

**Effects of windthrows
on the interaction between tree species
composition, forest dynamics and carbon
balance in Central Amazon**

DISSERTATION

Dr. rer. nat.

Daniel Magnabosco Marra

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composition, forest dynamics and carbon
balance in Central Amazon

Der Fakultät für Biowissenschaften, Pharmazie und Psychologie
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Dissertation

256 Seiten, 728 Literaturangaben¹, 69 Abbildungen², 22 Tabellen

Synopsis

This is a cumulative dissertation comprised of four original studies (three published papers and a *manuscript*) assessing interactions between large-scale wind disturbances and different attributes of Amazon forests. I combined detailed forest inventories with remote sensing data for a chronosequence of wind-disturbed sites in Central Amazon. This novel data set allowed me to investigate the effects of the complex and wide disturbance gradient created by windthrows on tree species composition, forest dynamics and biomass/carbon balance. Although Central Amazon forests seem to be resilient to windthrows, large-scale disturbances can shift soil carbon stocks and alter forest composition and dynamics for decades, with the potential to influence processes and mechanisms defining species diversity, distribution and carbon cycle processes.

¹Duplicated references from different studies are counted

²The Fig. 15 of this dissertation is also used in the *manuscript* (Paper 4); seven figures used in the *Introduction* of this dissertation were compiled from previous studies, including some listed in the *Appendices*

For Pedro Magnabosco (1923-2016, in memoriam)
and all those curious about nature.

A Pedro Magnabosco (1923-2016, in memoriam)
e a todos curiosos em descobrir a natureza.



Fig. 1. Aerial-view of a 2-yr-old blowdown in Central Amazon, Brazil. Picture: LMF/INPA.



Fig. 2. Ground-view of a 1-yr-old blowdown in Central Amazon, Brazil. Pictures: D. Magnabosco Marra.

‘Except where other powerful mechanical factors such as elephants are at work, only wind interferes profoundly with the forest equilibrium, changing at a stroke the conditions for regeneration, growth and reproduction in the lower layers.’ (Longman and Jeník 1974)

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PREFACE

PREFACE

The main goal of this dissertation was to assess the effects of windthrows or blowdowns on tree species composition and forest dynamics. Improving our knowledge on this topic is crucial for conservation and management of Amazon forests in face of land use intensification and gradual climate change that can result in more extreme weather events. To do so, I combined extensive fieldwork with remote sensing for establishing a forest chronosequence, a series of plots spanning a wide gradient of blowdown tree-mortality and varying in time after disturbance. In comparison to classical studies on canopy disturbance, mine has the uniqueness of including large natural gaps ($\geq 2,000 \text{ m}^2$). I used this chronosequence to monitor vegetation and soil attributes during succession. In addition to my extensive forest inventories, I was granted with a valuable data set that allowed me to parameterize specific tree biomass estimation models and make reliable estimates of biomass recovery after disturbance. The four papers comprising this dissertation add novel information on the importance of large-scale wind disturbances in driving tree species community composition and biomass/carbon balance in Amazon forests. In the ‘General Introduction’, I provide a general background on the main topic of this dissertation. In addition, I show how the different papers are connected to each other and fit into a larger research initiative. In the ‘General Methods’, I present detailed and complementary information that was not included in the papers. In the ‘General Discussion’, I make remarks and contextualize general results from the different papers.

SIGNIFICANCE STATEMENT

SIGNIFICANCE STATEMENT

A better understanding of tree species vulnerability and resilience to a range of disturbance intensities is key knowledge for the conservation and management of Amazon forests. In this dissertation I provide basic/primary information on how tree mortality associated with windthrows affects the structural and taxonomic attributes of Central Amazon forests, that in turn relate to spatial variations in biomass/carbon balance in a dynamic landscape. Although these forests seem to be resilient to windthrows, large-scale disturbances can alter forest dynamics for decades, with the potential to influence processes and mechanisms defining species diversity and distribution patterns. The data acquired within the projects related to this dissertation will be made freely available in the near future and may be applied to solve other questions on forest ecology and management.

SUMMARY

SUMMARY***Background***

Old-growth forests with native species provide essential goods and services for humans and are critical for biodiversity conservation and climate regulation. Large and contiguous remaining tropical forests such as the Amazon have a great importance at the regional and global scale. Amazon forests harbor thousands of tree species. In these forests, trees store *ca.* 90% of the total aboveground biomass/carbon and thus play a key role in global biogeochemical cycles. Tropical forests have long been described as an ecosystem at equilibrium. However, there is growing evidence that Neotropical forests (such as the Amazon) are in fact undergoing constant changes in dynamics, structure and species composition. Although changes are partly due to the intensification of different human disturbances and gradual climate change, Amazon forest dynamics is also likely to be associated with large-scale natural disturbances (e.g. windthrows). Apart from being threatened by intensive use leading to degradation (e.g. exploitation of timber, fibers and game meat), land-use changes (e.g. extensive agriculture and mining) and landscape fragmentation including urbanization, old-growth forests are facing novel and more intense natural disturbances, such as flooding, drought and windstorms. Although there are still large uncertainties in the predictions of future weather scenarios, climate change is expected to increase the frequency of extreme weather events leading to disturbances in the Amazon region.

This study focuses on the role of windthrows or blowdowns, a prevalent natural disturbance in the Central Amazon, on species composition and forest dynamics. Like human impacts, natural disturbances lead to tree mortality and thus induce a loss of tree biomass. The capacity of these forest systems to recover to pre-disturbance biomass levels is referred to as biomass resilience. To date, most of the research on biomass resilience in tropical forests has been on the extremes of the extant disturbance gradient, i.e. either single tree falls or severe human disturbances (e.g. shifting agriculture, fire and logging). Consequently, our knowledge on the vulnerability and resilience of tropical forests to large-scale wind disturbances is scarce and biased. In addition, the large tree species diversity and complex structure of Amazon forests pose extra challenges to the understanding of the processes and mechanisms

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that regulate community composition, species distribution and biomass dynamics when tree communities are subject to more intense tree mortality regimes.

Canopy gaps created by windthrow events, or blowdowns, create a complex mosaic of forest patches covering the full spectrum of disturbance intensities and recovery dynamics in the Central and Western Amazon. Blowdowns are produced by downbursts associated with severe convective systems such as squall lines. These periodic events can cause widespread tree mortality and can produce large canopy gaps. In contrast to human disturbance or other types of natural disturbances such as fire, wind-disturbed forests experience rapid deposition of organic matter from the dead vegetation, and are to a lesser extent subject to soil compaction. More importantly, the complex shape of blowdowns creates an extensive contact zone with undisturbed areas that contain the original habitat structure and species pool. In the Amazon, a complex set of processes, including soil and precipitation gradients, topography and inundation regime, are related to the observed local and regional variations in forest structure (e.g. with respect to stem density, basal area and biomass) and floristic composition. Recent studies have shown that variations in the natural tree mortality regime can also influence attributes of Amazon forests and that related mechanisms seem to operate at different spatial scales.

Although windthrows have not typically been regarded as important drivers of forest structure and dynamics in the Amazon, this dissertation is the first compendium of empirical/observational studies assessing the different effects of windthrows. The ultimate goal of this dissertation was to address the effects of windthrows on species composition, forest structure and biomass/carbon dynamics, and how these interact with shifts in functional composition (i.e. successional groups and functional diversity in biomass gain mechanisms) during the recovery from wind disturbances that varied greatly in extent and intensity. In addition, I assessed short-term effects (7 yrs after the disturbance) of a single blowdown event on soil carbon stocks and soil organic carbon. Understanding forest vulnerability and resilience to blowdowns has important implications for understanding forest responses to human disturbance and for the adaptation of current forest management and conservation practices to more extreme weather conditions.

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Methods

To track the decadal impacts of windthrow disturbance in Central Amazon I combined field observations and remote sensing data. I analyzed a 25-yr chronosequence of Landsat 5 Thematic Mapper (TM) imagery to identify single blowdowns events. From these, I selected three blowdown sites that varied in time after disturbance (from the years 1987, 1996 and 2005), and in the total amount of disturbed area (from 75 ha to 900 ha). Blowdowns that topple between 6 and 8 trees in a given Landsat pixel (30 m x 30 m, normally containing *ca.* 55 trees) are detectable as an increase in the fraction of non-photosynthetic vegetation (Δ NPV), which is related to increases in the fraction of dead vegetation and exposed soil.

For each site in the chronosequence, I was able to estimate tree mortality associated with the blowdown events by using a locally field-calibrated model with Δ NPV as a single predictor. NPV images can be computed from Landsat images by using Spectral Mixture Analysis (SMA), which accounts for the *per*-pixel fraction of the following three selected endmembers: green vegetation/photosynthetic active (GV), dead plant material/non-photosynthetic vegetation/soil surface (NPV) and shade. Δ NPV is calculated by subtracting the NPV image containing the blowdown of interest from that of the previous year.

To see whether mortality patterns varied systematically across the landscape, I extracted terrain elevation data from a digital elevation model of the same area. I employed this data set to assign plots (sample units) to typical topographic classes (i.e. plateaus, slopes and valleys), which are likely to experience different wind velocities during a blowdown event, and thus have an effect on vegetation damage by wind. I monitored the tree community in each blowdown site in plots along transects crossing the entire disturbed area of forest patches as well as different topographic classes.

Between 2009 and 2015, I measured tree growth, recruitment and mortality (diameter at breast height [DBH] \geq 10 cm) at least twice (3-yr interval) in each blowdown site. Re-measurements after several years in the different sites (from 4 to 27 yrs after the disturbance) allowed me to test for patterns of forest recovery of a given plot, rather than inferring it from the chronosequence. To control for possible pre-disturbance differences within and among different blowdown sites, I established plots in adjacent non-disturbed patches (i.e. in the old-growth matrix). In addition, I used data from an old-growth forest unaffected by human disturbances or blowdowns for at least 55 yrs (to date). I carried out full botanical surveys in

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the blowdown sites and recorded the mode of tree death (i.e. snapped, uprooted and standing dead) and mechanisms of biomass gain and loss (i.e. growth, recruitment, resprouting and mortality). Botanical exsiccates were added to a local herbarium. The entire sampled area was 19.6 ha (596 plots) including *ca.* 13,000 trees from 68 families, 275 genera and at least 1,017 species. Soil samples were collected from the plateau plots of one blowdown site, 7 yrs after the disturbance. I analyzed soil carbon stocks from disturbed and undisturbed areas to assess whether there were discernable changes due to large litter inputs following blowdown events.

In the Amazon forests, predicting stand biomass at large spatial-scales is a challenging task due to the heterogeneity of successional stages, high tree species diversity and inherent variations in tree allometry and architecture. In order to assess biomass dynamics during recovery from wind disturbance, I parameterized aboveground biomass estimation models, reliable for estimating the biomass of forests subject to wide gradients of floristic composition and structure and thus strong variations in tree architecture. For doing so, I was granted access to a valuable and unique allometric data set containing 727 trees (DBH \geq 5 cm) of 135 species from a large variation of successional stages relating to different levels of disturbance (i.e. old-growth and secondary forests).

Results and Discussion [denotes original contributions of this dissertation]

[1] Tree mortality in the three study sites ranged from 0 to 70%. Vegetation damage was generally not strongly controlled by topography, but in one of the sites, mortality was highest on plateaus. Thus, variations in tree mortality and damage across the landscape may be controlled by variables such as wind speed, direction and duration of the particular storm event. As expected, measures of forest structure (i.e. stem density, basal area and biomass) correlated negatively with tree mortality caused by the blowdowns. Tree mortality intensity affected the size distribution of trees, fraction of resprouters, community composition and mean wood density. In contrast to studies on small treefall gaps and human disturbances, I observed a diverse set of species and genera with special requirements and recruitment strategies forming the initial post-blowdown cohort and leading to a peak of rarefied richness and diversity at intermediate disturbance levels.

[2] Short-term effects of windthrows included marginally higher soil carbon stocks in disturbed areas than in undisturbed areas. These results indicate that a significant part of the

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plant litter input associated with large windthrow events is not immediately decomposed and directly emitted to the atmosphere (e.g. as CO₂ and CH₄). Instead, it is partly incorporated into the soil leading to the observed increase in soil carbon stocks. The degree of increase is related to soil clay content and tree mortality intensity. Thus, in addition to the well-documented influences of soil texture, soil carbon stocks in these forests are influenced by the tree mortality regime. In contrast to other types of disturbance, the higher carbon content and potentially higher nutrient availability in soils in areas recovering from windthrows may favor forest regrowth and increase vegetation resilience.

[3] By analyzing the allometric data of 727 trees, I found that good model fits for individual tree biomass do not necessarily translate into reliable predictions of biomass at the landscape level. When comparing biomass predictions at the landscape level using my different models and an available pantropical model, I observed systematic biases of up to *ca.* 40%. This result has important implications for biomass assessments in hyperdiverse and structurally complex tropical forests. My study yielded two biomass estimation models that performed satisfactorily across different forest structures and species composition, i.e. produced low values of bias and error. These models included predictors reflecting inherent variations in species architecture, which allowed me to reliably estimate biomass recovery and dynamics in the blowdowns sites.

[4] By assessing biomass dynamics along the chronosequence of blowdown sites (i.e. 4-27 yrs after disturbance and 0-70% tree mortality intensity) and the old-growth control forest, I found that blowdowns changed forest structure and reduced biomass stocks of the disturbed forests for at least three decades. Following disturbance, biomass resilience was enhanced by recruitment and growth of pioneer and mid-successional species, which accounted for more than twice the biomass accumulation of that observed in the old-growth forest. Biomass dynamics was dominated by 20 genera, belonging to different successional groups, whose performance was controlled by variations in tree mortality intensity. While observed reductions in biomass resilience of late-successional trees were associated with species loss, an increase in biomass resilience of pioneer trees was associated with species enrichment. Although the richness of mid-successional species decreased under high disturbance intensities, biomass resilience increased systematically due to species from key genera such as *Inga*, *Guatteria*, *Ocotea* and *Tapirira*.

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Conclusion

Results from the different studies presented in this dissertation indicate that the gradients of wind disturbance encompassed in large blowdown gaps produce decadal landscape-level shifts in different attributes of Central Amazon *terra firme* forests, including tree species composition and biomass/carbon dynamics. I showed that biomass resilience following disturbance is a process supported by a very high number of species, each performing the task of restoring biomass in different niches along the disturbance intensity gradient. This is in contrast to the widely held view that a limited number of pioneer species generally dominates early successional biomass dynamics. Moreover, blowdowns can shift soil carbon stocks, and therefore associated nutrient availability, independently of variations in soil texture.

Questions still remain about the legacy of blowdowns in Amazon forest landscapes. However, my findings support the idea that an increased frequency of blowdowns can be expected to increase the area of forests with a characteristic and predictable structure, floristic composition and soil carbon stocks, which differs significantly from forests undisturbed for centuries or longer. Notably, shifts in species composition and forest structure due to blowdowns produce long-term changes in biomass stocks and dynamics. Overall, this dissertation sheds new light on tropical forest vulnerability and resilience. Moreover, it suggests that blowdowns are likely to have an important impact on observed patterns of tree species diversity, distribution and carbon cycle processes in Amazon forests.

ZUSAMMENFASSUNG

ZUSAMMENFASSUNG***Auswirkungen von Sturmwurf auf die Interaktion zwischen Baumartenzusammensetzung, Walddynamik und Kohlenstoffbilanz im Zentral-Amazonas******Hintergrund***

Urwälder mit heimischen Arten bieten wichtige Güter und Dienstleistungen für den Menschen und sind von entscheidender Bedeutung für den Erhalt der Artenvielfalt und die Regulation des Klimas. Die noch verbliebenen großen, zusammenhängenden tropischen Wälder, wie der Amazonas, sind regional und global von großer Bedeutung. Diese Wälder beherbergen tausende von Baumarten, sie speichern *ca.* 90% der gesamten oberirdischen Biomasse / des Kohlenstoffs und spielen somit eine wichtige Rolle für das Funktionieren von Ökosystemen. Tropische Wälder wurden lange als ein Ökosystem im Gleichgewicht beschrieben. Allerdings gibt es immer mehr Hinweise darauf, dass neotropische Wälder (einschließlich des Amazonas) in der Tat einer ständigen Veränderung der Dynamik, Struktur und Artenzusammensetzung unterliegen, die im Zusammenhang mit der Intensivierung der verschiedenen menschlichen Störungen und des allmählichen Klimawandels stehen. Abgesehen davon, dass Urwälder durch intensive Nutzung (z.B. Holz, Fasern und Wild), Landnutzungsänderungen (z.B. extensive Landwirtschaft und Bergbau) und schnelle Landschaftszerschneidung (z.B. Urbanisierung) bedroht sind, sind sie auch mit neuen und intensiveren natürlichen Störungen, wie Überschwemmungen, Dürren und Stürmen konfrontiert. Obgleich Prognosen zukünftiger Wetterszenarien noch mit großen Unsicherheiten behaftet sind, wird erwartet, dass der Klimawandel extreme Wetterereignisse in der Amazonas-Region häufiger werden lässt.

Diese Studie konzentriert sich auf die Rolle von Wind, einer weit verbreiteten natürlichen Störung im zentralen Amazonas. Neben anthropogenen Einflüssen können auch natürliche Störungen zu Baummortalität führen und damit zu einem Verlust von Baumbiomasse. Die Fähigkeit von Waldökosystemen, die durch die Störung verlorene Menge an Biomasse wiederaufzubauen, wird als Biomasse-Resilienz bezeichnet. Bis heute bezieht sich ein Großteil der Forschung zu Biomasse-Resilienz in tropischen Wäldern auf die Extreme der Störungsgradienten, also entweder Verjüngung in Kronenlücken oder schwere anthropogenen Störungen (z.B. Wanderfeldbau, Feuer und Abholzung). Entsprechend ist unser Wissen über

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die Vulnerabilität und Resilienz tropischer Wälder in Bezug auf großräumige Windstörungen gering und unvollständig. Gleichwohl stellen die hohe Baumartenvielfalt und die komplexe Struktur der Amazonaswälder zusätzliche Herausforderungen für das Verständnis der Prozesse und Mechanismen dar, die Artzusammensetzung, die Artverteilung und die Biomassedynamik regulieren, wenn die Wälder intensiveren Mortalitätsregimes unterworfen sind.

Kronenlücken, entstanden durch Wind- (windthrow) und Sturmwurf (blowdown), schaffen ein komplexes Mosaik aus Waldflächen, welches das gesamte Spektrum der Störungsintensitäten und Regenerationsdynamik im Zentral- und West-Amazonas abdeckt. Sturmwürfe werden von Fallböen im Zusammenhang mit starken konvektiven Systemen wie Sturmfronten verursacht. Diese periodischen Ereignisse können zu weiträumiger Baummortalität führen und große Kronenlücken erzeugen. Im Gegensatz zu anthropogenen oder anderen natürlichen Störungen wie Feuer, stellen Sturmwürfe in Wäldern Ereignisse mit raschem Anfall toten organischen Materials dar und unterliegen in geringerem Umfang Bodenverdichtung. Wichtiger noch ist, dass die komplexe Form von Sturmwürfen eine ausgedehnte Kontaktzone mit ungestörten Bereichen ermöglicht, die ursprüngliche Habitatstruktur und den ursprünglichen Artenpool enthalten. Im Amazonas steht eine Reihe komplexer Prozesse, einschließlich Boden- und Niederschlagsgradienten, Topographie und Überflutungsregimes, hinter den beobachteten lokalen und regionalen Schwankungen der Waldstruktur (z.B. Stammdichte, Grundfläche und Biomasse) und der floristischen Zusammensetzung. Jüngere Studien haben gezeigt, dass auch Veränderungen im natürlichen Baummortalitätsregime Eigenschaften von Amazonaswäldern beeinflussen und dass die damit verbundenen Mechanismen auf verschiedenen räumlichen Skalen wirken.

Windwürfe wurden typischerweise nicht als wichtige Einflussfaktoren der Eigenschaften und Dynamiken von Baumgemeinschaften im Amazonas angesehen. Diese Dissertation ist mithin das erste Kompendium empirischer / observationaler Studien, die unterschiedlichen Wirkungen von Windwürfen im Amazonas untersuchen. Das Ziel dieser Arbeit war es, die Auswirkungen von Windwürfen auf die Artzusammensetzung, Waldstruktur und Biomasse- / Kohlenstoffdynamik und deren Wechselwirkung mit Veränderungen der funktionalen Zusammensetzung (d.h. sukzessionale Gruppen und Mechanismen des Biomasseaufbaus) während der Erholung von Windstörungen, die stark in Umfang und Intensität variieren zu

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untersuchen. Darüber hinaus habe ich die kurzfristigen Auswirkungen (7 Jahre nach der Störung) eines einzelnen Sturmwurfereignisses auf Bodenkohlenstoffvorräte und organischen Kohlenstoff im Boden untersucht. Das Verständnis der Vulnerabilität durch und der Resilienz nach Sturmwürfen hat wichtige Implikationen für das Verständnis der Reaktion von Wäldern auf anthropogene Störungen und die Anpassung von Bewirtschaftung und Schutzmaßnahmen an extremere Wetterbedingungen.

Methoden

Um die langjährigen Auswirkungen von Windstörung im zentralen Amazonas zu verfolgen, habe ich Feld- und Fernerkundungsdaten kombiniert. Ich habe eine 25-Jahres-Chronosequenz von Landsat 5 Thematic Mapper (TM) Bildern analysiert, um einzelne Sturmwurfereignisse zu identifizieren. Aus diesen habe ich drei Sturmwurfflächen ausgewählt, die sich im Zeitpunkt der Störung (in den Jahren 1987, 1996 und 2005) und dem insgesamt getroffenen Bereich (75 ha bis 900 ha) unterscheiden. Sturmwürfe, die 6-8 Bäume in einem Landsat Pixel (30m x 30m, mit normalerweise *ca.* 55 Bäumen) getroffen haben, sind erkennbar als eine Zunahme des Anteils der nicht-photosynthetisch aktiven Vegetation (Δ NPV), der wiederum mit dem Anteil toter Vegetation zusammenhängt.

Für jede Fläche der Chronosequenz konnte ich die Baummortalität der Sturmwürfe abschätzen, indem ich ein lokal im Feld kalibriertes Modell verwende, mit Δ NPV als einzigem Prädiktor. NPV-Bilder können vom Landsat-Bildern durch Spectral Mixture Analysis (SMA) berechnet werden, die die pro-Pixel-Anteil der folgenden drei ausgewählten Faktoren ermittelt: grüne / photosynthetisch aktive Vegetation (GV), abgestorbenes Pflanzenmaterial / nicht photosynthetisch aktive Vegetation (NPV) und Schatten. Δ NPV wird durch Subtraktion des NPV Bildes, das den Sturmwurf enthält mit dem des Vorjahres berechnet.

Um zu sehen, ob die Sterblichkeitsmuster systematisch über die Landschaft variierten, habe ich Geländehöhendaten aus einem digitalen Höhenmodell des gleichen Bereichs extrahiert. Mit diesen Daten habe ich die Plots (Probeneinheiten) in typische topographische Klassen (d. h. Plateaus, Hänge und Täler) gruppiert, bei denen es wahrscheinlich ist, dass sie während eines Sturmwurfereignisses unterschiedliche Windgeschwindigkeiten erfahren und sich somit in Bezug auf den Schaden der Vegetation durch Wind wie auch der Folgereaktion unterscheiden. Ich habe die Bäume in jeder Sturmwurffläche auf Plots entlang von

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Transekten, die das gesamte gestörte Gebiet mit verschiedener Bereichen und Toposequenzen schneiden, erfasst.

Zwischen 2009 und 2015 habe ich auf jeder der Sturmwurfflächen Wachstum, Verjüngung und Mortalität der Bäume (Brusthöhendurchmesser [BHD] ≥ 10 cm) mindestens zweimal (3 Jahres-Intervall) gemessen. Wiederholungsmessungen nach mehreren Jahren (4-27 Jahre nach der Störung) haben es mir ermöglicht, nach Mustern der Waldregeneration auf den Plots selbst zu suchen, statt mit einer Chronosequenz verschiedener Plots arbeiten zu müssen. Um mögliche Unterschiede innerhalb und zwischen den verschiedenen Sturmwurfflächen zu berücksichtigen, habe ich auch in benachbarten, nicht gestörten Flächen (d. h. in der Urwaldmatrix) Plots angelegt. Darüber hinaus habe ich Daten eines Urwaldes genutzt, der seit mindestens 55 Jahren von anthropogenen Störungen oder Sturmwurf unbeeinflusst ist.

Ich habe in den Sturmwurfflächen eine vollständige floristische Erhebung durchgeführt und den Mortalitätsmodus der Bäume (d. h. gebrochen, entwurzelte und stehend tot), sowie die Mechanismen der Biomasse Zu- und Abnahmen (d. h. Wachstum, Verjüngung, Stockausschlag und Mortalität) bestimmt. Botanische Belege wurden in ein lokales Herbarium überführt. Die gesamte Untersuchungsfläche betrug 19,6 ha (596 Plots) und enthielt *ca.* 13000 aufgenommene Bäume aus 68 Familien, 275 Gattungen und mindestens 1017 Arten. Bodenproben wurden vom Plateau einer Sturmwurffläche 7 Jahre nach der Störung gesammelt. Ich habe Bodenkohlenstoffvorräte aus gestörten und ungestörten Bereichen untersucht, um herauszufinden, ob es merkbare Unterschiede durch den hohen Anfall toten Materials nach Sturmwurfereignissen gibt.

Aufgrund der Heterogenität der Sukzessionsstadien, der hohe Baumartenvielfalt und inhärenten Schwankungen der Baumallometrie und -architektur ist die Biomasseschätzung im Amazonas auf großer räumlicher Skala eine anspruchsvolle Aufgabe. Um die Biomassedynamik während der Erholung von Windstörungen einschätzen zu können, habe ich Modelle zur Schätzung der oberirdischen Biomasse parametrisiert, die zuverlässige Schätzungen der Biomasse von Wäldern mit langen Gradienten floristischer Zusammensetzung und Struktur und den dadurch bedingten starken Schwankungen der Baumarchitektur liefern. Dafür erhielt ich Zugang zu einem wertvollen und einzigartigen Allometrie-Datensatz, der 727 Bäume (BHD ≥ 5 cm) von 135 Arten aus einer großen

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Bandbreite von Sukzessionsstadien unterschiedlicher Störungsintensität (d.h. späte Sukzession und Sekundärwald) enthält.

Ergebnisse und Diskussion

[1] Die Baummortalität reichte von 0 bis 70 % in den drei untersuchten Gebieten. Der Vegetationsverlust war in der Regel nicht von der Topographie beeinflusst, außer in einem Gebiet, wo die Mortalität auf Plateaus am höchsten war. Variationen der Mortalität und großflächiger Schaden an der Vegetation waren von Windgeschwindigkeit und -richtung sowie der Dauer des entsprechenden Sturmes beeinflusst. Wie erwartet waren Attribute der Waldstruktur (z.B. Stammdicke, Grundfläche und Biomasse) negativ mit der Baummortalität korreliert, welche durch Sturmwurf verursacht wurde. Die Intensität der Baummortalität beeinflusste ihrerseits die Größenklassenverteilung der Bäume, den Anteil neu auskeimender Bäume, die Artenzusammensetzung und die mittlere Holzdichte im Bestand. Im Gegensatz zu Studien über kleine Kronenlücken und anthropogene Störungen habe ich ein breites Spektrum von Baumarten und Gattungen mit unterschiedlichen Bedürfnissen und Verbreitungsstrategien untersucht, die die Vegetation direkt nach einem Sturmwurf darstellt. Sturmwürfe führten bei mittlerer Störungsintensität zur höchsten exklusiven Artenvielfalt (rarefied species richness) und Diversität.

[2] Kurzfristige Effekte von Windwürfen beinhalteten marginal höhere Kohlenstoffvorräte im Boden von gestörten Flächen im Vergleich zu ungestörten Flächen. Die organische Kohlenstoffkonzentration des Bodens war in gestörten Flächen signifikant höher als in ungestörten Flächen. Meine Ergebnisse weisen darauf hin, dass ein wesentlicher Teil des organischen Materials, das durch große Sturmwürfe zerstört wurde, nicht umgehend zersetzt und in die Atmosphäre abgegeben wird (z.B. als CO₂ und CH₄). Stattdessen wird es teilweise in den Boden eingebunden, was zu dem beobachteten Anstieg der entsprechenden Kohlenstoffvorräte führte. Dabei hängt die Menge des Anstiegs vom Tonanteil des Bodens und der Stärke der Baummortalität ab. Somit sind die Kohlenstoffvorräte im Boden dieser Wälder nicht nur, wie bislang gut dokumentiert, von der Bodentextur abhängig sondern auch von den Baummortalitätsregimes. Im Gegensatz zu anderen Störungsarten könnten der höhere Kohlenstoffgehalt und die damit einhergehende potenziell höhere Nährstoffverfügbarkeit im Boden von Gebieten die sich von einem Sturmwurf erholen das Wachstum und die Resilienz der Vegetation begünstigen.

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[3] Durch die Analyse allometrischer Daten von 727 Bäumen habe ich herausgefunden, dass gute Modellanpassungen für individuelle Baumbiomassen nicht unbedingt zu verlässlichen Schätzungen der Biomasse auf Landschaftsebene führen. Bei der Schätzung der Biomasse auf Landschaftsebene, für die ich verschiedene von mir erstellte Modelle sowie ein vorhandenes pantropisches Modell genutzt habe, habe ich systematische Abweichungen von bis zu ca. 40% gefunden. Dieses Ergebnis hat eine wichtige Bedeutung für Biomasseschätzungen artenreicher und strukturell komplexer tropischer Wälder. Ich habe zwei Modelle zur Schätzung der Biomasse erstellt, die zufriedenstellende Schätzungen für unterschiedlich strukturierte Wälder und Baumartenzusammensetzungen lieferten. Bei diesen beiden Modellen hatten die geschätzten Werte nur geringe Abweichungen von den Originalwerten und die Schätzungen wiesen nur geringe Fehler auf. Die entsprechenden Modelle beinhalteten Prädiktoren, welche die inhärenten Variationen der Architektur der Arten widerspiegeln. Das erlaubte mir, die sich erholende Biomasse sowie die Dynamik in den durch Sturmwurf gestörten Flächen zuverlässig zu schätzen.

[4] Indem ich die Biomassedynamik entlang von Chronosequenzen in den durch Sturm zerstörten Flächen (4 – 27 Jahre nach der Störung und 0 – 70 % Baummortalität) mit alten ungestörten Kontrollflächen verglichen habe, konnte ich feststellen, dass Sturmschäden die Waldstruktur ändern und die Biomassevorräte verringern. Diese Änderungen sind in den gestörten Wäldern für mindestens drei Jahrzehnte nachweisbar. Nach einer Störung wurde die Biomasseressilienz durch Ansiedlung und Wachstum von Pionierbaumarten sowie Baumarten mittlerer Sukzessionsstadien gefördert. Der Biomassezugewinn in diesen gestörten Wäldern war annähernd doppelt so hoch wie der von alten, ungestörten Wäldern. Die Biomassedynamiken wurden von 20 Gattungen dominiert, welche zu unterschiedlichen sukzessionellen Gruppen gehören und deren Wuchsleistung von der Stärke der Baummortalität abhängig war. Eine geringere Biomasseressilienz von spät-sukzessionellen Arten war mit Artenverlust assoziiert, während eine höhere Biomasseressilienz von Pionierbaumarten mit Artengewinn assoziiert war. Obwohl die Artenvielfalt mittlerer Sukzessionsstadien bei hohen Störungsintensitäten abgenommen hat, stieg die Biomasseressilienz systematisch aufgrund von Arten wichtiger Gattungen, wie beispielsweise *Inga*, *Guatteria*, *Ocotea* und *Tapirira*.

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Schlussfolgerung

Die Ergebnisse der Studien, welche ich in meiner Dissertation vorgestellt habe, deuten darauf hin, dass unterschiedlich starke Windschäden in großen Sturmwurfblöcken zu jahrzehntelang sichtbaren Änderungen in *terra firme* Wäldern im Zentral Amazonas führen. Zu diesen Veränderungen gehören die Baumartenzusammensetzung sowie Biomasse- bzw. Kohlenstoffdynamiken. Ich konnte zeigen, dass die Biomasseresilienz nach einer Störung ein Prozess ist, der durch eine hohe Anzahl von Arten gestützt wird. Dabei realisieren unterschiedliche Arten die Biomasseerneuerung in verschiedenen ökologischen und zeitlichen Nischen entlang eines Gradienten der Störungsintensität. Diese Erkenntnisse stehen im Kontrast zu der weitverbreiteten Meinung, dass wenige Pionierbaumarten die Biomassedynamiken von früh-sukzessionellen Beständen dominieren. Darüber hinaus können Sturmschäden Kohlenstoffvorräte und damit einhergehende Nährstoffverfügbarkeiten im Boden verändern. Das geschieht unabhängig von Variationen der Bodentextur.

Es bleibt offen, was die langfristigen Folgen von großen Sturmwürfen in Amazonas Wäldern sind. Meine Ergebnisse stützen jedoch die These, dass häufigere Sturmwürfe jene Waldflächen erhöhen, die eine entsprechend charakteristische und vorhersagbare Struktur aufweisen. Dazu gehören eine veränderte floristische Zusammensetzungen und Kohlenstoffvorräte im Boden, die sich signifikant von Wäldern unterscheiden die über Jahrhunderte ungestört waren. Änderungen in der Artenzusammensetzung und der Waldstruktur die von Sturmwürfen verursacht wurden, führen zu langfristigen Veränderungen der Biomassevorräte und -dynamiken. Diese Dissertation wirft ein neues Licht auf die Verwundbarkeit und Resilienz tropischer Wälder und die Ergebnisse deuten darauf hin, dass Sturmschäden möglicherweise einen wichtigen Einfluss auf die Diversität und Verteilung von Baumarten, sowie den Kohlenstoffkreislauf in Amazonas Wäldern haben.

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1.1. Amazon forest

Forests cover *ca.* 30% of the Earth's land area (FAO 2012) but old-growth forests with native species account only for about one-third of this area (FAO 2010). Large and contiguous old-growth tropical forests such as the Amazon are subject to substantial changes in structure and species composition due to the intensification of human activities, gradual climate change and extreme weather events (Allan 2011; Min et al. 2011; IPCC 2014; Tan et al. 2015). In contrast, these forests provide essential goods and services for humans (i.e. food, water and timber) (Trumbore et al. 2015) and are critical for biodiversity conservation (Gibson et al. 2011) and maintenance of biomass and carbon stocks (IPCC 2007; FAO 2010; Poorter et al. 2015). Since changes in land-use and terrestrial carbon cycle are related to the increase in the concentration of atmospheric greenhouse gases (Allan 2011), old-growth forests are also important for mitigating climate change (Bonan 2008; Nepstad et al. 2008; Costa and Pires 2010; Pöschl et al. 2010; IPCC 2014).

The Amazon spreads over nine countries in South America covering an area larger than Western Europe and accounting for about 40% of the remaining tropical forest worldwide (FAO 2010). This vast contiguous tropical forest is estimated to host 16,000 tree species (ter Steege et al. 2013), at least 750,000 insect species (Adis 1990) and more than 2,500 species of mammals, birds, reptiles and amphibians (Mittermeier et al. 2003). Brazil contains *ca.* 60% of the biome (*ca.* 4,196,943 km²) (IBGE 2004) in nine of its country states (Fig. 8). In this region live 246 indigenous ethnic groups (only *ca.* 25% of the pre-European number) speaking more than 150 languages (ISA 2016). This region was estimated to host more than 10,000 tree species (Hubbell et al. 2008), with *terra firme* forests hosting more than 280 tree species ha⁻¹ (de Oliveira and Mori 1999). A recent inventory of the Brazilian flora confirmed that this region harbors at least 4,725 tree species, from which *ca.* 10% are endemic (Zappi et al. 2015). As in other tropical regions, deforestation, fire and fragmentation are the main processes driving losses of pristine Amazon forests (Hansen et al. 2013). Although successful initiatives have been reducing deforestation rates in Brazil over the last years (Nepstad et al. 2014), accumulated deforestation (1970-2015) is 664,936 km², or *ca.* 16% of the total biome area (Fig. 3) (INPE 2016).

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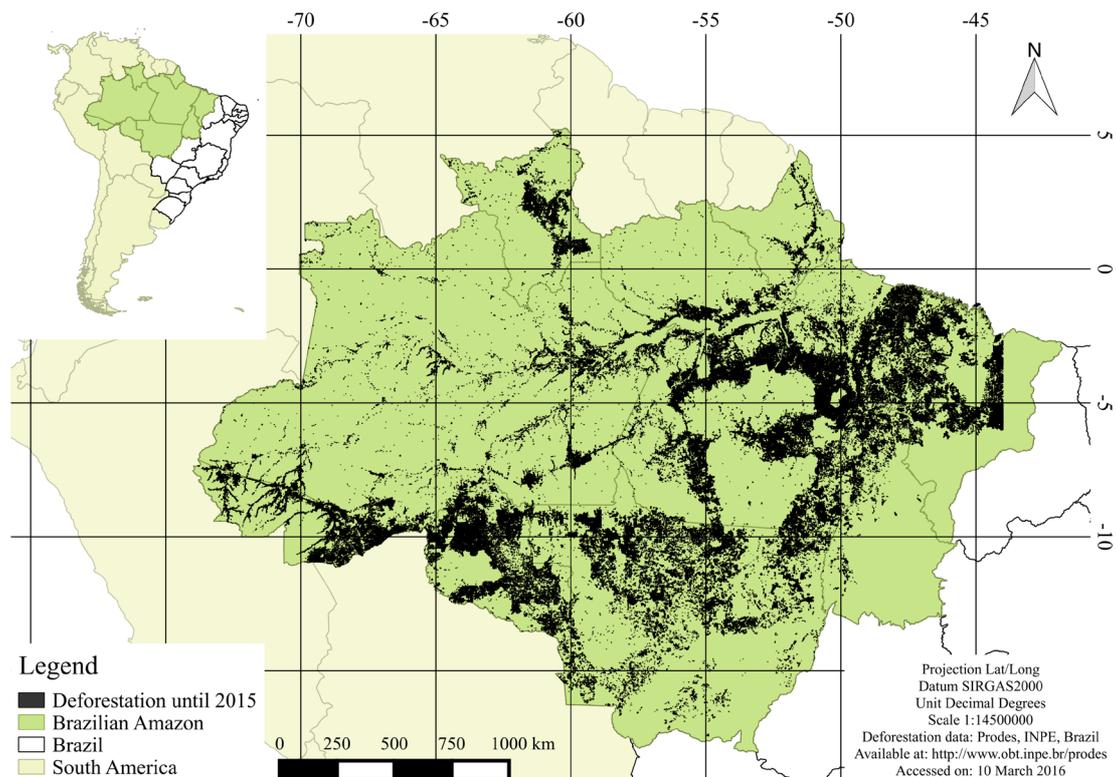


Fig. 3. Brazilian Amazon forest comprising *ca.* 60% of the total area (*ca.* 7,000,000 km²) of the biome in nine country states (i.e. *Acre*, *Amapá*, *Amazonas*, *Maranhão*, *Mato Grosso*, *Pará*, *Rondônia*, *Roraima* and *Tocantins*). The accumulated deforestation (664,936 km², between 1970 and 2015) is shown in black and old-growth areas in green.

Strong evidence supports that the Amazon forest has been influenced by large human populations over thousands of years, e.g. through the management of soils and the domestication of plant species (Prance 1972; Clement et al. 2015; Junqueira et al. 2016). Nonetheless, over the last few decades, increasing of human pressures and ongoing degradation is changing the forests' integrity at unprecedented rates (Lewis et al. 2015; Trumbore et al. 2015). Combating climate change by reducing C emissions is stimulating mechanisms and opportunities for developing countries to preserve old-growth tropical forests. These include the Reducing Emissions from Deforestation and Forest Degradation (REDD+) program from the United Nations Framework Convention on Climate Change (UNFCCC). However, there is accumulating evidence that climate change is related to observed changes on the frequency of extreme weather events and forest disturbances (Dale et al. 2001; Silva Dias et al. 2002; Werth and Avissar 2002; Min et al. 2011; IPCC 2014;

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Duffy et al. 2015), that may threaten the integrity of stored C. In this scenario, assessing forest vulnerability and resilience (i.e. species resistance and responses) to different levels of disturbances is a key and urgent knowledge gap that must be filled to establish efficient management and conservation strategies. My main motivation to develop this dissertation was the lack of information on Amazon forest succession and recovery following large-scale natural disturbances such as windthrows.

1.2. Tree-mortality disturbance

Naturalists have long been intrigued by the beauty, complexity and diversity of the Amazon forests (Wallace 1889; von Humboldt and Bonpland 1907; Roosevelt 1914). Apart from the great and incomparable contribution of classical studies to our current knowledge, they inevitably sparked a 'romantic' and 'mythological' view on the ecology and functioning of these forests. Although human perceptions vary between individuals and cultures (Prance 1972; Silva et al. 2007; Rametsteiner et al. 2009), Amazon forests are still popularly associated with myths (e.g. environmental homogeneity, steady-state, large trees and closed canopy) (CDEA 1992). As in other ecosystems, such associations do not represent the dynamic status of old-growth forests (Wirth et al. 2009). In fact, there is accumulating evidence supporting that old-growth tropical forests are not in a steady-state, but in a continuous recovery-process from different types of human and natural disturbances (Cole et al. 2014) that can affect tree community dynamics, structure and species composition (Baker et al. 2014; Brienen et al. 2015; Johnson et al. 2016; van der Sande et al. 2016).

A major mechanism of disturbance in old-growth forests is tree mortality and consequent gap-formation, that can be associated with endogenous (e.g. tree senescence, disease) or exogenous phenomena (e.g. natural disturbances) (Sousa 1984; Lugo and Scatena 1996; Foster et al. 1998). Current textbook knowledge is that small canopy-gaps (< 2,000 m²) usually caused by the mortality of one or a few trees dominate the disturbance dynamics in tropical old-growth forests (Hubbell et al. 1999; Sheil and Burslem 2003; Espírito-Santo et al. 2014; Baker et al. 2015). Treefall gaps create space for new trees and can promote changes in light conditions, temperature, humidity and soil properties (Putz 1983; Vitousek and Denslow 1986; Denslow 1987; Brokaw and Scheiner 1989). The natural regeneration in gaps can be dominated by growth of understory trees, resprouting of broken/damaged individuals or recruitment of new species (Sousa 1984; Guariguata and Pinard 1998; Nicotra et al. 1999;

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Vieira and Scariot 2006). Tree recruitment, which can influence the structure and composition of the regenerating forest (Schupp et al. 1989; Clark et al. 1999), is also influenced by environmental and biotic characteristics such as the species pool (seed- and seedling-banks), dispersion, competition and predation (Garwood 1989; Schupp 1990; Dalling et al. 2002; Terborgh et al. 2008; Marra et al. 2014b). General knowledge states that changes in species composition following gap formation relate to ecological characteristics of the regenerating species, which may have specific traits, requirements and thus ability to establish under different biotic and abiotic conditions (Swaine and Whitmore 1988; Nicotra et al. 1999; Poorter 1999; Poorter et al. 2004). Therefore, gap-recovery can include changes in the abundance of species from different successional groups (i.e. light demanding and fast-growing pioneers species, mid-successional or secondary-growth species, and late-successional or slow-growing species) (Denslow 1980a; Popma et al. 1988; Swaine and Whitmore 1988).

To date, available studies that aimed at assessing the effects of tree mortality disturbance on tropical forest dynamics, composition and diversity focused almost exclusively on small-scale disturbances (usually $< 2,000 \text{ m}^2$). Still, these studies yielded contrasting results (Denslow 1980b; Uhl et al. 1988; Hubbell et al. 1999; Chazdon et al. 1999; Brokaw and Busing 2000; Molino and Sabatier 2001; Roxburgh et al. 2004; Bongers et al. 2009; Baker et al. 2015), indicating that both niche- (i.e. light- and/or gap-partitioning) and neutral-based process can be relevant for defining the composition of the regenerating community (Grubb 1977; Vandermeer 1996; Brokaw and Busing 2000; Franklin et al. 2002; Poorter 2007). In short, despite notable efforts made to address the effects of tree mortality disturbance on old-growth forests, our current knowledge is still limited by spatial constraints that impel the assessment of landscape-scale natural processes (Leibold et al. 2004; Chave and Norden 2007; Chambers et al. 2013; Asner 2013). More importantly, we still do not know how the different dimensions of disturbances (i.e. intensity, frequency, duration, spatial scale and points of contact/interaction with the old-growth matrix) (Lugo and Scatena 1996) interact and influence different attributes of diverse and complex tropical forests. Consequently, important questions regarding species vulnerability and responses to disturbances remain unsolved (Foster et al. 1998; Turner et al. 1998; Sutherland et al. 2013); especially when accounting for disturbances that can create gaps $\geq 2,000 \text{ m}^2$ such as those promoted by large-scale windthrow events in Amazon (Negrón-Juárez et al. 2011).

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1.3. Downbursts and forest blowdowns in the Amazon

A downburst wind is a strong downdraft that induces an outburst of highly divergent and damaging winds rushing towards the ground (Fujita 1976). Downbursts are formed in association with severe convective systems (e.g. storms, thunderstorms and squall lines) (Fig. 4a) that can also produce heavy rain and hail (Fujita 1976; Fujita 1990; Garstang et al. 1998). A downburst with winds spreading horizontally more than 4 km is defined as a ‘macroburst’, whereas a downburst with winds spreading horizontally up to 4 km is defined as a ‘microburst’ (Fig. 4b) (Fujita 1990). Microbursts, which have a smaller dissipation area, usually produce stronger wind gusts than macrobursts. The winds typically lasts a few seconds but can reach speeds $> 150 \text{ km h}^{-1}$, often causing severe and extensive building and vegetation damage, and aircraft accidents (Fujita 1976; Fujita 1990).

In contrast to large-scale tropical and continental cyclones, storms and thunderstorms can form and dissipate rapidly in most parts of the world (Fujita 1990). Thunderstorms are associated with cumulonimbus clouds, which in Amazon can form alone or in clusters along cold front squall lines (Leary and Houze Jr 1979; Garstang et al. 1994; Cohen et al. 2009; Negrón-Juárez et al. 2010b). These towering vertical clouds result from updraft air currents that carry moist and warm air upwards into the storm. Cumulonimbus clouds can rise vertically to the tropopause and often beyond (Fig. 4a). Thunderstorms are formed when tall layers of moist and warm air reach higher and cooler regions of the atmosphere, creating convective cells (Fig. 3a). While the updraft feeds moist and warm air into the storm, the downdraft dissipates heavy rain and eventually microbursts (Fig. 4b) (Kuo 1965; Leary and Houze Jr 1979; Harding 2011). In thunderstorms, microbursts can be formed by air entrainment via evaporation or water loading via precipitation (Orville et al. 1989). Dry air entrainment occurs when dry air mixes in with the rainfall. Once the drier and colder air penetrates into the cloud, it causes the water to evaporate through evaporative cooling (i.e. ‘absorption of latent heating’), which reduces the air temperature drastically. The heavier cold air will then sink through the towering cloud, gaining speed while descending. The interaction/contact with warmer and less dense air closer to the ground may speed up air descent rates further through the cloud. Heavy rainfall also associated with cumulonimbus is a second important process creating microbursts through water loading. The weight of ‘thick

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water columns' with kilometers of height drags dry air towards the ground (Fujita 1976; Orville et al. 1989; Fujita 1990; Garstang et al. 1998; Harding 2011).

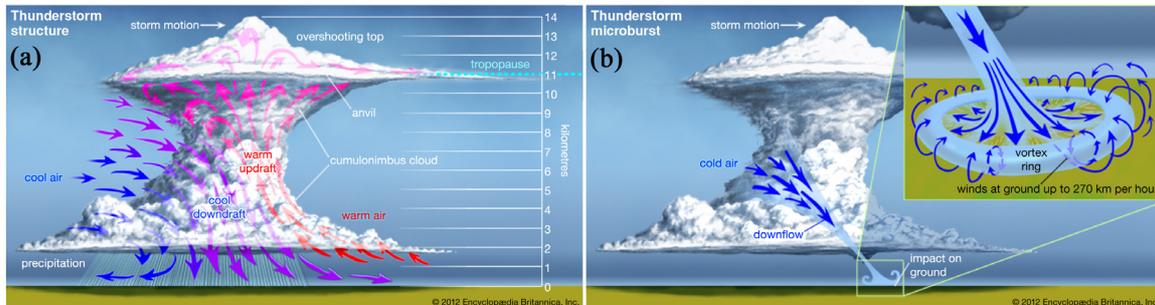


Fig. 4. (a) Towering thunderstorm structures (e.g. cumulonimbus clouds with *ca.* 12 km height) are formed from powerful warm updrafts (red arrows) associated with cool downdrafts (blue arrows). While updrafts are associated with convection, downdrafts are associated with cool and dry air masses. Under specific conditions, the downdraft can produce strong wind gusts. (b) Microbursts are formed from downdrafts inside the cloud. They form from via evaporative cooling causing downdraft (blue arrows) due to abrupt changes in air temperature and pressure inside the cloud. In case of heavy rainfall, air dragging via water loading can also speed up air sinking through the cloud. In the Amazon region, macrobursts and microbursts (see the definition in the text) can produce wind gusts that last a few seconds but exceed 150 km h^{-1} . The winds spread out in different directions (inset) and can cause severe building damage and blow down large forest patches. Images source: modified from Encyclopedia Britannica. Available at: <http://www.britannica.com>. Last access on: 21 March 2016.

Forest blowdowns of varying sizes were first detected for a large portion of the Amazon due to their linear and 'fan-shaped' damage geometry and spectral characteristics on Landsat Thematic Mapper (TM) images (Nelson et al. 1994; Nelson and do Amaral 1994). Dead vegetation creates a typical non-photosynthetic spectral pattern (Nelson et al. 1994; Nelson and do Amaral 1994; Chambers et al. 2007) identified in the bands 3, 4 and 5 (bands 4, 5 and 6 in Landsat 8). This 'dead vegetation' signal persists for *ca.* 1 yr before early colonizer species dominate the surface (Nelson 1994; Nelson and do Amaral 1994; Chambers et al. 2007). Nonetheless, older blowdowns can be tracked by using other features such as geometry and other spatial characteristics (Nelson et al. 1994; Araujo et al. 2013). These blowdowns were later associated to downbursts (i.e. macro and microbursts) (Garstang et al. 1998). Amazon convective-downbursts contain a significant ($> 35\%$) vertical component of velocity and usually occur together with heavy rainfall. The damage is also characterized by

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an acute angle between the borders, with trees diverging outward from the ‘center’ of the ‘fan-shaped’ patch (Fig. 5) (Garstang et al. 1998). Defoliation and uprooting were the main observed modes of tree damage/mortality in blowdown patches that have been overflowed (Nelson and do Amaral 1994).

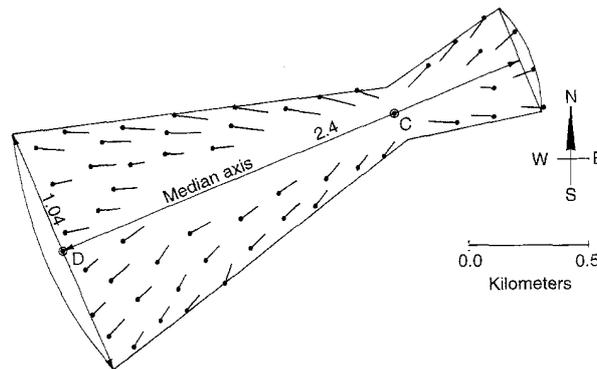


Fig. 5. Proposed ‘fan-shaped’ geometry of the vegetation damage associated to Amazon microbursts. Figure source: Garstang et al. 1998.

Over the past several years, a number of studies have shown that in the Central and Western Amazon, storm propagating blowdowns from 0.1 (Negrón-Juárez et al. 2011) to thousands of hectares are an important disturbance regime (Nelson et al. 1994; Espírito-Santo et al. 2010; Negrón-Juárez et al. 2010b; Araujo et al. 2013; Chambers et al. 2013; Asner 2013; Negrón-Juárez et al. 2016). Espírito-Santo et al. (2010) detected 279 blowdowns (occurred between 1999 and 2001) along an East-West gradient of Landsat TM imagery crossing the Amazon basin. These blowdowns accounted for a total disturbed area of 21,931 ha, with the smaller and larger blowdowns having five and 2,223 ha, respectively (Fig. 6). While blowdowns smaller than 50 ha were the most frequent, blowdowns with area > 101 ha accounted for more than 60% of the total analyzed disturbed area (Espírito-Santo et al. 2010). A similar approach was employed earlier by Nelson et al. (1994), who detected 330 blowdown patches (occurred between 1987 and 1989) varying from 30 to 3,500 ha and accounting for a total disturbed area of 90,000 ha. For an East-West gradient in the Amazon basin, the frequency of blowdowns seems to be positively correlated with precipitation and storm rates, with more frequent and larger blowdowns associated with the Central and West portion of the basin (Fig. 6) (Nelson et al. 1994; Espírito-Santo et al. 2010; Espírito-Santo et al. 2014).

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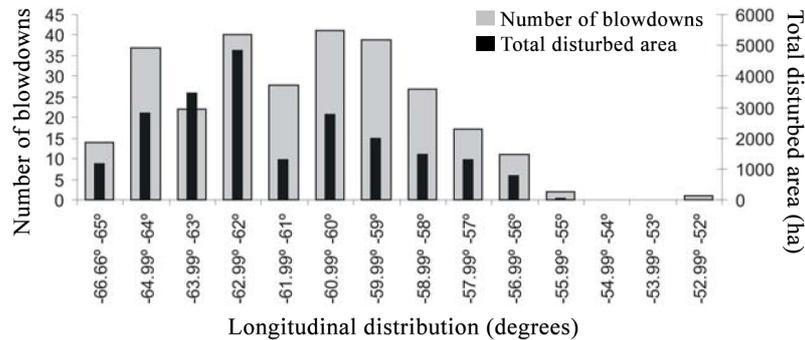


Fig. 6. East-west distribution and total disturbed area of 279 blowdowns events identified in 27 Landsat TM images (from 1999 to 2001) forming an East-West transect across the Amazon. Figure source: modified from Espírito-Santo et al. 2010.

A higher frequency of destructive downbursts was also reported for the late dry season in Central and Western Amazon, with potential hazard to river craft and aviation (Nelson and Amaral 1994; Garstang et al. 1998b; RI Negrón-Juárez [unpublished data]). However, to date, there is no study that has assessed the frequency distribution of small-scale blowdowns over large regions and its possible relationship with variations in precipitation. Although blowdown patches with total area between *ca.* 1,000 m² (1 pixel of a Landsat image with 30 m x 30 m spatial-resolution) and < 5 ha were neglected by previous studies (Nelson et al. 1994; Espírito-Santo et al. 2010; Espírito-Santo et al. 2014), these are important disturbance mechanism in these forests (Negrón-Juárez et al. 2011; Negrón-Juárez et al. 2016). For instance, in the Manaus region, the cumulative disturbance of this small-scale disturbances in 2008 was equivalent to *ca.* 40% of the total deforestation in the year (Negrón-Juárez et al. 2011). As previously mentioned, blowdowns can also be formed in storms propagated with squall lines (Fujita 1990; Garstang et al. 1994). In January 2005, a basin-wide squall line event propagated blowdowns that caused an estimated mortality of 525 ± 121 million trees (Negrón-Juárez et al. 2010b). A large disturbed patch created by this event was analyzed in different studies comprising this dissertation and other topic-related studies.

Indeed, like other closed canopy forests worldwide (Bormann and Likens 1979; Lieberman et al. 1989; Scatena et al. 1996; Lindroth et al. 2009; Zeng et al. 2009), Central and Western Amazon forests comprise a mosaic of forest patches (Fig. 7) recovering from complex windthrows varying in size and frequency (Chambers et al. 2013; Negrón-Juárez et

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al. 2016). By integrating old-growth forest data on tree mortality with remote sensing disturbance probability distributions, Chambers et al. (2013) parameterized an individual-based simulation model (TRECOS) to assess possible effects of wind-driven mortality on biomass balance. Simulations from this model suggest that tree biomass stocks in old-growth Central Amazon forests vary constantly, driven by a continuous cycle of recovery from wind disturbance. As pointed by previous studies (Nelson et al. 1994; Espírito-Santo et al. 2010; Espírito-Santo et al. 2014), the simulations with TRECOS also indicate a lower return-frequency probability for larger blowdown events (Chambers et al. 2013). Although these simulations do not account for vegetation responses, they show that a significant fraction of the tree mortality associated with wind disturbances is not accounted for in available permanent plots in the Amazon. These results emphasize that an important disturbance process may be missing in regional and continental biomass/carbon balance assessments (Fisher et al. 2008; Chambers et al. 2009a). Note that, despite the strong influence of precipitation and soil gradients (Malhi et al. 2006; Banin et al. 2012; Quesada et al. 2012), even small variations in the tree mortality regime have been reported as a prevalent mechanism defining structural and taxonomical attributes of Amazon forests. This tradeoff seems to operate at the local- (Toledo et al. 2011), regional- (Schietti et al. 2016) and continental-scale (Johnson et al. 2016).

Prior to this dissertation, there were only two studies describing short-term effects of blowdowns in the Amazon. In Mato Grosso (southeast Amazon), a blowdown caused *ca.* 10% of biomass reduction in an old-growth forest (Silvério 2015). In areas subjected to damage by forest fires before the blowdown, wounded trees close to the forest edge were more susceptible to damage and mortality. Diameter at breast height (DBH) correlated positively with damage probability, suggesting that in this forest larger trees are more susceptible to damage from wind (Silvério 2015). In Central Amazon, large blowdown gaps (*ca.* 6yr-old) were reported to have lower basal area, biomass and wood density than that from nearby old-growth forest plots (Chambers et al. 2009b). The fast-recruitment of pioneer species with lower wood density and biomass was attributed to the observed patterns. As already mentioned, similar effects were not consistently observed within small treefall gaps (Hubbell et al. 1999; Chazdon et al. 1999; Molino and Sabatier 2001). Still, catastrophic tree mortality disturbances can also change soil attributes due to uprooting of trees, litter

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accumulation and decomposition (Putz 1983; Vitousek and Denslow 1986; Kramer et al. 2004; Don et al. 2012).

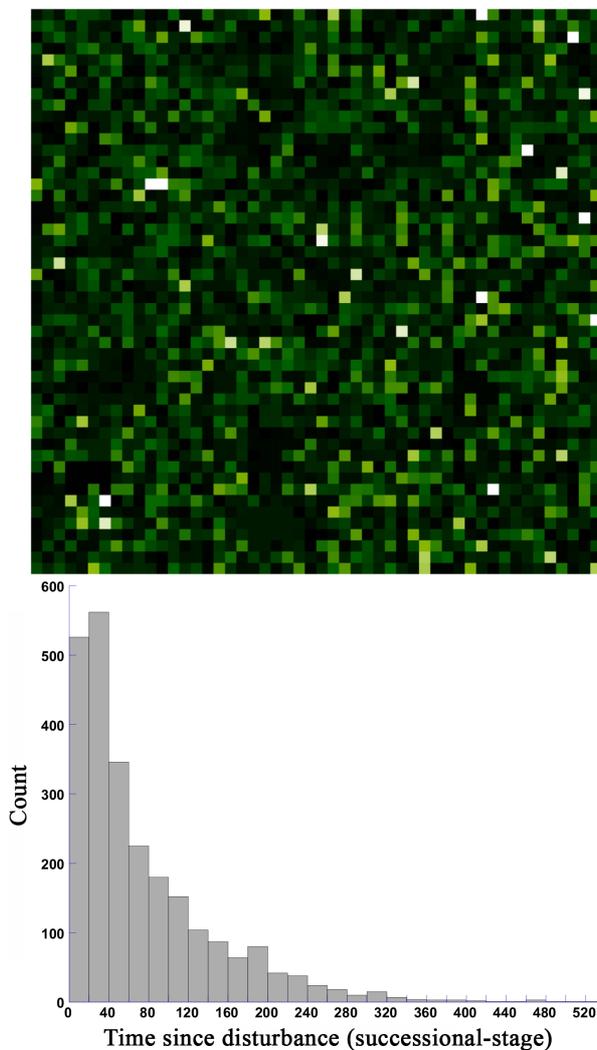


Fig. 7. Spatial distribution in time since last episodic succession-inducing disturbance (t_e) estimated from an individual-based simulation model (TRECOS) that integrates field plot data and remote sensing disturbance probability at the end of a 2,000-yr run (light pixels, old patches; dark pixels, young patches). The distribution of t_e ranging from 1 to >500 yrs is shown in the histogram. Median t_e for the 400-m² cells was 51 yrs (mean, 73.9 yrs), which is less than the time required for a patch to approach steady-state conditions in terms of biomass or tree species composition, resulting in a highly dynamic old-growth Central Amazon forest mosaic. Maximum t_e (534 yr) demonstrated that a significant number of patches at the tail of this distribution are at a mature state, and trees exceeding 500 yrs are found in these forests (Chambers et al. 1998; Vieira et al. 2005). Figure source: modified from Chambers et al. 2013.

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In this dissertation, I aimed to provide the first empirical assessment of forest succession and biomass/carbon dynamics following large-scale wind disturbances in the Amazon (Fig. 8). Specifically, I tested the effects of blowdowns on species composition, forest dynamics and important components of the carbon balance in Central Amazon *terra firme* forests. In addition, together with colleagues, I assessed for the first time the effects of blowdowns on soil carbon stocks.

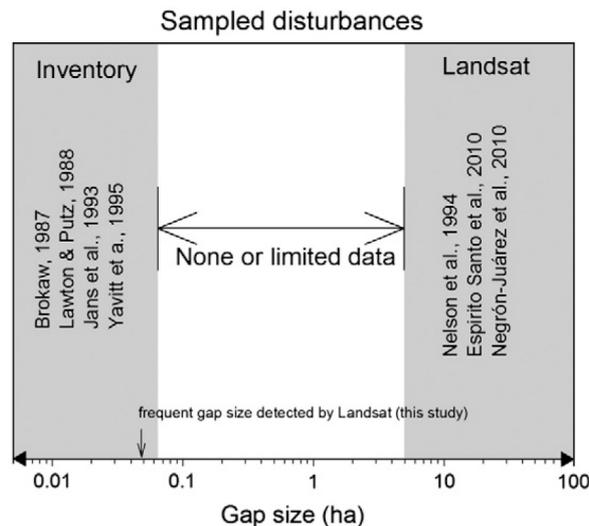


Fig. 8. Up to date monitoring of canopy gaps. Note that the different papers included in this dissertation (Marra et al. 2014a; Magnabosco Marra et al. 2016a; Santos et al. 2016; Magnabosco Marra et al. 2016b) contributed with novel information on the white area, for which data is scarce for the entire Amazon. Figure source: Negrón-Juárez et al. 2011.

1.4. General framework

The different studies comprising this dissertation fit into a larger framework that combines initiatives and groups from four countries (i.e. Brazil, Germany, Peru and USA) (Fig. 9). The main project started in 2006 with the ultimate goal of assessing the effects of windthrows on the structure and dynamics of Amazon *terra firme* forests. In a first stage, we focused on developing and improving remote sensing techniques for detecting and quantifying tree mortality associated with blowdowns. Apart from establishing robust routines for detecting and quantifying blowdown patches (Chambers et al. 2007; Negrón-Juárez et al. 2010b), our group also proposed a new approach showing the importance of small-scale blowdown events (Negrón-Juárez et al. 2011). During this first phase, the

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initiative was funded by the National Aeronautics and Space Administration (NASA) within the NASA Biodiversity Project (Project 08-BIODIV-10), and by the Brazilian Council for Scientific and Technological Development (CNPq) within the National Institute of Science and Technology (INCT) *Madeiras da Amazônia*.

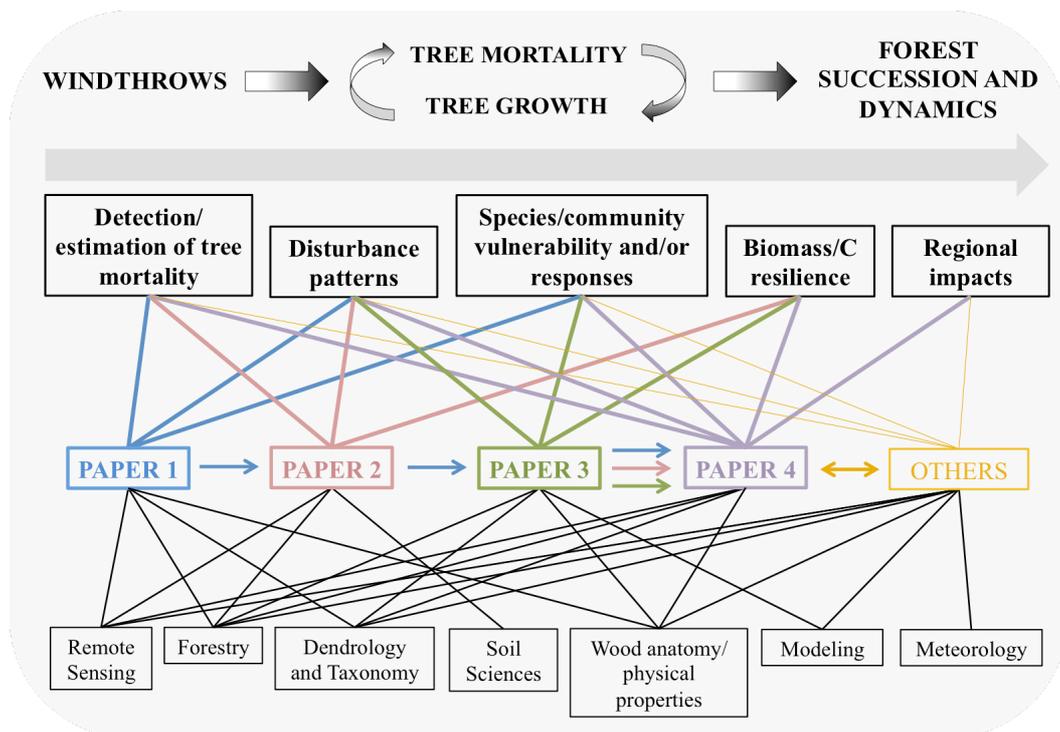


Fig. 9. Framework describing assessed interactions between windthrows, forest succession and dynamics. Upper black boxes with bold-case indicate the different aspects and processes analyzed in this dissertation and additional topic-related studies. Color bolded boxes in the middle indicate the papers included in this dissertation (i.e. Paper 1- Marra et al. 2014a *PLoS ONE*; Paper 2- Santos et al. 2016 *Biogeosciences*; Paper 3- Magnabosco Marra et al. 2016a *Biogeosciences*; and Paper 4- Magnabosco Marra et al. 2016b in preparation for *Ecological Monographs*). Lower black-boxes indicate data sources and methodological approaches applied in different studies. Arrows between color boxes indicate the information flow between the different studies. Color lines indicate the aspects and processes addressed by each of the papers. Back lines indicate the different data sources and approaches employed in each of the papers. ‘Others’ refers the topic-related studies developed between 2009 and 2016, in which I contributed with research design, grant submission, data collection and processing, data analysis, analytical tools and for which I wrote and/or edited parts of the respective papers. They included: Chambers et al. 2009 *Ecol Lett*; Negrón-Juárez et al. 2010 *Geophys Res Lett*; Negrón-Juárez et al. 2011 *Remote Sens Environ*; Chambers et al. 2013 *PNAS*; Ribeiro et al. 2014 *JARQ*; Ribeiro et al. 2016, *For Ecol and Management* (in review); and Negrón-Juárez et al. 2016 *Sci Adv* (in review).

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In 2010, based on small-scale observations of short-term effects of single blowdowns in the region of Manaus (Chambers et al. 2009b; Magnabosco Marra 2010), the initiative expanded to other sites in Central (Brazil: Manaus, Presidente Figueiredo and Manacapuru) and Western Amazon (Peru: Iquitos region). In this second phase, preliminary results from other studies from our (Fisher et al. 2008; Chambers et al. 2009a; Chambers et al. 2013) and other groups (Lloyd et al. 2009; Gloor et al. 2009), motivated the implementation a forest monitoring project that could allow to asses long-term effects of blowdowns across this regional gradient (Brazil-Peru). To do so, we combined remote sensing with forest inventories in different blowdown events varying in time after disturbance. I was in charge of leading the activities in Central Amazon, including the identification and selection of blowdown sites, setting up the infra-structure for accessing the areas (i.e. road and trails), building up campsites, establishing permanent plots for monitoring the vegetation, collecting botanical samples and identifying tree species.

In 2011, I joined the workgroup *Spezielle Botanik und Funktionelle Biodiversität* (AG Wirth) from the *Universität Leipzig* and started to develop this dissertation. For doing so, I got financial support from the International Max Planck Research School for Global Biogeochemical Cycles (IMPRS-gBGC), the Biogeochemical Processes Department from the Max Planck Institute for Biogeochemistry (MPI/BGC-Jena) and the Research Group Functional Biogeography (MPI/BGC-Jena). In 2012, together with research partners from the *Instituto Nacional de Pesquisas da Amazônia* (INPA), I wrote a proposal and got a grant from the *Conselho Nacional de Desenvolvimento Científico e Tecnológico* (CNPq) to develop a project entitled Succession After Windthrows (SAWI). With the SAWI, I could re-measure all the permanent plots established between 2008 and 2011 and investigate the short-term effects of blowdowns in the soils of one study site from our chronosequence. In addition, I had access to valuable data sets produced by the *Laboratório de Manejo Florestal* (LMF/INPA). These included: (1) forest inventory data from two 5-ha permanent plots (total of 250 subplots) in old-growth forest, which were installed in 1996 and are monitored since 1998 (*Projeto Jacaranda*); and (2) allometric data on 727 trees harvested in a contiguous forest (*Projeto Piculus*). The *Projeto Jacaranda* was funded by the INPA and the Japan International Cooperation Agency (JICA). The *Projeto Piculus* was funded by the INPA, the *Financiadora de Estudos e Projetos* (Finep) from the Brazilian Ministry of Science and Technology and the Pilot Program to Conserve the Brazilian Rainforests (PPG7).

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Within the scope of this large and interdisciplinary initiative, the specific goal of this dissertation was to cover the biotic and abiotic facets of the disturbance-recovery process, with a special focus on the interactions between disturbance and vegetation leading to shifts in forest dynamics and biomass/carbon balance. To do so, I carried out four interactive studies, including three peer-reviewed papers and an additional manuscript to be submitted to the *Ecological Monographs*. These studies are complementary to topic-related studies in which I also contributed (Fig. 9, referred as ‘Others’; references are given in the *Appendices* of this dissertation). Overall, they provide novel and complementary evidence on the importance of periodic wind disturbances on complex landscape process defining tree community attributes in Amazon *terra firme* forests.

1.5. Disturbance patterns and effects of windthrows on structural and taxonomical attributes

In the first paper of this dissertation (Marra et al. 2014a), I assessed the landscape-level effects of tree mortality caused by a single blowdown associated with a squall line event on taxonomical and structural attributes of a Central Amazon *terra firme* forest. By using field and remote sensing data, I investigated the short-term effects of large blowdown gaps (> 2,000 m²) created during a single storm event in January 2005 near Manaus, Brazil. Specifically, I aimed to address (i) how forest structure and composition vary with disturbance gradients and (ii) whether tree diversity is promoted by niche differentiation related to windthrow events at the landscape scale. In contrast to a categorical comparison between blowdown gaps and undisturbed forests (Chambers et al. 2009b; Negrón-Juárez et al. 2011), in this study I looked at the differential effects of tree mortality intensity on community composition, diversity and structure (Fig. 10). To this end, I applied data collected 4 yrs after disturbance and data from a contiguous old-growth forest (i.e. *Projeto Jacaranda*), which I used as a control. These study sites are located at the *Estação Experimental de Silvicultura Tropical* (EEST), a 21,000 ha reserve owned and administered by the LMF/INPA. Parts of the EEST were hit by blowdowns formed along a squall line event that propagated along the Amazon basin in January 2005. The geographical range and tree mortality associated to this event were also assessed and reported by our group (Negrón-Juárez et al. 2010b). A detailed description of the studied areas is given in the ‘General Methods’ section of this dissertation and in paper 1 (Marra et al. 2014a).

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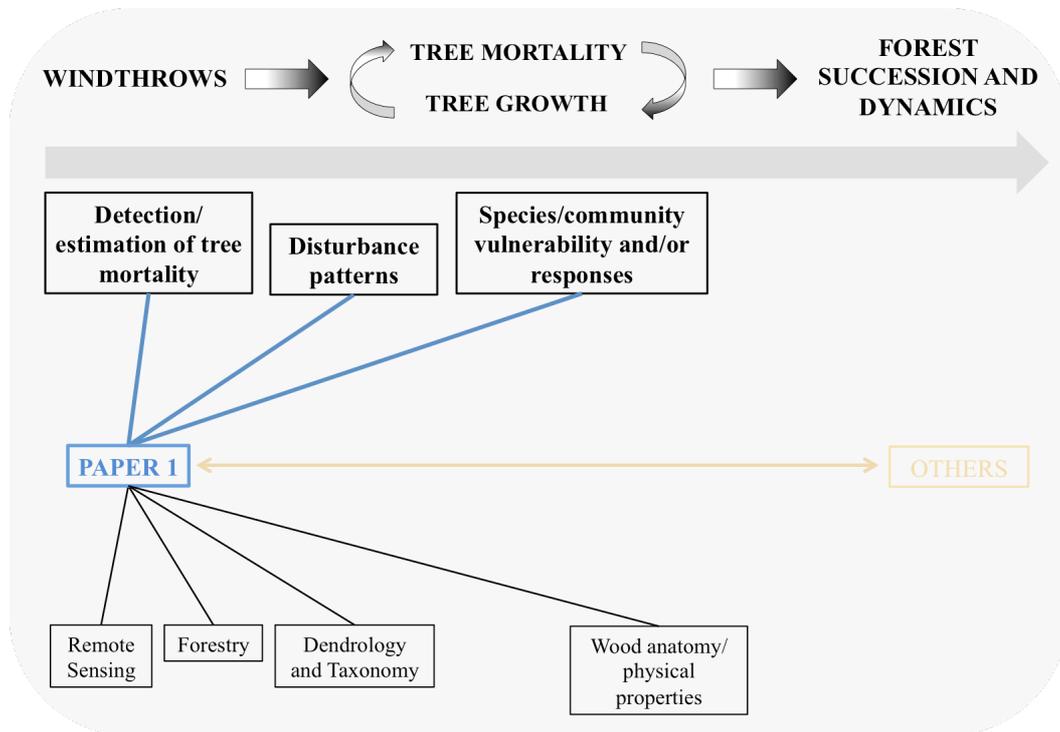


Fig. 10. Framework describing the aspects and processes (upper boxes), sources and methodological approaches (lower boxes), and previous studies considered in the conception of paper 1 (Marra et al. 2014a) comprising this dissertation. This study was motivated by the results from Chambers et al. (2009), who reported significant differences in structure and wood density between blowdown gaps and an undisturbed forest. Here, I investigated differences in taxonomical and structural forest attributes and possibly relationships with tree mortality intensity. To do so, I combined remote sensing for assessing tree mortality intensity at the landscape-level, with a detailed forest inventory for assessing tree community attributes.

Innovative measures of tree mortality caused by the blowdown, allowed me to assess differential effects of the observed gradient of tree mortality typical of these Central Amazon forests. Furthermore, it allowed me to assess how variations in tree mortality intensity affect different forest attributes. I could also reveal the different modes of tree mortality associated with windthrows. More importantly, I showed that variations in tree mortality intensity and associated environmental heterogeneity can promote tree species diversity by favoring a diverse set of species differing from that observed in old-growth forests. The novel results reported in paper 1, suggest that large, intermediate and small canopy gaps created by blowdowns are each characterized by unique recovery processes. These results also indicate that blowdowns can influence patterns of forest structure and species composition at the

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landscape scale. In the context of the NASA Biodiversity and SAWI projects, this paper directly motivated other studies (Ribeiro et al. 2016; Negrón-Juárez et al. 2016), including paper 2, paper 3 and paper 4 of this dissertation (Magnabosco Marra et al. 2016a; Santos et al. 2016; Magnabosco Marra et al. 2016b).

1.6. Windthrows and soil carbon

It has been reported that both small treefall gaps and large-scale natural disturbances can change soil attributes. The greater canopy openness in gaps allows increased light availability and air circulation. Furthermore, the exposure of mineral soil from deeper horizons due to uprooting of trees, as well as the higher litter inputs due to tree mortality, can change soil attributes such as mineral composition, texture, temperature and moisture (Putz 1983; Vitousek and Denslow 1986; Turner et al. 1998; Don et al. 2012). Importantly, soil attributes can also have strong effects on Amazon tree communities, defining species distribution, tree density and biomass (Castilho et al. 2006; John et al. 2007; Quesada et al. 2012; Johnson et al. 2016; Schiatti et al. 2016).

In paper 1, I documented the most important tree modes of death and how tree mortality intensity varied at the landscape-level, resulting in lower observed values for structural variables such as tree density and basal area in highly (and recently) disturbed areas (Marra et al. 2014a). These observed short-term reductions in tree density also indicated a strong gradient of litter deposition associated to differences in tree mortality intensity. In paper 2 of this dissertation, I looked for possible effects of variations in tree mortality intensity on soil carbon stocks (Fig. 11) (Santos et al. 2016). To do so, I assessed soil carbon stocks of the disturbed forest described in paper 1 (Marra et al. 2014a), 7 yrs after disturbance.

This study is the first report showing tradeoffs between tree mortality associated with blowdowns and variations in soil carbon stocks in Amazon forests. I show that greater inputs of litter released from dead trees in disturbed areas resulted in higher soil carbon stocks. Moreover, I show that although clay content is positively related to the soil carbon content, even clay-poor soils can incorporate a significant amount of the organic and mineral carbon available in the litter after disturbance. These results suggest that a significant fraction of the landscape variation in soil carbon stocks, at least for the Central Amazon, can be attributed to variations in the tree mortality regime (i.e. forest dynamics). The higher carbon availability

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that I observed and the possibly higher nutrient availability in soils from large canopy gaps created by wind disturbance are potential aspects favoring forest recovery, as demonstrated in the paper 4 of this dissertation (Magnabosco Marra et al. 2016b).

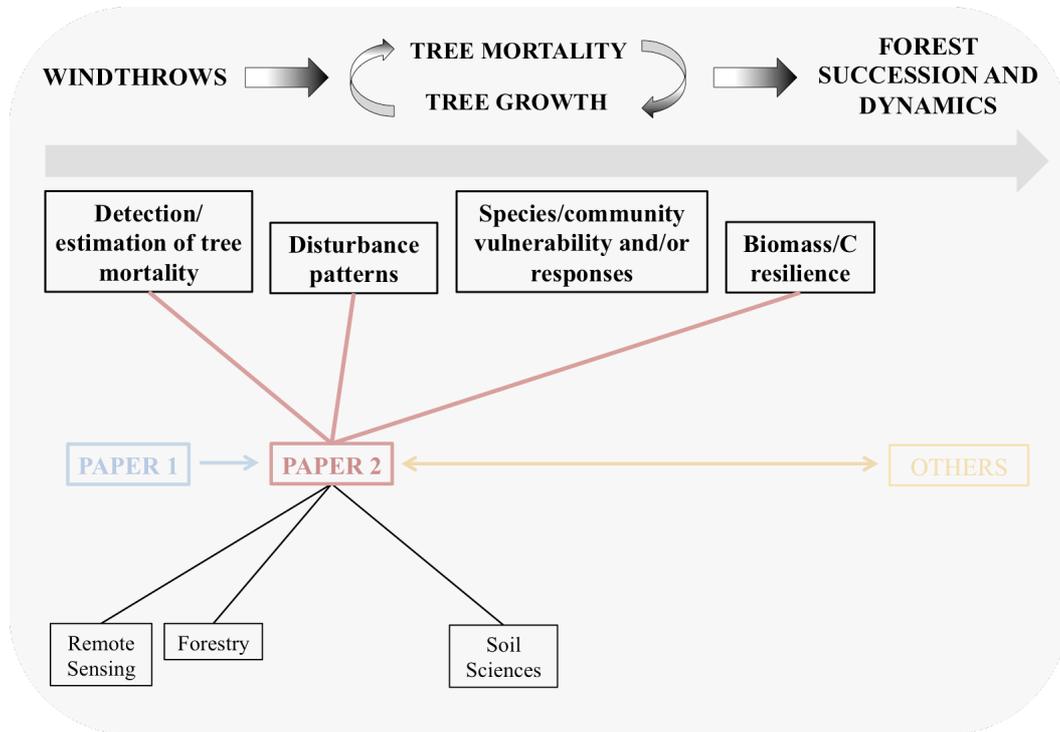


Fig. 11. Framework describing the aspects and processes (upper boxes), sources and methodological approaches (lower boxes), and previous studies considered in the conception of the paper 2 comprising this dissertation (Santos et al. 2016). Here, I assessed tradeoffs between vegetation dynamics (i.e. differences in the tree mortality regime) and soil carbon stocks. To do so, I sampled soils along a gradient of tree mortality associated with the blowdowns studied in paper 1 (Marra et al. 2014a).

1.7. Predicting biomass of complex wind-disturbed forests

Although tropical forests account only for 7-10% of the land surface (Bonan 2008), they harbor more than 90% of the world's estimated tree species (Fine et al. 2008) and store *ca.* 25% of terrestrial (below- and aboveground) carbon stocks (Bonan 2008; FAO 2010; Poorter et al. 2015). Worldwide, Latin American forests play a crucial role in this context, in particular the Amazon forest (Bonan 2008; Saatchi et al. 2011). Despite large uncertainties associated with current biomass/carbon estimates (Saatchi et al. 2007; Clark and Kellner 2012; Feldpausch et al. 2012; Mitchard et al. 2014), the Amazon basin is estimated to store

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ca. 90 Pg C (Houghton et al. 2001; Feldpausch et al. 2012), equivalent to *ca.* 35% of the world's forest carbon stock (Saatchi et al. 2011).

Uncertainties in Amazon biomass estimates at local and regional scales arise both from the parameterization and application of biomass estimation models. This issue has long been a focus of debate (Chave et al. 2005; Saatchi et al. 2007; Clark and Kellner 2012; Chave et al. 2014; Marvin et al. 2014; Sileshi 2014). At the local-scale, model parameterization with a data set that does not represent the target forest (i.e. size distribution, tree species diversity and respective variation in architecture) or a wrong/inadequate statistical approach, can yield a model that produces biased stand-level predictions (Clark and Kellner 2012; Sileshi 2014). Also, the use of site-specific models for estimating the biomass of forests different than that where these models were fit (i.e. different structure and floristic composition), can lead to biased predictions.

Generic models combining global and/or pantropical allometric data sets are of a great importance since they include many species growing at different conditions and climates, thus representing a wide spectrum of potential predictors for tree biomass (Brown et al. 1989; Chave et al. 2005; Chave et al. 2014). However, these models may fail to represent allometries in regions/forests not included or poorly represented in the data set used for the model parameterization (Nogueira et al. 2008; Lima et al. 2012; Ngomanda et al. 2014). Still, when applied at the large scale, generic global or pantropical models are usually constrained by the availability of remote sensing and field/plot-based data for the calibration of the sensors (Saatchi et al. 2007; Clark and Kellner 2012; Marvin et al. 2014; Mitchard et al. 2014). In the Amazon forest, this issue is of a great importance.

The network of permanent plots installed within the *Projeto Jacaranda*, NASA Biodiversity and the SAWI projects provide an extensive and unique database for assessing the biomass recovery trajectory of Amazon forests disturbed by large-scale wind disturbances. Nonetheless, the issues mentioned above related to the estimation of biomass in tropical forests become critical when one aims at estimating the biomass of complex wind-disturbed forests. In these forests, tree mortality associated with different levels of disturbance produce strong spatial variation in floristic composition, structural and architectural attributes (Chambers et al. 2009b; Ribeiro et al. 2014; Marra et al. 2014a; Negrón-Juárez et al. 2016).

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In paper 3, I parameterized biomass estimation models adequate to estimate aboveground biomass of Central Amazon *terra firme* forests encompassing the full tree mortality gradient typical of this region (Fig. 12). To parameterize biomass estimation models, I used an allometric data set on 727 trees including a large variation of successional stages relating different levels of disturbance (i.e. old-growth and secondary forests), and including a high number (135) of species (LMF/INPA) (Fig. 12). By applying a differential modeling approach (Wirth et al. 2004; Mascaro et al. 2011), I was able to ‘correctly’ deal with the heteroscedascity intrinsic to allometric data, a condition that has been neglected or not well treated in many studies (Mascaro et al. 2011; Sileshi 2014). The ample data set that I used, allowed me to fit generic models that account for important variations in species architecture, typical of diverse tropical forests (Hallé 1974; Poorter et al. 2003; Kitajima et al. 2005; Poorter et al. 2006; Banin et al. 2012). In addition, I assessed allometric differences related to species belonging to different successional groups. By pooling pioneer, mid- and late-successional species in separate groups, I fit specific biomass estimation models that account for such related differences.

My results indicated that in species-rich and structurally complex tropical forests, using biomass estimation models fit with an inappropriate modeling approach or with a single independent variable (e.g. DBH), can also lead to biased stand-level estimates of aboveground biomass (Magnabosco Marra et al. 2016a). In forests subjected to strong environmental gradients, DBH might not reflect site-specific differences in e.g. tree height, wood density and species architecture, which have a strong influence on AGB estimates (Baker et al. 2004a; Feldpausch et al. 2011; Banin et al. 2012; Feldpausch et al. 2012; Sileshi 2014).

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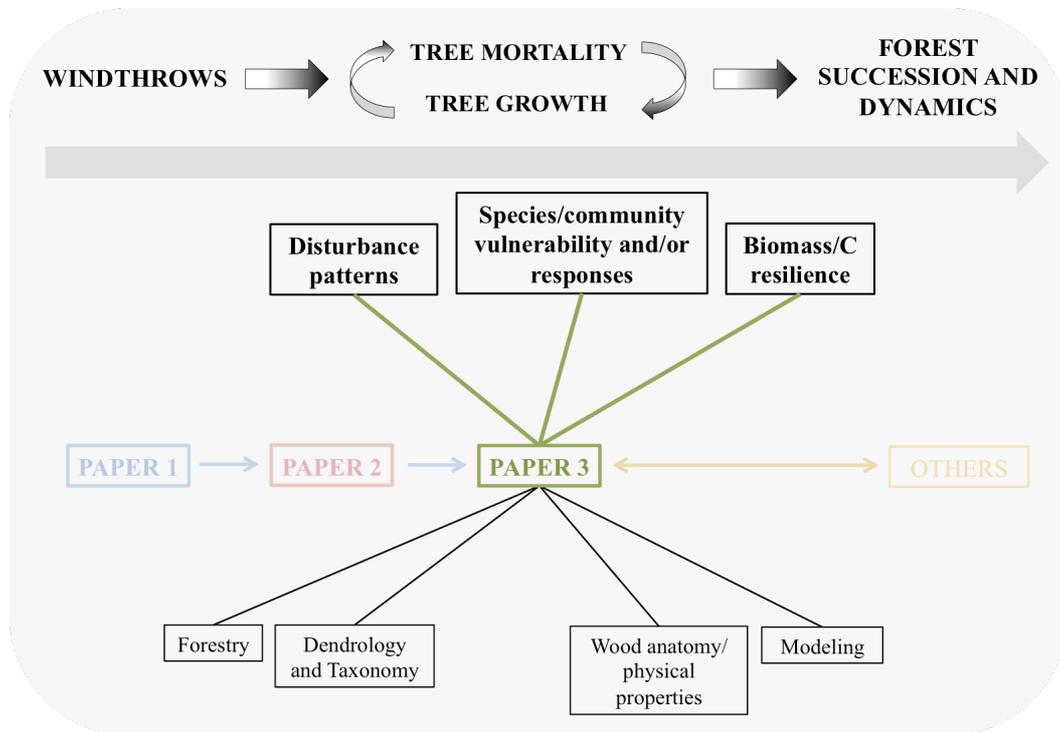


Fig. 12. Framework describing the aspects and processes (upper boxes), sources and methodological approaches (lower boxes), and previous studies considered in the conception of the paper 3 comprising this dissertation (Magnabosco Marra et al. 2016a). Here, I parameterized biomass estimation models for estimating the aboveground biomass of hyperdiverse and structurally complex Central Amazon forests subject to a wide tree mortality gradient created by windthrows. To do so, I applied allometric data on 727 trees belonging to at least 135 species, which represented local variations in species diversity and respective architecture.

1.8. Exploring mechanisms of biomass resilience to windthrows

Large-scale natural disturbances leading to catastrophic tree mortality can shift old-growth forests towards earlier successional stages (Longman and Jenik 1974; Everham and Brokaw 1996; Turner et al. 1998; Cole et al. 2014). The capacity of a forest to recover pre-disturbance conditions (i.e. resilience) depends on vegetation resistance and responses (Holling 1973; Harrison 1979; Peterson et al. 1998), and recovery often involves progressive changes in forest structure and floristic composition (Everham and Brokaw 1996; Guariguata and Ostertag 2001; Chazdon 2003). In the absence of periodic large-scale disturbances, old-growth forests can exhibit a steady-state (i.e. equilibrium) behavior, in which tree communities can remain stable until the next large disturbance.

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Old growth Amazon forests have long been assumed to be at equilibrium, with treefall gaps associated with background tree mortality (Lugo and Scatena 1996) being the major disturbance regime (reported as lower than $5\% \text{ yr}^{-1}$ in Amazon forests) (Phillips et al. 2004; Gloor et al. 2009; Espírito-Santo et al. 2014). While gap-phase regeneration following treefall disturbances seems to fail in explaining landscape variations in tree species composition and diversity in these and other tropical forests (Uhl et al. 1988; Hubbell et al. 1999; Baker et al. 2015), there is growing evidence supporting that even the variations in background tree mortality captured in available small permanent plots can significantly influence forest structure attributes (Toledo et al. 2013; Johnson et al. 2016; Schiatti et al. 2016).

In fact, recent studies also support that old-growth forests are not at equilibrium, but in a continuous recovery-process from different types and levels of disturbance (Cole et al. 2014) likely to drive observed shifts in dynamics (Baker et al. 2004b; Brien et al. 2015), species and trait composition (van der Sande et al. 2016). The occurrence of periodic blowdowns across vast areas of the Amazon (Nelson et al. 1994; Fisher et al. 2008; Chambers et al. 2009a; Chambers et al. 2013; Asner 2013) corroborates this ‘non-equilibrium’ hypothesis. Basin-wide effects of large blowdowns on forest composition and dynamics, however, remain uncertain but presumably depend on the frequency and size distribution of these events (Gloor et al. 2009; Espírito-Santo et al. 2010; Chambers et al. 2013; Espírito-Santo et al. 2014). Although this issue was not addressed in this dissertation, it is evident that the wide range of tree mortality intensities produced by blowdowns (Nelson and do Amaral 1994; Negrón-Juárez et al. 2010b; Negrón-Juárez et al. 2011; Marra et al. 2014a; Rifai et al. 2016) is not captured by most of the available plot-based inventories in the Amazon (usually $< 5\%$) (Lewis et al. 2004; Phillips et al. 2004; Brien et al. 2015).

General research on tropical forest resilience focused on small gap-phase regeneration (Grubb 1977; Denslow 1980a; Uhl et al. 1988; Hubbell et al. 1999; Bongers et al. 2009) or stand-removing human disturbances (Finegan 1996; Guariguata and Ostertag 2001; Poorter et al. 2016) that include soil alterations, nutrient removal and fire (Chazdon 2003; Chazdon et al. 2007). Here, I assumed that these extremes do not represent the entire disturbance gradient typical of Central and Western Amazon forests affected by periodic blowdowns (Nelson et al. 1994; Chambers et al. 2013; Negrón-Juárez et al. 2016). Although there is an expressive number of studies on patterns of tree damage and mortality in tropical and subtropical forests

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frequently affected by wind disturbances (e.g. hurricanes, typhoons and tornadoes), long-term monitoring and assessments of forest resilience to extreme natural disturbance events are scarce (Everham and Brokaw 1996; Scatena et al. 1996; Mascaro et al. 2005). The lack of knowledge on the recovery process across the full disturbance gradient of wind-disturbed Amazon forests and on the importance of windthrows for the biomass/carbon balance in these forests were my main motivations for developing the paper 4 of this dissertation (Fig. 13) (Magnabosco Marra et al. 2016b).

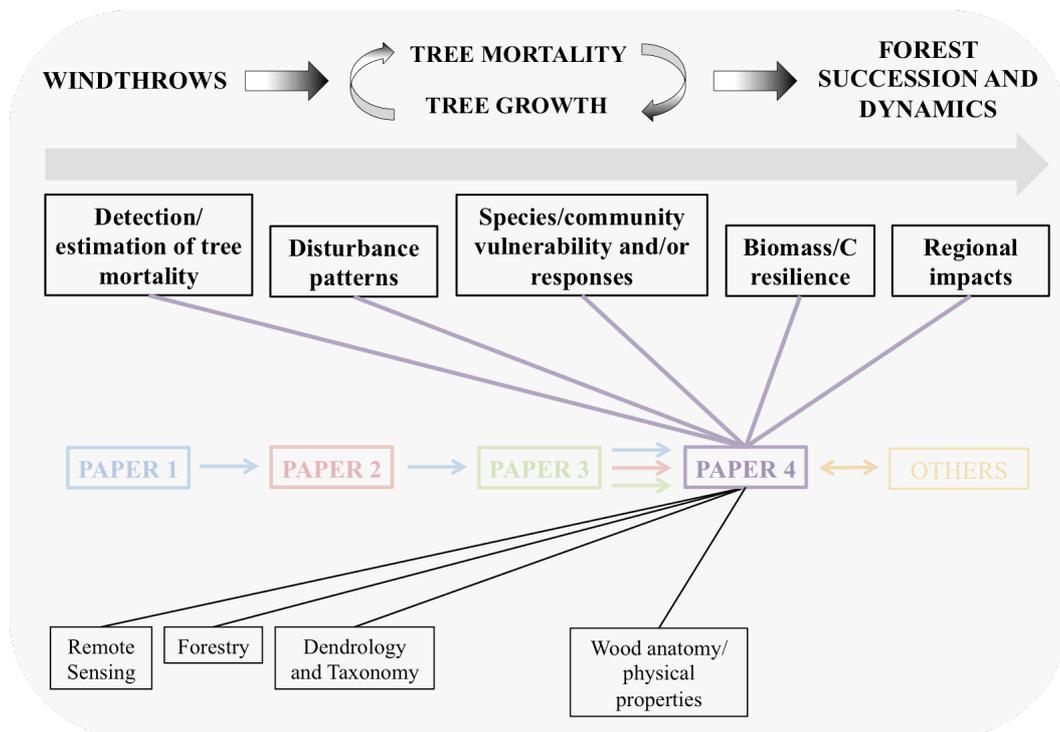


Fig. 13. Framework describing the aspects and processes (upper boxes), sources and methodological approaches (lower boxes), and previous studies considered in the conception of the paper 4 comprising this dissertation (Magnabosco Marra et al. 2016b). Here, I assessed the biomass recovery process and its interactions with shifts in taxonomical attributes of tree communities during succession after windthrows. This study combines most of the previous knowledge and data acquired during the NASA Biodiversity and SAWI projects. In addition, it includes data acquired within the *Projeto Jacaranda* on an old-growth forest, which I used as a control.

In paper 4, I assessed interactions between taxonomical attributes and resilience mechanisms during the biomass recovery process following different blowdown events (Fig. 13). To this end, I combined my forest inventory data in a chronosequence approach and most of the previous knowledge acquired by our research group within the last nine years.

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Although these forests seem to have high biomass resilience to windthrows, I detected decadal effects of initial tree-mortality on taxonomical and structural attributes, including functional composition (i.e. importance of pioneer, mid- and late-successional species) and species richness. I was for the first time able to provide a detailed picture of biomass recovery and could show how many and which species are performing different biomass gain mechanisms along the gradient of disturbance intensity and recovery-time. The variation in these attributes along the disturbance gradient typical of blowdowns marked a clear partitioning of biomass stocks and dynamics (i.e. biomass gain and losses). My results support that blowdowns produce non-negligible effects on these forests and are likely to contribute to broad scale patterns of species diversity and biomass dynamics.

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A detailed description of the employed methods is given in the different papers comprising this dissertation. Here, I present additional information not covered by these individual papers. To this end, I also provide figures from topic-related studies, including some in which I am a co-author. The references for the topic-related papers in which I am a co-author are given in the ‘Appendices’ section of this dissertation. The allometric data used in the paper 3 (Magnabosco Marra et al. 2016a) and the forest inventory data on the old-growth forest used as a control in the papers 1 and 4 (Marra et al. 2014a; Magnabosco Marra et al. 2016b) were granted by the LMF/INPA. The forest inventory and soil data on the wind-disturbed forests, which were collected within the NASA Biodiversity and SAWI projects, are planned to be made available in the short future. The metadata from paper 1 (Marra et al. 2014a) and paper 2 (Santos et al. 2016) are available on the German Centre for Integrative Biodiversity Research (iDiv) data portal (idata.idiv.de). For using these data contact D. Magnabosco Marra, J.Q. Chambers (jchambers@lbl.gov) or N. Higuchi (niro@inpa.gov.br).

2.1. Study-sites selection

Long-term studies describing forest recovery after large-scale natural-disturbances are rare. Aspects such as the relatively low frequency, predictability and detectability, have limited our capacity of studying the ecological and evolutionary importance of these disturbances. Accessibility, logistics and safety issues are other prevalent factors limiting our knowledge about large-scale disturbances.

Over the last years, the improvement and availability of satellite images, remote sensing tools and the more recent emergence of open source software for image analysis (R Core Team 2014; Conrad et al. 2015; Google Earth Engine Team 2015; QGIS 2016), amplified our capacity of detecting, estimating the magnitude and distribution of large-scale disturbances such as blowdowns across the Amazon (Nelson et al. 1994; Chambers et al. 2007; Espírito-Santo et al. 2010; Negrón-Juárez et al. 2010b; Negrón-Juárez et al. 2011; Chambers et al. 2013; Espírito-Santo et al. 2014; Negrón-Juárez et al. 2016). In contrast, the high tree mortality associated with these events creates large gaps, difficult to be accessed (Figs. 1 and 2). The enormous amount of woody debris from the dead trees, a dense community of canopy species (e.g. lianas and epiphytes) brought to the ground together with

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falling trees and the formation of treefall pits and mounds, provide extra restrictions/difficulties for the implementation of a forest monitoring project. Although a considerable amount of necromass is decomposed within the first years, the natural regeneration of fast-growing species (i.e. herbs, shrubs, lianas and trees) promptly fills the forest understory, which in heavily damaged areas will remain more dense and closed for years (D. Magnabosco Marra and G.H.P.M. Ribeiro, personal observations). Still, when aiming to exclude the influence of more recent human disturbances, the remoteness and lack of infrastructure such as roads and trails, increase logistic and access difficulties.

The goal of this dissertation could not have been achieved without the use of remote sensing data from satellites. Non-photosynthetic vegetation (NPV) has high reflectance in the band 5 of Landsat imagery (Fig. 14) (Nelson 1994; Chambers et al. 2007; Negrón-Juárez et al. 2010a; Negrón-Juárez et al. 2011). I used this signal, which lasts for about a year, to identify the three wind-disturbed forests comprising my chronosequence.

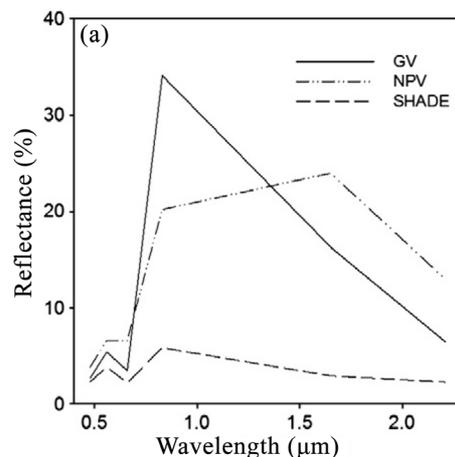


Fig. 14. Reflectance signatures (also known as endmembers) (Adams et al. 1995; Adams and Gillespie 2006; Somers et al. 2011) used to detect forest blowdowns in the different studies comprising this dissertation. Non-photosynthetic vegetation (NPV) has high reflectance in the band 5 (centered at 1.65 μm) of Landsat imagery, distinct from that of green vegetation (GV) and shaded pixels. Figure source: modified from Negrón-Juárez et al. 2011.

The old-growth forest (Og) that I used as a control is located north of Manaus, at the EEST/INPA (Fig. 15). In this area, there are 250 permanent subplots (400 m^2 , each) installed along two transects with 2,500 m length, each (Fig. 16). These plots were installed in 1996 as part of the *Projeto Jacaranda* (Higuchi et al. 1998b; Silva et al. 2003) and have been

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monitored by the LMF team (every two or three years) since 1998. This 10-ha area includes the typical topographical variation of the forests from Central Amazon (i.e. plateaus, slopes and valleys) (Braga 1979; Ranzani 1980) and harbors more than 700 tree species (Carneiro 2004; Carneiro et al. 2005; Teixeira et al. 2007). The topographic gradient, high species diversity, long-term monitoring and history of use (i.e. no great disturbance within the last 5-6 decades), make this forest a perfect site to be used as a reference in my chronosequence approach.

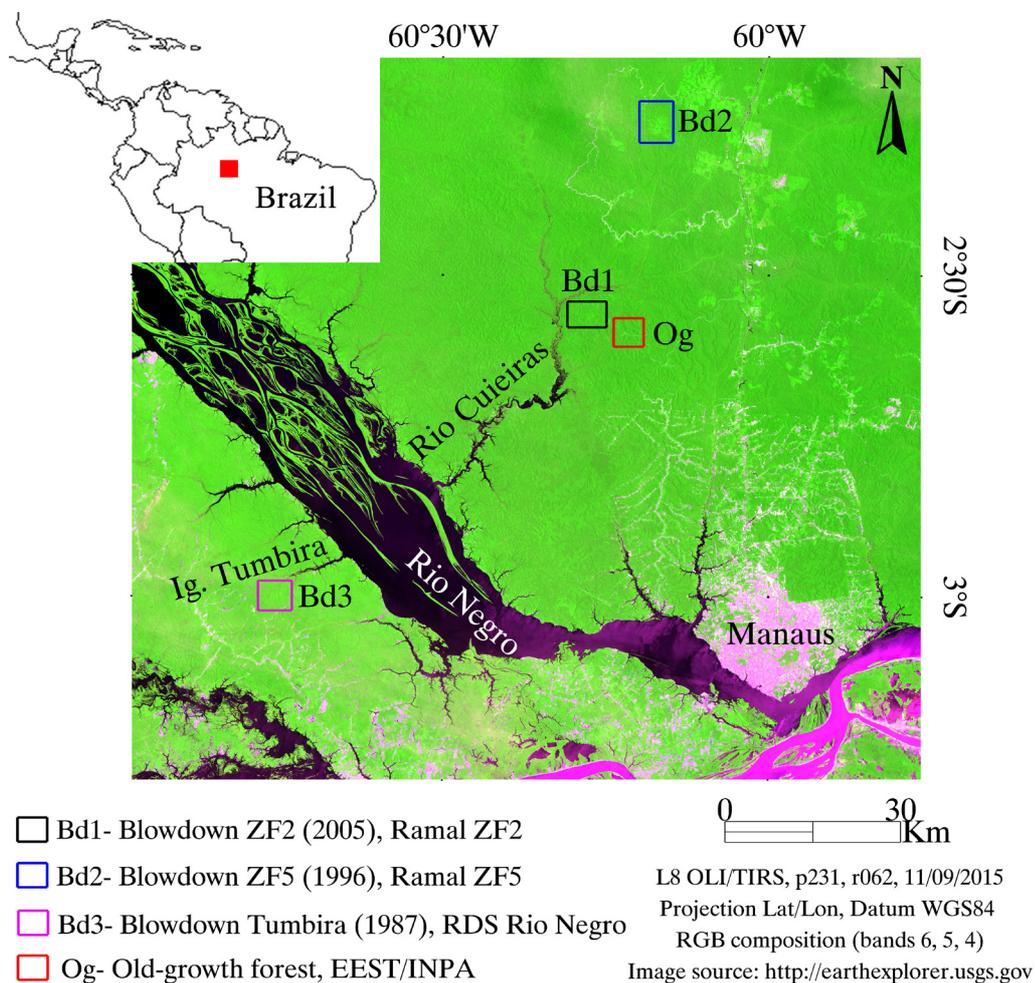


Fig. 15. Study sites (year of blowdown) comprising the forest chronosequence studied in this dissertation. The selected sites are covered by typical *terra firme* forest.

Downbursts associated with the squall line event from 2005 produced severe vegetation damage in different regions of the Amazon (Negrón-Juárez et al. 2010b),

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including *ca.* 250 ha (Bd1) of old-growth forests of the EEST/INPA an adjacent area owned and administered by the *Superintendência da Zona Franca de Manaus* (SUFRAMA) (Figs. 15 and 16). Blowdown patches were identified in RGB compositions (bands 5, 4 and 3) of Landsat 5 TM images by their high short-wave infrared reflectance (red channel), which indicates dead vegetation (NPV) (Figs. 16-18). Recognized disturbed areas were confirmed with a field survey led by the LMF/INPA. Later, disturbed areas were also visualized from a helicopter flight (Fig. 1).

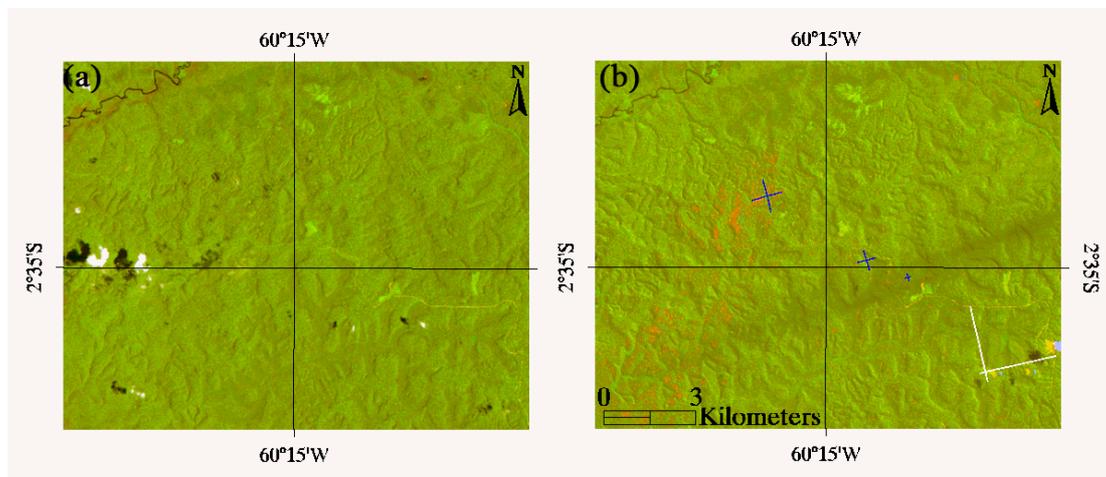


Fig. 16. Contiguous old-growth *terra firme* forest in the region of Manaus, Central Amazon, Brazil, shown in RGB composition (bands 5,4,3) of Landsat 5 TM imagery. Changes in surface reflectance from (a) Oct/2004 to (b) Jul/2005 indicate tree mortality caused by a blowdown event from 2005. Patches exhibiting high short-wave infrared reflectance (red channel) indicate non-photosynthetic vegetation (NPV) (green channel, near infrared) (b). The total affected area by this single event was *ca.* 250 ha. The transects used to sample the ZF2 (Bd1) site and the old-growth control forest (Og) (see Fig. 15), are shown in blue and white, respectively (b). Images source: <http://earthexplorer.usgs.gov>.

In the Bd1, I installed six transects of varying lengths to survey the vegetation in the summer of 2009 (4 yrs after disturbance) (Fig. 16). Subplots were installed along six transects of varying size allocated in disturbed areas including the local variation in topography and in blowdown tree-mortality intensity. For the allocation of the transects, I considered changes in NPV, previous description of disturbed areas (Guimarães 2007), observations from field surveys conducted between 2007 and 2009, and logistic constrains. Apart from the papers 1, 2 and 4 included in this dissertation, several other studies were developed in the Bd1 and

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adjacent disturbed areas (Guimarães 2007; Negrón-Juárez et al. 2010b; Bordon 2012; Araujo et al. 2013; Chambers et al. 2013; Ribeiro et al. 2014; Negrón-Juárez et al. 2016).

The selection of the blowdown sites *ZF5* (Bd2) and *Tumbira* (Bd3) (Fig. 15) was done in cooperation with R.I. Negrón-Juárez and J.Q. Chambers. Due to well-known logistic limitations intrinsic to all studies carried in remote areas of the Amazon, site accessibility was also considered as a selection criterion. For that reasons, we focused our search in the region of Manaus. We also searched blowdowns in Landsat 5 TM imagery data over a 27yr- period (from 1979 to 2005). We systematically scanned pairs of images (from consecutive years) searching for ‘fan-shaped’ and irregular disturbed patches. We excluded blowdowns occurring close to main rivers (i.e. *igapó* and *várzea*) (Junk et al. 2011), in other upland forest types (i.e. *campina* and *campinarana*) (Braga 1979), close to roads and human settlements. The Bd2 and Bd3 sites spanned the maximum amplitude of time after disturbance and tree mortality intensity that we found within the considered time-period.

The Bd2 site, which is accessible from the *Ramal-ZF5* road, is located *ca.* 35 km north from the Bd1 (Fig. 15). This area is owned and administrated by the SUFRAMA. Similar to the sampling method adopted in the Bd1 (later also employed in Iquitos [Peru] within the NASA Biodiversity project), in the Bd2 I sampled the vegetation along a 3 km length transect crossing a single disturbed patch of *ca.* 900 ha (Fig. 16). Subplots were first measured in this area in the summer of 2010 (14 yrs after disturbance).

The Bd3 site is located at the *Reserva de Desenvolvimento Sustentável do Rio Negro* (RDS Rio Negro), a 102,978.83 ha reserve. This area is accessible by boat, navigating through the *Rio Negro* and the *Igarapé Tumbira* (Fig. 15). In this site, I sampled the vegetation along two 1.5 km length transects crossing a total disturbed area of *ca.* 75 ha (Fig. 18). The first survey was conducted in the summer of 2011 (24 yrs after disturbance).

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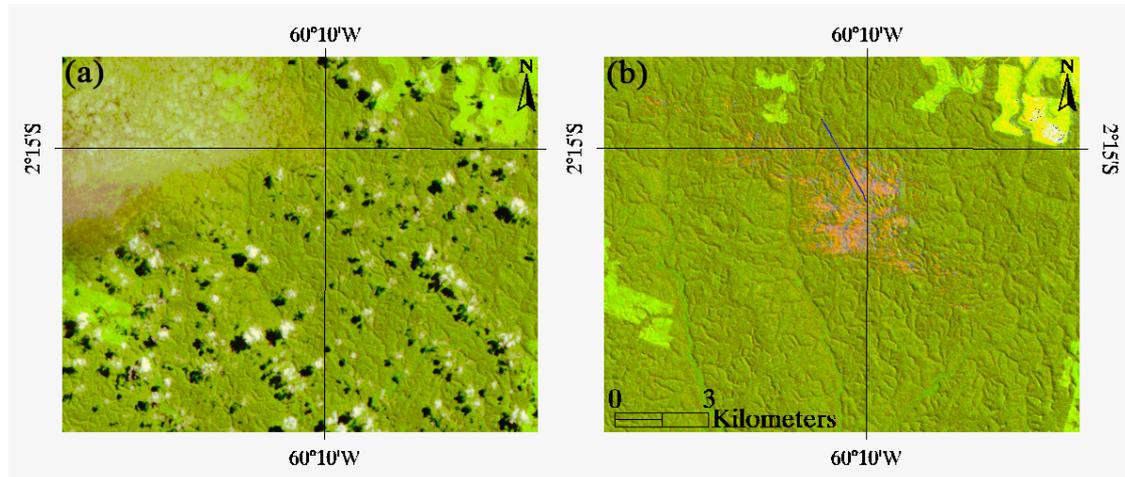


Fig. 17. Contiguous old-growth *terra firme* forest in the region of Presidente Figueiredo, Central Amazon, Brazil, shown in RGB composition (bands 5,4,3) of Landsat 5 TM (TM) imagery. Changes in surface reflectance from (a) Jul/1996 to (b) Jun/1997 indicate tree mortality likely to be caused by a single downburst from 1996. Patches exhibiting high short-wave infrared reflectance (red channel) indicate non-photosynthetic vegetation (NPV) (green channel, near infrared) (b). The total affected area by this single event was *ca.* 900 ha. The transect used to sample the ZF5 (Bd2) site is shown in blue (b). Images source: <http://earthexplorer.usgs.gov>.

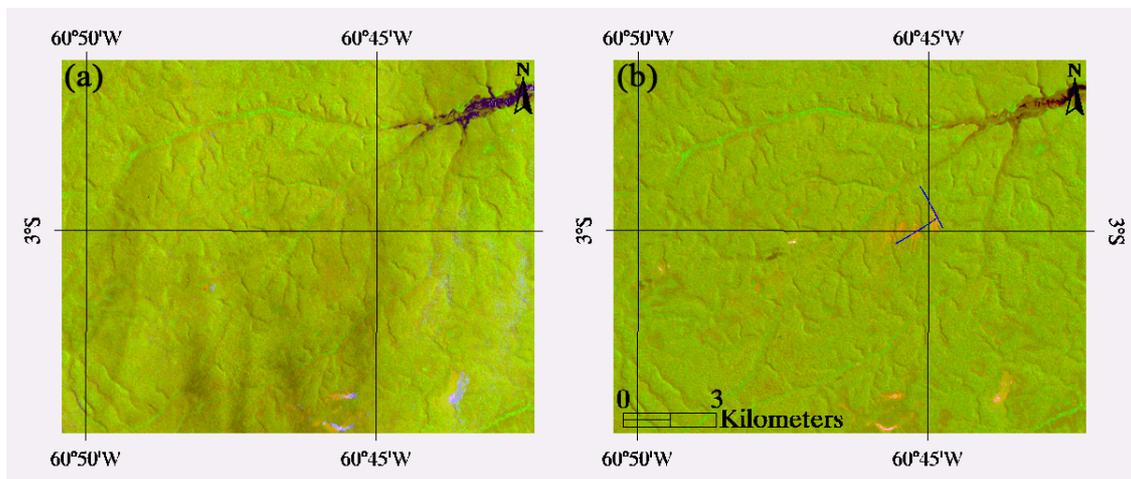


Fig. 18. Contiguous old-growth *terra firme* forest in the region of Manacapuru, Central Amazon, Brazil, shown in RGB composition (bands 5,4,3) of Landsat 5 TM imagery. Changes in surface reflectance from (a) Aug/1986 to (b) Jul/1987 indicate tree mortality likely to be caused by a single downburst from 1987. Patches exhibiting high short-wave infrared reflectance (red channel) indicate non-photosynthetic vegetation (NPV) (green channel, near infrared) (b). The total affected area by this single event was *ca.* 75 ha. The transect used to sample the Tumbira (Tum) site is shown in blue (b). Images source: <http://earthexplorer.usgs.gov>.

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Before installing transects and subplots for carrying vegetation and soil surveys, I visited the selected sites and carefully inspected for differences in vegetation type, topography, soil texture and color (through manual and visual inspection), and history of use. Note that the Bd1, Bd2 and Og sites belong to a contiguous forest (Fig. 15). Although the Bd3 site is located on other side of the *Rio Negro*, this area is also covered by similar and comparable *terra firme* (upland) forest. This assumption was confirmed by the results presented in the ‘Supporting information’ section of the paper 4.

2.2. Tree mortality estimates

Since changes in the fraction of NPV (hereafter referred as Δ NPV) relate to changes in the fraction of dead vegetation, I was able to use Δ NPV images to estimate the tree mortality associated with the blowdowns included in my forest chronosequence. For each blowdown site, I produced a Δ NPV value on a *per-pixel-basis* by subtracting the NPV image of the year before the blowdown (2 yrs for the Bd2 site) from that of the same year of the blowdown. The Δ NPV images were then used to estimated tree mortality intensity with an estimation model that has pixel Δ NPV-value as predictor (Negrón-Juárez et al. 2010a; Negrón-Juárez et al. 2011).

I produced NPV images for the selected blowdowns by employing Spectral Mixture Analysis (SMA) (Adams et al. 1995) on the Landsat 5 TM imagery. This technique allows for the quantification of the *per-pixel* fraction of the following three selected endmembers (Somers et al. 2011): green vegetation /photosynthetic active (GV), dead plant material/non-photosynthetic vegetation (NPV) and shade. I used the shade endmember to account for differences in angle, topography, shading, and shadows (Adams et al. 1995). At last, I normalized the fractions of GV and NPV by removing the shade as $GV/(GV+NPV)$ and $NPV/(GV+NPV)$ (Negrón-Juárez et al. 2010; Negrón-Juárez et al. 2011; Negrón-Juárez et al. 2016). For the analysis presented in the papers comprising this dissertation, I used images processed by R.I. Negrón-Juárez. With that, I aimed to standardize results from my studies with those from our research group (Negrón-Juárez et al. 2010b; Negrón-Juárez et al. 2011; Chambers et al. 2013). For further details on the image processing procedures and SMA routine, consult the ‘Material and Methods’ section of the paper 1 (Marra et al. 2014a), the ‘Methods’ section of the paper 4 (Magnabosco Marra et al. 2016b) and topic-related studies

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from our research group (Negrón-Juárez et al. 2010b; Negrón-Juárez et al. 2011; Chambers et al. 2013; Negrón-Juárez et al. 2016).

Field-measures of tree mortality were obtained for my study region within the first year after the 2005 blowdown event in 30 plots of 20 m x 20 m for trees ≥ 10 cm DBH (Guimarães 2007). Blowdown tree-mortality intensity (%) was linearly and positively correlated with ΔNPV (Fig. 19) (Negrón-Juárez et al. 2010b). To estimate blowdown tree-mortality in the sites included in my forest chronosequence, I used this linear model, which has Landsat-derived ΔNPV as single predictor (Negrón-Juárez et al. 2010b):

$$\text{Tree mortality (\%)} = (103.22 \times \Delta NPV) - 3.22 [1].$$

To support the classification of the subplots comprising my forest chronosequence into typical topographic classes (i.e. plateaus, slopes and valleys), I extracted terrain elevation data from a digital elevation model (Shuttle Radar Topographic Mission –SRTM) (<http://glovis.usgs.gov>).

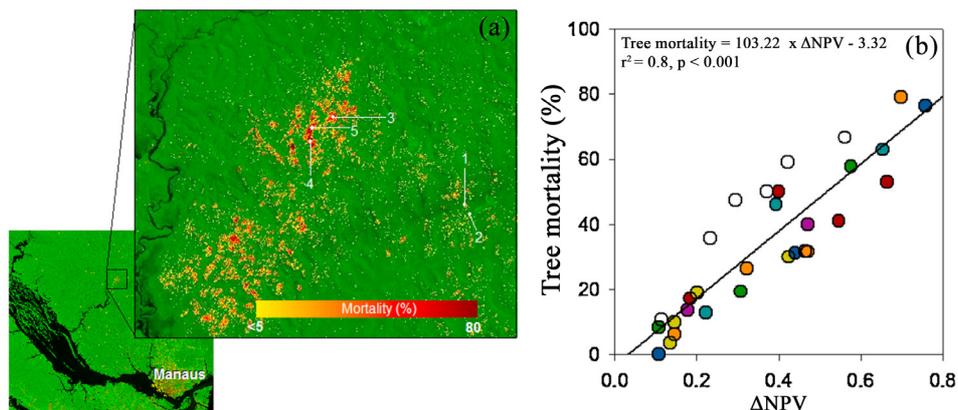


Fig. 19. Relationship between Landsat-derived ΔNPV and field-measured tree mortality in our study region (Bd1 and Og, see Fig. 15). (a) Tree mortality was measured in 30 plots (20 m x 20 m) allocated in five sites covering a 0-80% gradient of tree mortality (Guimarães 2007; Negrón-Juárez et al. 2010b). (b) The strong relationship between ΔNPV and field-measured tree mortality data allows the estimation of tree mortality at this region. Figure source: modified from Negrón-Juárez et al. 2010.

For the old-growth forest used as control (Og) (Figs. 15 and 16), I used measures of tree mortality calculated from ΔNPV only in paper 1 (Marra et al. 2014a). In that case, I applied census data from 2004-2006 and estimated tree mortality by using a ΔNPV image

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obtained by subtracting the 2005 from the 2004 NPV image, which corresponds to the period between the two forest inventories (see details in the ‘Material and Methods’ section of paper 1). Although regular surveys (*ca.* once a month) of the LMF/INPA team assure that no large blowdowns occurred in this area since 1996, I checked for representative changes in NPV over the time-period considered for selecting the blowdown sites (1979-2005). I did not find strong changes in NPV over large areas of the Og site during this entire period. Since changes in NPV can be detected at the pixel level (30 m x 30 m) (Negrón-Juárez et al. 2011), this approach allowed me to detect even small or single treefall gaps (*ca.* 1,000 m²), typical of old-growth forests (i.e. background tree mortality). Nonetheless, I did not remove subplots showing these small-scale disturbances. Together with regular field surveys, the lack of large changes in NPV assure that, apart from being free of human disturbances for 5-6 decades, no large-scale natural disturbance occurred in the Og site over the last years. This careful assessment, allowed me to use this forests as a control for assessing the magnitude of observed changes in the disturbed forests (i.e. Bd1, Bd2 and Bd3).

2.3. Vegetation and soil sampling

The sampling design adopted in the studies comprising this dissertation was defined and constrained by specific aspects of wind-disturbed forests. These are: (1) strong and complex gradients of tree mortality influenced by biotic and abiotic aspects such as species vulnerability (Negrón-Juárez et al. 2016; Ribeiro et al. 2016; Rifai et al. 2016) and the still unknown interaction between wind and Amazon forest canopies; and (2) access and displacement restrictions in disturbed areas, specially at early-successional stages (Figs. 1 and 2).

I sampled the vegetation in subplots installed along transects (Fig. 20) of varying lengths. With this method, I was able to reduce effort during installation (e.g. trail opening and maintenance, logistics to transport materials/equipment's, number of employed personal and ergonomics) and monitoring of subplots (e.g. displacement and logistics to transport materials/equipment's and samples). More importantly, this method allows sampling communities subjected to strong biotic and abiotic gradients (Felfili 1995; Schietti et al. 2016). Therefore, sampling along transects allowed me to cover the entire disturbance gradient associated with the different blowdowns and previous important landscape variations.

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The starting and end point of the different transects were defined in order to cover the entire tree mortality gradient found in each site, but also undisturbed areas used to compare the old-growth forest of each blowdown site with that from the old-growth control forest. The transects also crossed entire toposequences in order to account for possible gradients in wind-damage due to topography. Since soil texture in these forests is known to vary along the topographic gradient (higher clay content in plateaus and sand in valleys) (Ranzani 1980; Telles et al. 2003), sampling along transects also allowed me to account for possible structural and floristic variation due to this aspect (Chauvel et al. 1987; Castilho et al. 2006). This method was also compatible with that adopted in the *Projeto Jacaranda*, i.e. the Og site included in my chronosequence (Higuchi et al. 1998b; Higuchi et al. 2003; Teixeira et al. 2007). For additional information about specific sampling aspects from each site comprising the chronosequence, consult paper 4 (Table S1 of the ‘Supporting information’ section) (Magnabosco Marra et al. 2016b).

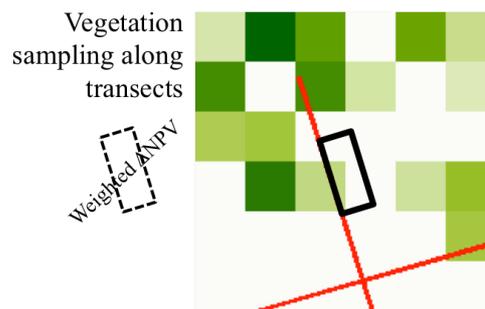


Fig. 20. Sketch showing the allocation of subplots installed along transects crossing forest blowdowns in Central Amazon *terra firme* forests. The transects cross the entire disturbed patches accounting for the available tree mortality gradient, i.e. from undisturbed (white pixels) to heavily damage areas (dark-green). For each subplot, I was able to estimate tree mortality associated to the blowdowns by using weighted Δ NPV values in a locally field-calibrated model (Negrón-Juárez et al. 2010b).

The forest chronosequence studied in this dissertation (i.e. the three blowdown sites and the old-growth forest) comprised 596 subplots. Subplots were permanently delimited with plastic signs/flags. In blowdown site, I measured DBH of all trees ≥ 10 cm DBH (Fig. 21). Recorded trees were tagged with aluminum numbered tags. Wounded trees and those with irregular trunks (buttresses) or aerial roots were measured above these irregularities. In all cases, the height at which measures were taken was marked with paint. With this I aimed

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to avoid inducing measurement error when re-measuring the trees. In order to quantify forest dynamics (tree growth, recruitment and mortality rates), all trees were measured at least two times in different intervals. I used three consecutive measures from the Og site, from the years 2002, 2004 and 2006 (2yr-intervals). The blowdown sites were monitored between 2009 and 2015. Re-measurements were taken with 3yr-intervals. To reduce measurement errors, the trees were always measured by the same team.



Fig. 21. Forest inventory routine and overall aspect of subplots installed in the three blowdown sites located in Central Amazon, Brazil (Fig. 15). Pictures: D. Magnabosco Marra and G.H.P.M. Ribeiro.

Most of the novel and complementary knowledge presented in the studies comprising this dissertation required a detailed assessment of the flora. In all the studied sites, great effort was made to collect samples and to identify recorded tree species (Figs. 22 and 23). I continuously collected botanical samples in the blowdown sites between 2009 and 2015. Apart from that, a great effort has been undertaken just after the first forest inventory was completed (Fig. 22). In total, I collected *ca.* 2,100 samples. To do so, I counted on the support from A.F. Neves, I.G. de Souza and S.L. Pereira. I identified botanical samples with the support from V.M.C. Carneiro and F.Q. Reis. The botanical exsiccates collected within the SAWI project were incorporated to the herbarium of the *Instituto Federal de Educação,*

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Ciência e Tecnologia do Amazonas (IFAM) (Fig. 23). Extensive botanical sampling and detailed species identification were carried out in the Og site as part of the *Projeto Jacaranda* (Higuchi et al. 2003). Botanical exsiccates were incorporated to the herbarium of the INPA and the collection of the EEST/INPA (Carneiro 2004; Carneiro et al. 2005).



Fig. 22. (a) Equipment for collecting botanical samples within our study sites in Central Amazon, Brazil. Tree climbing with spurs (b) and belt (c) for collecting samples (d) with a pruner connected to a 11 m telescopic aluminum stick (e). In the field, botanical samples were preserved in alcohol (f) and later dried in an electric-drier (g) at *ca.* 65°C. Binoculars were also used to recognize known species and those for which samples have been already taken (h). Pictures: D. Magnabosco Marra and G.H.P.M. Ribeiro.

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Fig. 23. I collected at least one botanical sample (three replicates) from all species sampled in the blowdown sites. (a) Most of the samples were identified in the field. Species that were identified in the field were identified by consulting specialists or comparing botanical exsiccates with holotypes from the herbaria of the IFAM and INPA (b-e). Botanical exsiccates collected within the SAWI project were incorporated to the herbarium of the IFAM (f). Pictures: D. Magnabosco Marra.

The soil study presented in paper 2 (Santos et al. 2016) of this dissertation was proposed within the scope of the SAWI project. This study was also part of the Master's dissertation of L.T. dos Santos, undertaken at the INPA under supervision by N. Higuchi and me. This study also counted on fundamental support from P.B. de Camargo and S.E. Trumbore. Soil samples were collected from the Bd1 site in the summer of 2012, thus 7 yrs after disturbance (Fig. 24). Since soil texture differences related to topographic variation can also affect other soil attributes in these forests (Ranzani 1980; Telles et al. 2003), we sampled soils only in plateau subplots of the Bd1 site.

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Fig. 24. Overall aspect of plateau subplots from the *ZF2* site (Bd1) (see Fig. 15), 7 yrs after disturbance. Subplots were allocated along a wide disturbance gradient, including from 0-70% blowdown tree-mortality intensity. Note the large amount of litter and wood debris covering the soil. Pictures: D. Magnabosco Marra.

We sampled a 30 cm depth profile and bulk density in 16 subplots covering a wide gradient of tree mortality. Soil clay content was determined with texture analysis using the pipetting method (Gee and Bauder 1986), with data from two profiles sampled in each plot. The 16 subplots were selected from the available 144 subplots installed in the Bd1 site (Marra et al. 2014a) to cover the maximum range of tree mortality intensity found in plateaus (0-70%). In most of the subplots that experienced high tree mortality intensities, 7 yrs after disturbance there was still higher amount of litter and wood debris than that from undisturbed subplots (Figs. 24 and 25). To cover the strong heterogeneity of microsites found our study site (i.e. root, trunk and crown zones of downed trees), we sampled six soil profiles (0-30 cm depth) in each subplot. In addition, we collected samples in 5 cm tall cylinders (98 cm³) for assessing bulk density. Soil analyzes were carried out at the *Laboratório Temático de Solos e Plantas* (LTSP) of the INPA and the *Centro de Energia Nuclear na Agricultura* (CENA) of the *Universidade de São Paulo* (USP).

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Fig. 25. Soil sampling seven years after blowdown (Bd1 site, see Fig. 15). An auger was used to take samples from three depths (0-30 cm) and 5 cm tall cylinders (98 cm³) were used to collect bulk density samples. In our sampling design, we accounted for disturbance heterogeneity within plots, including root, trunk and crown zones of downed trees. Pictures: D. Magnabosco Marra.

2.4. Allometric data

The magnitude and high tree species diversity of the Amazon forests (de Oliveira and Mori 1999; Ribeiro et al. 1999; Zappi et al. 2015) impose extra challenges to the development of forestry and ecological research involving observational and/or empirical data acquisition. The assessment of complex processes and mechanisms needed to address simple questions, commonly demand long-term sampling effort in an interdisciplinary framework (Fig. 9). For the development of the paper 3, I benefited from a valuable allometric data set collected along more than two decades by LMF/INPA team (Carvalho Jr et al. 1995; Santos 1996; Higuchi et al. 1998a; Silva 2007).

The results obtained in paper 1 of this dissertation indicated that forest recovery following blowdowns is a complex and dynamic process involving strong landscape variations in forest structure and floristic composition (Marra et al. 2014a). The regenerating forest can harbor species with different ecology, requirements, wood density and architecture than those found in old-growth communities. The mortality of large late-successional species combined with a fast recruitment of pioneer and mid-successional species can also lead to strong differences in the size distribution of trees. As I have shown in paper 3 of this dissertation (Magnabosco Marra et al. 2016a), reliable biomass estimates for these structurally complex and hyperdiverse forests, requires allometric models capturing strong gradients in the size distribution and floristic composition. As already noticed, the models need to include predictors accounting for allometric differences related to species from

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different successional groups (i.e. pioneer, mid- and late-successional), different wood density and architecture (e.g. crown size and shape, total height and DBH:height relationship). For these reasons, I could not satisfactorily apply the biomass estimation models available for this study region. For instance, local models parameterized with data exclusively collected in old-growth (Higuchi et al. 1998a; Silva 2007) or secondary forests (Nelson et al. 1999), may not represent the species mixture found in blowdown areas, i.e. from early-recruited pioneers to late-successional survivors. By contrast, global and pantropical models combine different data sets and thus include a wide range of species. Nonetheless, these models may fail on capturing allometric variations along succession in an specific forest type (Magnabosco Marra et al. 2016a).

The allometric data set applied in the paper 3 (Magnabosco Marra et al. 2016a) of this dissertation is probably one of the largest allometric data sets collected in a contiguous forest. This data set contains 727 trees ≥ 5 cm DBH and belonging to 135 species. Trees were harvested through the plot-based destructive method, in which all the trees from a plot within a given area were felled (see details in the ‘Material and methods’ section of paper 3). The sampled areas included an old-growth and two secondary *terra firme* forests located at the EEST/INPA. Data acquisition (Fig. 26) followed pre-established sampling protocols developed by the LMF/INPA over the last decades (Carvalho Jr et al. 1995; Santos 1996; Higuchi et al. 1998a; Silva 2007; Lima et al. 2012; Ribeiro et al. 2014). Adopted procedures are also prescribed by the IPCC (Penman et al. 2003; IPCC 2007).

The biomass estimation models parameterized in paper 3 (Magnabosco Marra et al. 2016a), include predictors accounting for architectural variations due to strong changes in floristic composition. Based on morphological and ecological attributes, I classified these 727 tree species into successional groups. I also compiled wood density values from the available literature (see details on the ‘Material and methods’ section of the paper 3). For the biomass-carbon transformations presented in the ‘General Discussion’ section of this dissertation and ‘Discussion’ section of the paper 4, I assumed carbon to be 48.5% of the dry biomass. This value, similar to that reported for other Amazon forests (Brown et al. 1995; Lima et al. 2012), is the mean carbon content of randomly selected trees from the allometric data set included in paper 3 (Silva 2007).

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Fig. 26. Acquisition of tree allometric data for the parameterization of aboveground biomass estimation models. The diameter at breast height (DBH) of target trees was measured before (a) felling operations. Total tree height and volume measurements were done after felling. Representative samples of the trunk, branches, leaves and flowers/fruits (when available) were taken from randomly selected trees for determining water and carbon content. When taking samples from trunk and branches, the mass of sawdust (b) was collected and weighted together with its respective stem section. Different tree compartments, i.e. trunk, coarse and fine branches, leaves and flowers/fruits, were weighted separately (c-h). Pictures: LMF/INPA.

2.5. Data analysis

A detailed description of the employed statistical methods is given in each of the studies comprising this dissertation. I developed all statistical analysis using the R platform (R Core Team 2014). R codes were written by myself, with occasional support from co-authors. When specific packages were used, these were specified in the correspondent papers. I parameterized biomass estimation models using the WinBUGS 1.4.3 software (Lunn et al. 2000). SMA and other remote sensing analyses were developed using the Environment for Visualizing Images software (ITT 2012). Soil samples from the paper 2 were analyzed by L.T. dos Santos, at the LTSP/INPA and CENA/USP. The deforestation data employed in the Fig. 7 was obtained from the *Instituto Nacional de Pesquisas Espaciais* (INPE) (<http://www.obt.inpe.br/prodes>). I produced the Fig. 7 in the Quantum GIS environment (QGIS 2016).

3. ORIGINAL CONTRIBUTIONS

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3.1. Paper 1

Marra DM, Chambers JQ, Higuchi N, Trumbore SE, Ribeiro GHM, Santos J dos, Negrón-Juárez RI, Reu B, Wirth C (2014a) Large-scale wind disturbances promote tree diversity in a Central Amazon forest. *PLoS ONE* 9: e103711. doi: 10.1371/journal.pone.0103711



Large-Scale Wind Disturbances Promote Tree Diversity in a Central Amazon Forest

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Abstract

Canopy gaps created by wind-throw events, or blowdowns, create a complex mosaic of forest patches varying in disturbance intensity and recovery in the Central Amazon. Using field and remote sensing data, we investigated the short-term (four-year) effects of large (>2000 m²) blowdown gaps created during a single storm event in January 2005 near Manaus, Brazil, to study (i) how forest structure and composition vary with disturbance gradients and (ii) whether tree diversity is promoted by niche differentiation related to wind-throw events at the landscape scale. In the forest area affected by the blowdown, tree mortality ranged from 0 to 70%, and was highest on plateaus and slopes. Less impacted areas in the region affected by the blowdown had overlapping characteristics with a nearby unaffected forest in tree density (583±46 trees ha⁻¹) (mean±99% Confidence Interval) and basal area (26.7±2.4 m² ha⁻¹). Highly impacted areas had tree density and basal area as low as 120 trees ha⁻¹ and 14.9 m² ha⁻¹, respectively. In general, these structural measures correlated negatively with an index of tree mortality intensity derived from satellite imagery. Four years after the blowdown event, differences in size-distribution, fraction of resprouters, floristic composition and species diversity still correlated with disturbance measures such as tree mortality and gap size. Our results suggest that the gradients of wind disturbance intensity encompassed in large blowdown gaps (>2000 m²) promote tree diversity. Specialists for particular disturbance intensities existed along the entire gradient. The existence of species or genera taking an intermediate position between undisturbed and gap specialists led to a peak of rarefied richness and diversity at intermediate disturbance levels. A diverse set of species differing widely in requirements and recruitment strategies forms the initial post-disturbance cohort, thus lending a high resilience towards wind disturbances at the community level.

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Introduction

Natural disturbances varying in size are suggested as major driver of tree species substitution across space and time, thus influencing vegetation structure, composition and diversity in forest ecosystems [1–4]. Disturbance dynamics in neotropical forests are considered to be dominated by small canopy gaps (<2000 m²) from small treefall events resulting from small-scale abiotic disturbances [5–7] and biotic interactions [8]. In contrast, widespread tree mortality caused by large-scale exogenous disturbances such as forest blowdowns are often regarded as rare events.

However, remote sensing studies confirm a broad range in the size and intensity of wind disturbances representing a continuum without simple distinctions between frequent and episodic events

[9–11]. In addition, widespread tree mortality associated with blowdowns is more prevalent in the Central and Western Amazon than the Eastern Amazon [12–14]. This has revived a classical question [1,5,15,16] on the ecological importance of large canopy gaps (2000 m²) and how these influence forest dynamics and tree diversity patterns at the landscape scale [11,14,17–20].

In Central Amazon forests, there is in fact a large gradient of gap sizes created by blowdowns, which leads to a spatially complex mosaic of successional pathways [10,20,21] and gap size distribution varies locally, for example with topography. Studies outside the Amazon report that gap size distributions resulting from wind disturbance vary predictably with elevation [22–24], with a greater fraction of large contiguous blowdowns on exposed ridges and plateaus. Blowdowns can raze thousands of trees locally, and with

this create a few large gaps (2000 m^2) as well as many smaller tree-fall gaps ($<2000\text{ m}^2$) [9,10,25].

Large blowdowns and small tree fall gaps may differ substantially in environmental conditions and thus may represent very different starting conditions for tree regeneration. In single-treefall gaps, soil and organic layer disturbance due to uprooting and snapping trees, as well as changes in nutrients and water availability can influence both mortality and recruitment rates as well as other factors vital for the maintenance of tree populations and communities [6,15,26–28]. Large blowdowns can include a wide range of variability in disturbance severity [22,29], which may affect the structure and composition in the recovering forest [30–33].

As a first order effect, gap formation by adult tree mortality is considered a key process as it increases the local availability of resources, most notably of light [5,34]. With the resulting increase in high-light microsites [26] forest patches gain the potential to promote light-demanding (pioneers) tree species specialized in colonizing and occupying gaps by efficient dispersal and rapid growth [2,34–36]. Nonetheless, the same traits that convey high growth potential for such light-demanding or pioneer species (e.g. high enzyme activity, low self-shading, and low wood density and construction costs) weaken their competitive strength under undisturbed conditions. Such traits may prevent them from enduring low light conditions, casting shade and outcompeting shade-tolerant and slower-growing (late-successional) trees in the longer term, resulting in relatively short life spans [37–41]. Light-demanding species thus depend on frequent gap formation to escape local extinction [2,5,6,34]. However, this binary mosaic view – pioneer versus late-successional species in gaps versus old growth forest – may be too simplistic for understanding the influence of a complex gradient ranging from single tree fall gaps to large blowdowns on landscape-level dynamics of highly-diverse tropical rain forests. Given the complexity of the disturbance mosaic, tropical tree species may not fall into two distinct successional groups but rather form a continuum from pioneer to late-successional strategies [37,42–44]. For example, small gaps ($<2000\text{ m}^2$) opened up by mortality events of one or a few trees maybe too dark for light-demanding species and colonization may depend on alternative mechanisms, such as growth-release of the understory sapling bank (advanced regeneration), resprouting of damaged trees, and lateral expansion of surviving trees. All three mechanisms may also be relevant in larger gaps ($>2000\text{ m}^2$) especially given distance-related limitation of seed dispersion. [31,45–48], but here high-light conditions also strongly promote the emergence of pioneer species [33,49]. However, the threshold disturbance intensity below which colonization by light-demanding species fails is not known. Moreover, it is not known whether there are specialists for intermediate levels of wind disturbance.

By combining a landscape-level approach with a detailed plot-scale analysis of high taxonomic resolution, we analyzed recruitment patterns along a large gradient of disturbance intensity and its potential relevance for maintaining tree species diversity in tropical forests. We hypothesize that the vast species pool of Amazonian forests contains species with strategies intermediate between the extremes of light-demanding and shade-tolerant species, thus enabling the forest vegetation to fully exploit the entire gradient of gap sizes and resource availability. We further hypothesize that a co-occurrence of light-demanding, shade-tolerant and intermediate species leads to a peak in diversity at intermediate disturbance intensities and gap sizes in early regeneration. To address these hypotheses we answered the following questions: 1. *Are there predictable patterns of disturbance intensity distributions for large blowdowns, and do these patterns*

differ between topography classes (valleys, slopes, and plateaus)? 2. Do severe blowdowns exert/promote selective mortality effects at individual and species dimensions? 3. How do pre-blowdown conditions, early vegetation responses and the relative importance of the regeneration mode (establishment from seed, resprouting and growth of survivors) interact with disturbance intensity? 4. What are the implications of these effects on community composition and species coexistence at the landscape scale?

Materials and Methods

Study sites

We conducted the research at the Estação Experimental de Silvicultura Tropical (EEST) ($2^{\circ}61'S$, $60^{\circ}20'W$) of the Instituto Nacional de Pesquisas da Amazônia (INPA) and adjacent-contiguous area (ZF2), which is administered by the Superintendência da Zona Franca de Manaus (SUFRAMA) ($2^{\circ}56'S$, $60^{\circ}26'W$), Amazonas, Brazil (Figure 1a). In January of 2005 storms propagating from southwest to northeast of Brazil caused large forest blowdowns across the central Amazon, including ~ 2500 ha of forest in the Manaus region [9]. At the ZF2, forest not known to have been previously disturbed near the Rio Cuieiras (a tributary to the Rio Negro) was heavily disturbed, as identified by field surveys and Landsat images (Figure 1).

The entire area is covered by *terra firme* forest. Prior to the 2005 disturbance there was no evidence of human intervention for at least the previous 40 years. In our Landsat chronosequence there was no signal of large natural disturbances affecting the area since 1979. Mean monthly temperature in this region is $26^{\circ}C$ with little seasonal variation [50,51] and annual rainfall is about 2600 mm, with a distinct dry season between July and September [52,53]. The local topography is undulating with a maximum altitudinal difference of about 140 m (40–180 m a.s.l.). Upland plateaus with high clay content (Oxisols) are cut by slopes and valleys dominated by soils with high sand content (Spodosols) and subject to seasonal flooding. The drainage network flows to tributaries of the Rio Negro or directly to the Rio Cuieiras. The *terra-firme* forest is characterized by a closed canopy with high tree species diversity [54–57] and a dense understory with abundant acaulescent palm species in plateaus and canopy palm species in valleys [57,58]. In this region, forest compositional and structural variations are correlated with water stress, soil and topography [54,59–61].

Forest inventory

We sampled three different patches directly affected by the 2005 blowdown (hereafter referred to as disturbed forest). To assess the entire disturbance gradient we installed three pairs of transects, measuring 200, 600 and 1000 m length by 10 m width respectively, for a total of six transects (Figure 1b – blue lines). We established 144 sub-plots of 10×25 m (total of 3.6 ha) within the 6 transects. At each sub-plot, we determined several measures of forest structure for trees with diameter at breast height (DBH) ≥ 10 cm. Diameters of live uprooted and damaged-snapped trees were usually measured above the DBH (1.3 m height) to avoid lesions and mechanical obstructions, such as trunks, branches, soil, etc. For species with buttressed and aerial roots, we measure the diameter just above these obstructions.

Considering previous studies [26,46,62] and field observations, we identified resprouting stimulated by mechanical injuries in individuals following uprooting and snapping (partial or total rupture of the crown). For botanical identification we collected samples from at least one individual of each species and for subsequent re-measurement we tagged all trees. We carried out

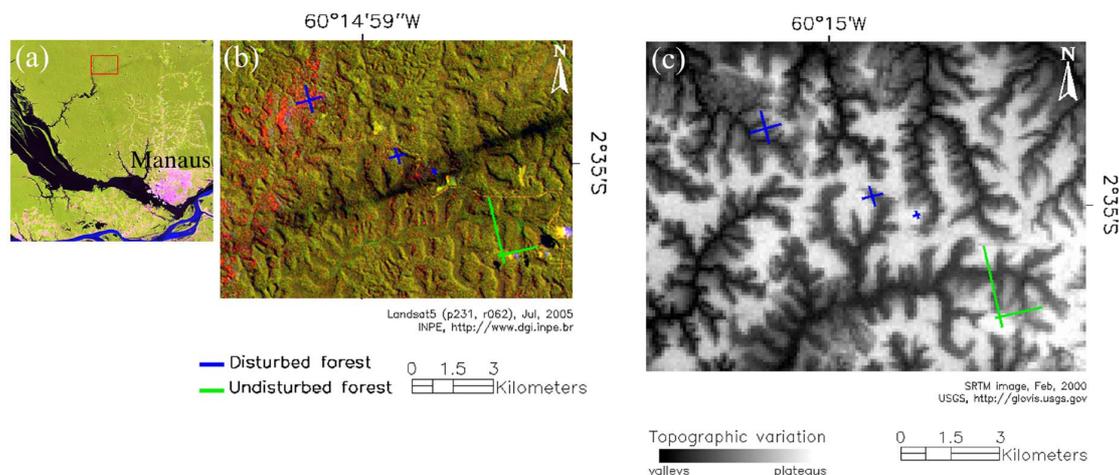


Figure 1. Study areas at the confluence of the Rio Solimões and Rio Negro, Amazonas, Brazil. Legend: (a) Landsat RGB composition of the studied areas (red inset); (b) sampled areas [short-wave infrared reflectance (red channel) indicate the 2005 blowdown tree mortality, measured by quantifying the differences on the no-photosynthetic vegetation (Δ NPV) fraction - SMA analysis]; (c) SRTM elevation model and topographic variation.

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identification to the species level [63–65] when possible, by comparing the collected material with specimens at the INPA and IFAM (Instituto Federal de Educação, Ciência e Tecnologia do Amazonas) herbariums, and also with the EEST botanical collection. Reproductive material (flowers and/or fruits) was collected when available, and added to the IFAM herbarium and to the EEST botanical collection. Our research did not involve endangered or protected species and no special permits were required to access the ZF2. We carried the forest inventory between June and September of 2009. Botanical samples were collected in two campaigns, in 2009 and 2011.

We used measurements from an undisturbed contiguous area (hereafter referred to as undisturbed forest) to compare with our data for the disturbed forest (Figure 1b – green lines). In this area, two transect plots measuring $20 \times 2,500$ m (10 ha) were installed in 1996 [66] and forest structure and dynamics are monitored in 250 sub-plots (20×20 m) using measures of growth, recruitment and mortality made every two years since 2000 [52,67]. We used data from 196 (total 7.8 ha) sub-plots in an area not affected by clouds in both 2004 and 2005 Landsat images, and estimated structural parameters at these sites in 2008. We used census data from these sites for the years 2004–2006 to obtain background forest mortality rates for an area not directly affected by the 2005 blowdown (as confirmed using our Landsat Δ NPV maps) [10]. Although much of the Amazon experienced drought in 2005 with potential effects on mortality [68,69], the region we studied was not unusually dry during this period [9,53].

The transects established in disturbed and undisturbed forests were perpendicularly oriented in north-south and east-west directions (Figure 1b). These transects cross several toposequences in order to represent the floristic and structural variation between plateaus, slopes and valleys (Figure 1c). For classifying sub-plots into topographic classes we used field observations, apparent soil texture, slope and altitude [56,57,66]. Slope was measured with a clinometer and sub-plot altitude data was assessed by using a Global Positioning System (GPS) receiver (*Trimble Nomad 900*) and a digital elevation model (Shuttle Radar Topographic Mission -SRTM) (<http://glovis.usgs.gov>). Higher altitude areas (>80 m a.s.l.) with lower slope (~ 0 – 10°) and higher clay content soils were

classified as plateaus. Areas with slope $>10^\circ$, mixed sand/clay texture soils, and located in interfluvial areas were classified as slopes. Areas with low elevation and relief with sandy soil and direct contact with perennial or intermittent water streams were classified as valleys (Figure 1). In the Manaus region, valleys can be also characterized by the high abundance of some palm species (e.g. *Mauritiella aculeata* (Kunth) Burret, *Oenocarpus batata* Mart. and *Manicaria saccifera* Gaertner) and for being partially inundated during the rainy season. In the disturbed forest we classified 44 (1.1 ha), 73 (1.8 ha) and 27 (0.7 ha) sub-plots in plateaus, slopes and valleys, while in the undisturbed forest plateaus, slopes and valleys represented 49 (2.0 ha), 96 (3.8 ha) and 51 (2.0 ha) sub-plots, respectively.

In both disturbed and undisturbed forests we counted dead trees and measured their DBH. In the disturbed forest, we classified mode of tree death related to the blowdown as snapped, uprooted or standing dead according to previous studies [9,25,62]. For both disturbed and undisturbed forests, we estimated tree density (trees ha^{-1}) and basal area ($\text{m}^2 \text{ha}^{-1}$). For the disturbed forest, we additionally estimated mean DBH (cm) and wood density (g cm^3) for each sub-plot. We compiled species wood density from available literature [70–73] to check for possible correlations between disturbance intensity measures and wood density variation. For species for which data were not available or the identification was only possible at the genus level, we used genus-level obtained by calculating the mean wood density of local congeneric species. For six trees (snapped or without leaves), we used family-level obtained by calculating the mean wood density of the recorded species from the respective family.

Satellite data and disturbance parameters

We used Landsat-5 thematic mapper images (Path 231, Row 062), obtained from Brazil's National Institute for Space Research (INPE, <http://www.dgi.inpe.br/CDSR/>) and the United States Geological Survey (USGS, <http://glovis.usgs.gov>) to assess disturbance intensity over the disturbed area, directly affected by the 2005 blowdowns. We first georeferenced (400 control points per image) the images using the NASA Geocover data set as a basemap (<https://zulu.ssc.nasa.gov/mrsid/>) and several reference

points across the EEST route were collected using a GPS (*Trimble Nomad 900*); we applied a mask to remove clouds, cloud shadows, land use, and water bodies; and removed smoke and haze contamination with the Carlotto technique [74]. Further, we carried out a spectral mixture analysis (SMA) [75] to determine the fractions of green vegetation (GV), nonphotosynthetic vegetation (NPV) and shade. We normalized the pixels without shade as $GV/(GV + NPV)$ and $NPV/(GV + NPV)$, resulting in shade-normalized GV and NPV fractions [76]. The ΔNPV reflects changes in nonphotosynthetic vegetation (NPV, wood, dead vegetation and surface litter) before and after the storm and was calculated as $NPV_{2005} - NPV_{2004}$. We carried out SMA analysis with the Environment for Visualizing Images software (ENVI, ITT Industries, Inc, Boulder CO, USA).

We assessed disturbance intensity in the disturbed forest by estimating three disturbance parameters on a per-pixel basis (30×30 m): sub-plot mortality, mortality in the area surrounding the sub-plot (hereafter referred to as neighboring mortality) and gap size; these three disturbance parameters derived from tree mortality measures (in percentage) obtained from a mortality estimation model which has the ΔNPV as predictor [$Y = 103.22 * \Delta NPV - 3.32$] ($r^2 = 0.8$ and $P < 0.001$) [9]. We used the four corner coordinates (northeast, northwest, southeast and southwest) to rasterize polygons representing our sub-plots on the ΔNPV image. The sub-plot's ΔNPV was obtained by calculating the area weighted mean ΔNPV value of those pixels included in its respective rasterized polygon. To increase the accuracy of this estimation, we resampled the ΔNPV image from its native resolution of 30×30 m to a 3×3 m grid size, which allowed improved estimation of the relative area within each pixel contributing to the total sub-plot area.

We applied the sub-plot's weighted mean ΔNPV in our mortality estimation model [9] to assess tree mortality at sub-plot level in the two forests. For the disturbed forest we calculated the neighboring mortality with the same equation by applying the mean ΔNPV value of the eight pixels directly adjacent to that pixel which included the geographic coordinates of the sub-plot's central point. Additionally, we estimated gap size as the area of virtual polygons formed by groups of contiguous pixels with $\Delta NPV \geq 0.16$. In these forests a $\Delta NPV \geq 0.16$ corresponds to a mortality rate of $\sim 13\%$ (~ 6 trees/pixel), which is conservatively above the minimum rate observed from smaller treefall gaps in local old growth forests ($\sim 2\%$) [67,77], and above the single-pixel mortality gaps obtained from field-measured mortality ($\sim 5\%$) [10,25]. In our mortality model [$Y = 103.22 * \Delta NPV - 3.32$], $\Delta NPV < 0.032$ produced negative mortality estimates, which occurred exclusively in the undisturbed forest and valleys of the disturbed forest. Because the model was adjusted only for disturbed areas, negative ΔNPV values cannot be interpreted as real gain in PV (or forest regrowth). In order to avoid negative mortality estimates, we applied a threshold ($\Delta NPV < 0.032$) below which we assumed mortality was zero for sub-plots. Neighboring mortality and gap size were only estimated for the disturbed forest. We computed sub-plot and neighboring mortality by using tools from the *raster* [78] and *maptools* [79] packages implemented in the R (*version 3.0.1*) software platform [80]. We computed gap size with the SAGA software (*version 2.0.8* <http://www.saga-gis.org>).

Statistical analysis

Disturbance patterns. To check for recognizable relationships between disturbance patterns and topography, we compared structural (tree density and basal area) and disturbance intensity (sub-plot mortality) of the different forests. For the disturbed forest, we tested for the effects of disturbance intensity measures (sub-plot

mortality, neighboring mortality and gap size) on subsequent structural and floristic variation in the different topographic classes of the disturbed forest.

To assess structural differences among topographic classes within the two forests, we classified sub-plots from the disturbed forest in two levels of disturbance. Non- and low-disturbance sub-plots ($\Delta NPV < 0.16$; hereafter referred as low disturbance) [10] were compared with sub-plots that experienced disturbance above this threshold ($\Delta NPV > 0.16$; hereafter referred to as high disturbance). We compared ΔNPV and structural measures of the two forests with factorial ANOVA. We used a Post-hoc Tukey test to evaluate significant differences among topographic classes. In disturbed forest, we related mode of death (snapped, uprooted and standing dead) among topographic classes with linear regressions and assessed whether mode of death is still recognizable and related to sub-plot mortality. With one-way ANOVA, we compared the mean DBH of dead trees among modes of death. Additionally, we tested for the effect of the disturbance intensity on subsequent structural variation by relating tree density and basal area to sub-plot mortality with linear regressions. The same analysis was applied to test for possible correlations between mean DBH of recorded dead trees and sub-plot mortality.

Selective mortality patterns. To address our questions related to selective mortality effects at individual and species level, we compared the size distribution of trees from the disturbed with the undisturbed forest. For the disturbed forest, we described the variation of genera's importance at low and high disturbance levels, and related species diversity measures to sub-plot mortality.

Due to the lower disturbance intensity that has been observed in valleys, and also to pre-blowdown distinct structural and floristic characteristics of the vegetation in the valleys, we only considered sub-plots established on plateaus and slopes for these analyses. To assess the influence of disturbance intensity on size distribution of trees and on the importance of genera, we also considered the classification described in section 2.4.1. We assessed the disturbance intensity effects on the size distribution of trees using Chi-squared tests comparing the diameter distribution of live and dead trees within the disturbed and undisturbed forests, and also within the levels of disturbance described above. For the disturbed forest, we additionally related the mean DBH of live trees to sub-plot mortality. We described community demographic patterns at the genus level for low and high disturbance sub-plots by estimating the Importance Value Index (IVI), calculated as the sum of relative density, frequency and dominance (basal area) of congeneric species [81]. To assess the effects of disturbance intensity on diversity patterns, we related with linear and polynomial regressions, species richness, Shannon diversity and species rarefaction to sub-plot mortality. These three measures were calculated for groups of five sub-plots, ranked and grouped by their sub-plot mortality value (23 in total). With this we avoided the tree density effect observed in those sub-plots with high mortality values, and thus few trees (e.g. with three trees); and were able to look for patterns at the community level.

Disturbance gradient effects and vegetation responses. To address our last two questions, on vegetation responses along the disturbance gradient and changes on community composition, we assessed the importance of resprouters and fast growing or pioneer species, and checked for variations in species composition with disturbance intensity measures.

With linear regressions we assessed the effect of sub-plot mortality, neighboring mortality and gap size on the fraction of resprouters; and effect of sub-plot mortality on mean wood density. We tested with one-way ANOVA for wood density and size differences between resprouters and non-resprouters. Further,

we related the fraction of pioneer species basal area to sub-plot mortality and mean wood density; and related the fraction of pioneer species with neighboring mortality and gap size. We consider as pioneers, light-demanding/fast-growing species typical for the region from the genera *Cecropia*, *Conceveiba*, *Inga*, *Laetia*, *Miconia*, *Pourouma*, *Tachigali* and *Vismia*. To reduce the influence of possible pioneer trees that were established before the blowdown, we only accounted for trees in these genera with $DBH \leq 25$ cm.

To test for the effect of disturbance intensity on floristic composition, we used nonmetric multidimensional scaling (NMDS) to reduce the dimensionality of the community species composition [82,83]. Ordinations were computed with two axes from one dissimilarity matrix generated by the abundance of all recorded species. We used Mantel-tests ($P < 0.001$) to test for the significance of the NMDS analysis. Finally, sub-plot mortality, neighboring mortality and gap size were used as predictors in linear regressions to assess the effects of disturbance intensity measures on the floristic composition variation detected by the first NMDS axis. Finally, to look in detail at possible variations on genera composition driven by the disturbance intensity, we fit a cubic smoothing spline function (degrees of freedom = 3) relating the abundance of the 25 most important genera (based on IVI values) to sub-plot mortality. As in our previous analyses (see section 2.4.2) only sub-plots established on plateaus and slopes were used for these last two analyses. All statistical analyses were performed in R (*version 3.0.1*) software platform [80]. We used the *vegan* package [84] for estimating diversity indices, species curves and to process the NMDS analysis. All other tests were custom written.

Results

Disturbance patterns

In the disturbed forest we sampled 1944 live and 363 dead trees. Our structural measures confirm a correlation between ΔNPV and tree mortality, and indicate that vegetation damage was partially controlled by topography.

Tree density and basal area in the sub-plots (250 m^2) of the disturbed forest ranged from 3 to 33 trees and from 0.08 to 2.23 m^2 , respectively. Mean tree density and basal area in the undisturbed forest was higher than in the low and high disturbance sub-plots (Table 1). Mean tree density and basal area in slopes from the high disturbance was lower than in slopes from the low disturbance and undisturbed forest (Table 1).

In the disturbed forest, ΔNPV ranged from -0.213 to 0.696 with an overall mean value of 0.176 ± 0.037 (mean $\pm 99\%$ CI), higher than from the undisturbed forest (0.038 ± 0.016 ; ranging from -0.168 to 0.202). Estimated sub-plot mortality in the disturbed forest ranged from 0 to 69.9% with an overall mean value of $16.2 \pm 3.4\%$, higher than from the undisturbed forest ($3.7 \pm 0.8\%$; ranging from 0 to 30.5). In the undisturbed forest, mortality rate computed from field data (2004–2006) was $1.6 \pm 0.7\% \text{ year}^{-1}$ and correlated positively but weakly with the estimated sub-plot mortality ($r^2 = 0.04$; $P = 0.004$; Pearson's $r = 0.20$). Plateaus, slopes and valleys from high disturbance sub-plots had higher mean ΔNPV and sub-plot mortality in comparison to low disturbance and undisturbed forest (Table 1). Plateaus and slopes from the high disturbance also had higher neighboring mortality and gap size than plateaus and slopes from the low disturbance. The disturbed sub-plots were set in gaps that ranged in size from 0–22.6 ha (6.5 ± 2.3), which correlated positively with mean sub-plot mortality ($r^2 = 0.37$; $P < 0.001$;

Pearson's $r = 0.60$). During the analyzed period we did not find gaps larger than three pixels (2700 m^2) in the undisturbed forest.

In the disturbed forest the density of dead trees ranged from 0 to 360 trees ha^{-1} and the mean (101 ± 22 trees ha^{-1}) varied among topographic classes ($F = 8.74$; $P < 0.001$). The mean density of dead trees in plateaus (104 ± 43 trees ha^{-1}) was similar to that for slopes (120 ± 31 trees ha^{-1}) ($P = 0.536$), but exceeded the mean density observed in valleys (44 ± 31 trees ha^{-1}) ($P < 0.01$, both). The total number of dead trees, both snapped and uprooted, correlated positively with sub-plot mortality in slopes in plateaus. In the disturbed forest plateaus and slopes, the density of live trees and basal area were negatively correlated with sub-plot mortality, while valleys were not affected (Table 2).

Selective mortality patterns

Our data show that the blowdowns promoted subsequent changes in forest structure, genera substitution and species demography. Four years after the blowdown event, differences in size-distribution, genera importance and diversity measures still correlated with levels of disturbance.

In the disturbed forest, the DBH of recorded dead trees ranged from 10 to 120 cm, with mean value (27.5 ± 2.3 cm) higher than from that from live trees of both disturbed (20.6 ± 2.3 cm) and undisturbed forest (21 ± 0.7 cm). DBH of dead trees did not vary among modes of death (ANOVA $F = 2.37$; $P = 0.125$), but for snapped and uprooted trees had a low correlation with sub-plot mortality ($r^2 = 0.02$; $P = 0.029$; Pearson's $r = 0.13$), with a non-variable mean value among modes of death (ANOVA $F = 2.37$; $P = 0.125$).

Even four years after the blowdown event, the DBH distribution comparisons indicated size distribution differences between trees of the disturbed and the undisturbed forests. The DBH distribution of dead trees in both low- and high-disturbance sub-plots (Figure 2a) did not follow that of the undisturbed forest before (2004) and after (2006) the blowdown event (Chi-squared test, $P < 0.001$). While the undisturbed forest had a higher abundance of dead trees within the smaller diameter classes, low and high disturbance forests had higher abundance of large trees exhibiting a log-normal distribution. The DBH distribution under low and high disturbance was also different (Chi-squared test, $P = 0.017$). Within live trees, both disturbed and undisturbed forests had higher abundance of small trees and exhibit the typical negative exponential DBH distribution of tropical forests (Figure 2b). The DBH distribution of live trees under low disturbance was similar to that of the undisturbed forest ($P = 0.490$), while under high disturbance forest it diverged from that observed within trees from the undisturbed and low disturbance forest ($P < 0.001$). The overall mean DBH of live trees was negatively related to sub-plot mortality in plateaus and slopes of the disturbed forest (Figure 2c).

In the disturbed forest, recorded trees were distributed in 51 families, 158 genera and 324 species or morphotypes. A total of 54 species ($\sim 16\%$) just occurred on plateaus, while 55 ($\sim 17\%$) and 20 ($\sim 6\%$) were restricted to slopes and valleys, respectively. Fifty eight species ($\sim 18\%$) occurred in all topographic classes. Fabaceae (66 species), Sapotaceae (26) and Lecythidaceae (23) were the richer families in number of species and together summed $\sim 40\%$ of all recorded trees and $\sim 36\%$ of the total richness. Eighteen families were represented by just one species. 129 species were represented by only a single tree. Heavily damaged sub-plots, especially those in gaps with large amounts of necromass, often had high density of lianas. Field observations showed that gaps in which wood decay was more advanced generally had a dense understory with seedlings dominated by the genera *Casearia* and

Table 1. Summary statistics (mean \pm 99% CI) of structure and disturbance intensity measures for different levels of wind-disturbance in a forest disturbed by a large blowdown, and an undisturbed forest, in Amazonas, Brazil.

TC	NS	TD	BA	Δ NPV	SP	NG	GS
UN	196	593 \pm 28*	27.7 \pm 2.1*	0.038 \pm 0.016*	3.7 \pm 0.8		
	49	632 \pm 46	29.1 \pm 4.4	0.048 \pm 0.036	4.6 \pm 1.9		
	96	590 \pm 34	26.8 \pm 2.9	0.047 \pm 0.022	4.2 \pm 1.3		
	51	560 \pm 44	28.2 \pm 3.7	0.011 \pm 0.030	2.0 \pm 0.9		
LD	75	583 \pm 46*	26.7 \pm 2.4*	0.050 \pm 0.016*	4.4 \pm 0.9	5.4 \pm 1.4*	1.1 \pm 0.9*
	12	643 \pm 5	28.0 \pm 0.2	0.048 \pm 0.002	5.2 \pm 0.1	8.4 \pm 0.2	0.4 \pm 0.04
	39	615 \pm 99	27.1 \pm 5.1	0.054 \pm 0.033	4.8 \pm 1.9	5.9 \pm 2.8	0.6 \pm 1.5
	24	500 \pm 78	25.3 \pm 5.3	0.046 \pm 0.029	3.2 \pm 2.0	3.2 \pm 2.5	1.9 \pm 3.4
HD	69	462 \pm 62*	19.9 \pm 4.9*	0.312 \pm 0.040*	28.9 \pm 4.2*	25.0 \pm 4.2*	12.6 \pm 2.7*
	32	554 \pm 98	25.5 \pm 8.9	0.326 \pm 0.064 [†]	30.4 \pm 6.7 [†]	26.0 \pm 5.3 [†]	9.2 \pm 3.3 [†]
	34	426 \pm 76 [†]	14.5 \pm 4.2 [†]	0.307 \pm 0.054 [†]	28.5 \pm 5.6 [†]	24.7 \pm 6.8 [†]	16.3 \pm 3.9 [†]
	3	600 \pm 158	21.5 \pm 7.0	0.208 \pm 0.040 [†]	18.2 \pm 4.1	16.8 \pm 7.8	6.6 \pm 13.3

Legend: UN- undisturbed forest; LD- low disturbance (up to 13% of mortality); HD- high/severe disturbance (greater than 13% of mortality); TC- topographic classes; NS- number of sampled sub-plots; TD- tree density (trees ha⁻¹); BA- basal area (m² ha⁻¹); SP- sub-plot mortality (%); NG- neighboring mortality (%); GS- gap size (ha).

*Significant differences (ANOVA) among levels of disturbance ($P < 0.001$).

[†]Significant differences (Tukey HSD) between same topographic classes ($P < 0.001$).

doi:10.1371/journal.pone.0110371.t001

Table 2. Linear regressions and Pearson's correlation relating structural variables to mortality intensity in a forest disturbed by a large blowdown, in Amazonas, Brazil.

Structure variables	Topographic classes ^y	N. of trees	Regression parameters [*]			F	r ²	P	Pearson's r
			a	b					
Dead trees	Plateau	114	1.5191	0.0456	6.00	0.125	0.018	0.354	
	Slope	219	2.1073	0.0564	13.5	0.159	<0.001	0.4	
	Valley	30	0.8224	0.059	2.43	0.052	0.131	0.297	
N. of snapped trees	Plateau	51	0.2713	0.0378	9.17	0.18	0.004	0.423	
	Slope	92	1.055	0.0129	2.08	0.028	0.153	0.168	
	Valley	19	0.5055	0.0405	2.38	0.086	0.135	0.294	
N. of uprooted trees	Plateau	44	0.8259	0.0074	0.34	0.008	0.559	0.09	
	Slope	105	0.5709	0.0548	16.45	0.188	<0.001	0.434	
	Valley	7	0.138	0.0248	0.86	0.033	0.362	0.182	
N. of standing dead trees	Plateau	19	0.4218	0.0004	<0.01	-0.023	0.954	0.008	
	Slope	22	0.4813	-0.0113	5.48	0.071	0.022	-0.267	
	Valley	4							
Live trees	Tree density (trees ha ⁻¹)	637	648.69	-3.000	2.46	0.055	0.123	-0.235	
		962	658.28	-8.290	29.36	0.293	<0.001	-0.54	
		345	494.97	3.3030	0.47	0.018	0.5	0.135	
Basal area (m ² ha ⁻¹)	Plateau		31.57	-0.2286	2.23	0.051	0.143	-0.224	
	Slope		29.14	-0.4966	36.2	0.337	<0.001	-0.582	
	Valley		25.25	-0.0742	0.05	0.002	0.819	-0.046	

^{*}Model: $y = a + bx + cI$.

^yDegrees of freedom for the topographic classes: plateaus (44); slopes (73); valleys (27).
doi:10.1371/journal.pone.0103711.t002

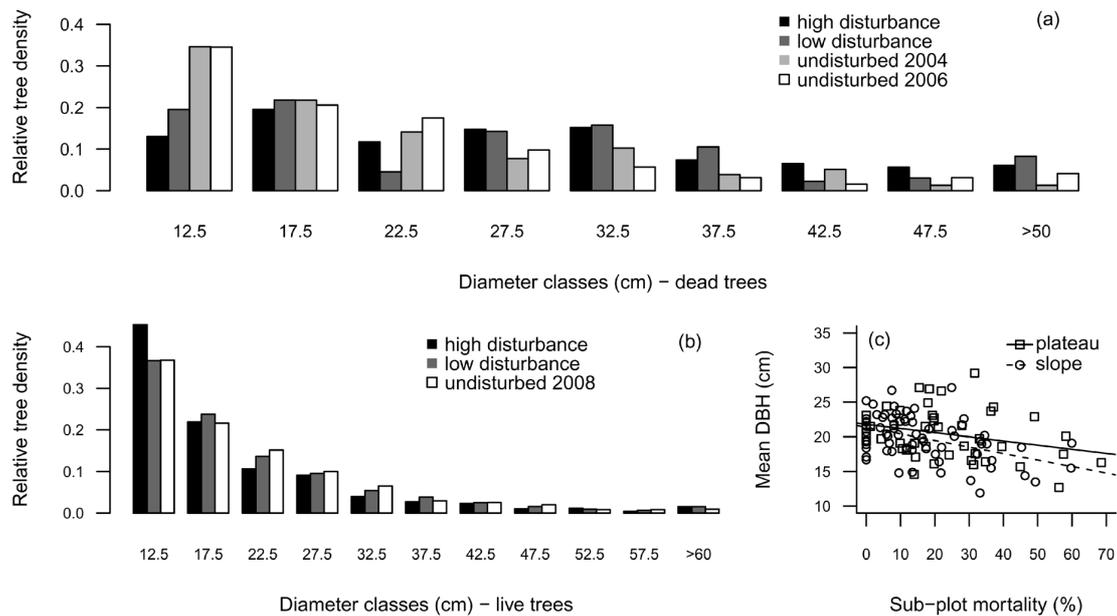


Figure 2. Tree size distribution (DBH \geq 10 cm) in plateaus and slopes of a forest disturbed by a large blowdown and an undisturbed forest, in Amazonas, Brazil. Legend: (a) diameter distribution of dead trees; (b) diameter distribution of live trees; (c) mean DBH of live trees in disturbed plateaus ($r^2=0.05$; $P=0.06$; Pearson's $r = -0.277$) and slopes ($r^2=0.19$; $P<0.001$; Pearson's $r = -0.451$) related to sub-plot mortality. doi:10.1371/journal.pone.0103711.g002

Laetia (Salicaceae), *Cecropia* and *Pourouma* (Urticaceae), *Conceveiba* and *Croton* (Euphorbiaceae), *Inga* and *Tachigali* (Fabaceae), *Miconia* (Melastomataceae), *Tapirira* (Anacardiaceae) and *Vismia* (Hypericaceae). Genera demographic analyses revealed differences between low (total of 258 species) and high disturbance (215). Ten genera among the 20 most important genera from the high and the low disturbance levels were different (Figure 3). The high disturbance level had both typical light-demanding/fast-growing (e.g. *Cecropia*, *Inga* and *Pourouma*) and shade-tolerant/slower-growing (e.g. *Brosimum*, *Pouteria*, *Sloanea* and *Vantanea*) exclusive genera within the 20 most important genera. *Eschweilera*, *Licania*, *Pouteria* and *Protium* had the highest IVI in both disturbance levels, but the contributions of the IVI estimators of these and other common genera varied between disturbance levels.

Species richness per sub-sub-plot varied from 3 to 25 species in the disturbed forest. For groups of plots, species richness was negatively related to sub-plot mortality ($r^2=0.39$; $P<0.001$; Pearson's $r = -0.64$) (Figure 4a). Shannon diversity also correlated negatively with sub-plot mortality ($r^2=0.39$; $P=0.002$; Pearson's $r = -0.61$). Nonetheless, at intermediate disturbance (20–50% of tree mortality), Shannon diversity was slightly lower or even similar to that from the less- and non-disturbed sub-plots (Figure 4b). Species rarefaction curve along the mortality gradient indicated that intermediate-disturbance areas can be more diverse than both heavily and undisturbed areas (Figure 4c).

Disturbance gradient effects and vegetation responses

Of the live trees recorded in the disturbed forest, 206 (~11% of total sampled) had crown or trunk injuries and 191 (~10%) had one of the mechanisms indicative of resprouting. 151 trees (~7%) belonged to light-demanding/fast-growing pioneer genera, and the mortality gradient appeared to amplify forest niches that lead to changes in species composition.

Resprouting trees were recorded in all the topographic classes and within different species. In slopes, the fraction of resprouters related positively to sub-plot mortality as well as to other disturbance intensity measures (Figure 5). In plateaus and slopes, the mean wood density correlated negatively with sub-plot mortality ($r^2=0.03$; $P<0.035$; Pearson's $r = -0.19$), but resprouters and non-resprouters had no significant differences in wood density ($F=0.262$, $P=0.609$), but did have in DBH ($F=4.87$, $P=0.027$).

In general, light-demanding/fast-growing genera (e.g. *Cecropia*, *Conceveiba*, *Inga*, *Casearia*, *Miconia*, *Pourouma*, *Tachigali*, *Tapirira* and *Vismia*) contributed less to total basal area in less disturbed sub-plots, while their basal area was positively related to sub-plot mortality in plateaus ($r^2=0.39$; $P<0.001$; Pearson's $r = 0.63$) and slopes ($r^2=0.27$; $P<0.001$; Pearson's $r = 0.52$) (Figure 6a). In contrast, the fraction of basal area contributed by these fast-growing species was negatively related to sub-plot mean wood density, also exclusively in plateaus ($r^2=0.30$; $P<0.001$; Pearson's $r = -0.56$) and slopes ($r^2=0.31$; $P<0.001$; Pearson's $r = -0.57$) (Figure 6b). The fraction of these typical pioneer species was positively related to neighboring mortality in plateaus ($r^2=0.32$; $P<0.001$; Pearson's $r = 0.58$) and slopes ($r^2=0.46$; $P<0.001$; Pearson's $r = 0.67$) (Figure 6c). Gap size was also positively related to these group of species in plateaus ($r^2=0.14$; $P=0.013$; Pearson's $r = 0.34$) and slopes ($r^2=0.21$; $P<0.001$; Pearson's $r = 0.44$) (Figure 6d).

The NMDS stress value was 0.286, and the first two axes captured 34% of the floristic variation (Figure 7a and Table 3). Floristic similarities within heavily damaged sub-plots increased due to the higher abundance of light-demanding and fast-growing species. Sub-plot mortality related positively to the variations in species composition captured by the first NMDS axis (Figure 7b). The same pattern was observed for neighboring mortality and gap size, which correlated more strongly (Table 3).

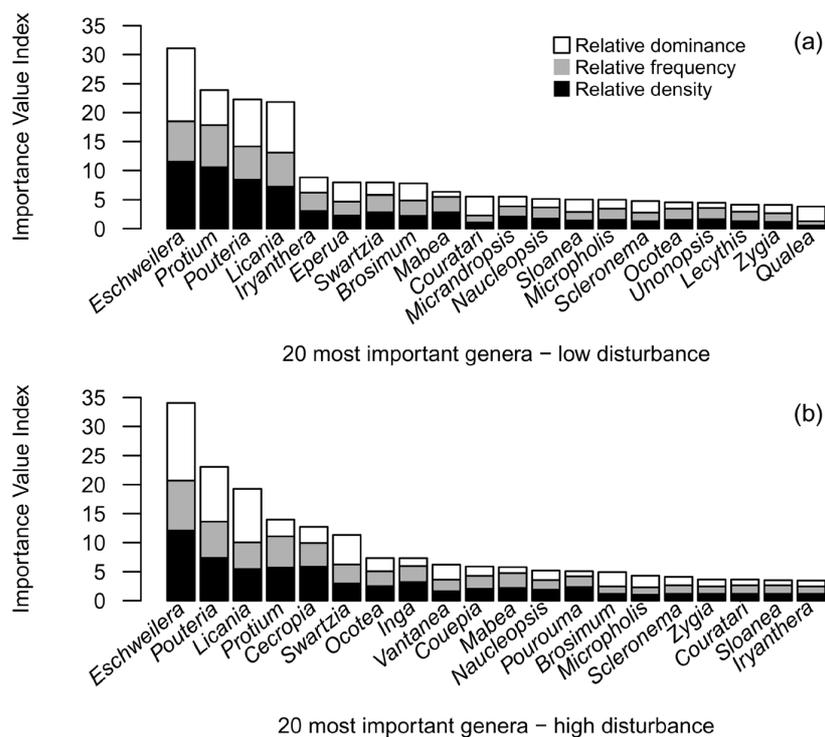


Figure 3. Genera importance ranking over plateaus and slopes of a forest disturbed by a large blowdown, in Amazonas, Brazil. Legend: (a) Importance Value Index (IVI) of the 20 most important genera recorded under low disturbance (up to 13% of tree mortality); (b) IVI of the 20 most important genera recorded under high disturbance (up to 70% of tree mortality). doi:10.1371/journal.pone.0103711.g003

The demographic patterns of the 25 most important genera in the community (identified in Figure 3) and the variations in species composition (Figure 7) corroborate our results related to genera abundance variation in respect to disturbance intensity (Figure 8). The genera abundance curves show that these 25 genera are not equally distributed along the landscape and that part of this variation was regulated by variations in sub-plot mortality. Interestingly, the abundance of these genera varied along the mortality gradient revealing five distinct groups (identified using colors in Figure 8) which had their optimum under specific disturbance intensities. This pattern indicates that there exist specialist guilds for each different level of disturbance/resource. Moreover, areas where the tree mortality driven by the blowdown

ranged between 20–50% are those which provide gap space and light conditions, thus favoring a wider range of species with different requirements.

Discussion

Disturbance patterns

Mortality rate and structural measurements of the undisturbed forest were similar to those reported in other undisturbed forests nearby [52,67,77,85]. Tree mortality levels observed in the disturbed forest were in accordance with patterns described in earlier studies [9,10,25] also in Amazon and even higher than in hurricane-damaged forests [30,45,47,86].

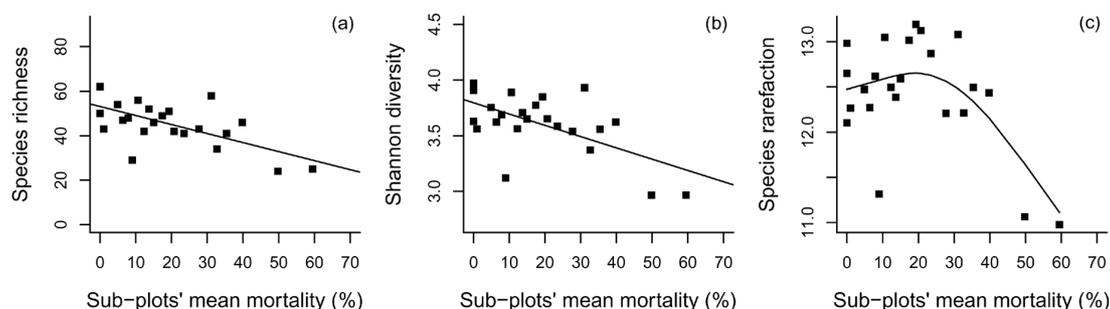


Figure 4. Species richness and diversity measures related to a mortality gradient in plateaus and slopes of a forest disturbed by a large blowdown, in Amazonas, Brazil. Legend: (a) species richness; (b) Shannon diversity; (c) species rarefaction. doi:10.1371/journal.pone.0103711.g004

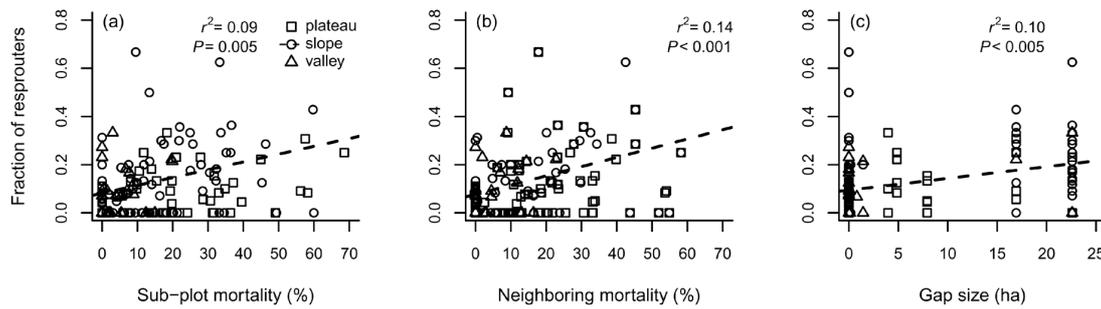


Figure 5. Fraction of resprouting tree species related to disturbance intensity measures from a forest disturbed by a large blowdown, in Amazonas, Brazil. Legend: (a) fraction of resprouters related to sub-plot mortality (slopes Pearson's $r=0.33$); (b) fraction of resprouters related to neighboring mortality (slopes Pearson's $r=0.38$); (c) fraction of resprouters related to gap size (slopes Pearson's $r=0.33$). doi:10.1371/journal.pone.0103711.g005

Wind-related mortality caused by snapping and uprooting was greatest in more exposed areas, including plateaus and the top of slopes (Table 2). As a consequence of lower disturbance intensity, structural patterns were not altered by blowdowns in the valleys (Table 1). This may indicate that strong winds did not reach the valley floors, or that the vegetation in valleys is less affected by wind damage, as has been observed in other tropical and subtropical forests affected by cyclones [23,24,29,48,87]. We also did not observe uprooted canopy palm trees in valleys and just 14 snapped and/or standing dead ones. As there is no evidence that caulescent palm tree species that occur in these valleys are less susceptible to wind damage (see species in item 2.2), we assume that valley floors are indeed better protected from strong winds.

Although in these forests vegetation damage was partially controlled by abiotic aspects such as wind characteristics and topography [22,29,88], resolution of this question requires more information on individual-species traits, such as anatomic-morphological variations among individuals and species, size distribution and populations range, and individual pre-disturbance conditions (pest-attack, biological interactions, age, etc.).

In the disturbed forest, measures of forest structure, including tree density and basal area, were lower four years following the blowdown event (Table 1). The topographic variation of measures of structure was amplified by the landscape driven differences in mortality. Immediate tree mortality effects on tree density and basal area reduction are directly dependent on the disturbance

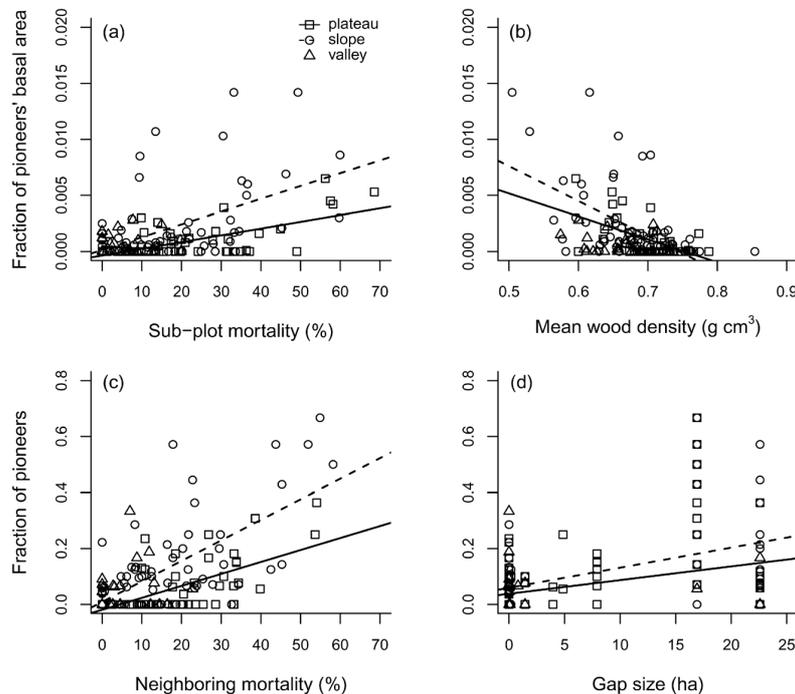


Figure 6. Pioneer (light-demanding and fast-growing) tree species importance related to disturbance intensity measures and wood density in a forest disturbed by a large blowdown, in Amazonas, Brazil. Legend: (a) fraction of pioneers' basal area related to sub-plot mortality; (b) fraction of pioneers' basal area related to sub-plot mean wood density; (c) fraction of pioneers related to neighboring mortality; (d) fraction of pioneers related to gap size. doi:10.1371/journal.pone.0103711.g006

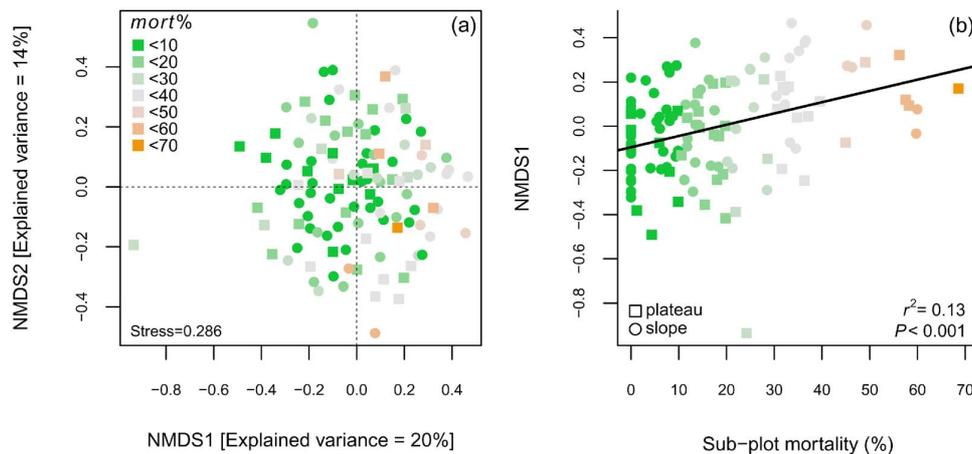


Figure 7. NMDS ordination diagram of 117 sub-plots sampled in plateaus and slopes of a forest disturbed by a large blowdown, in Amazonas, Brazil. Sub-plot mortality caused by the blowdown is highlighted by the color-scale. Legend: (a) NMDS scores computed from a dissimilarity matrix with the abundance of all recorded species; (b) first NMDS axis related to sub-plot mortality. doi:10.1371/journal.pone.0103711.g007

intensity – i.e. the fraction of trees killed by wind (Table 2). In heavily damaged areas with the highest estimated mortality rates, structural measures were lower than the early-successional stages found in other nearby and smaller disturbed forest patches [89] and anthropogenic disturbances in the same forest type [41,90]. At these sites, forest recovery will depend on species responses to the light gradient in gaps, which was supported for our results related to the third and fourth questions. Within the disturbed areas, the correlation of percent mortality with structural characteristics also showed that areas less affected by wind damage were similar to the undisturbed forest sub-plots.

The observed higher mortality within plateaus and slopes of the undisturbed forest was also related in nearby unaffected *terra-firme* forest, where under regular disturbance regimes, standing death can be expected to be more frequent in plateaus, and uprooting and snapping more frequent in slopes and in valleys [91]. Thus, competition can be more important in plateaus and exogenous disturbances dominant in slopes and valleys, which will cause differences in the size-density distribution of trees related to topographic position [92]. Despite such findings, our study indicates that for the Central Amazon forests, most notably in plateaus and slopes, tree mortality is also regulated by wind disturbance regimes such as blowdowns of varying size.

Although in the undisturbed forest we only observed small gaps, in the disturbed forest large gaps (2000 m²) were common and changed forest structure, particularly in plateaus and slopes. Such results suggest that severe disturbances are required to form large gaps. The higher values of tree density and basal area observed in plateaus may indicate a variation in forest vulnerability due differences in species composition, or possibly higher resilience of plateaus.

Selective mortality patterns

We expected to see large emergent to be more prone to wind damage than smaller ones. While we did observe differences in DBH distribution of dead trees between undisturbed and disturbed forests that suggests lower proportional mortality for smaller trees (despite potential biases introduced because smaller dead trees decompose faster), we also observed no correlation between the DBH of dead trees and sub-plot mortality, indicating

that size selective mortality did not depend on disturbance intensity.

Observed reductions in mean DBH and wood density in the live trees in highly damaged areas of the disturbed forest (Figure 2c) likely reflect fast recruitment of light-demanding and fast-growing species with shorter life span and generally lower wood density values [15,34,71]. Chambers *et al.* (2009b) compared non-disturbed and smaller blowdown gaps with ~10 years-succession and reported similar patterns, except for tree density, which was lower in our four-years disturbed plots. The substantial increase in the fraction of small trees with increasing sub-plot mortality also evidentiate the recruitment of shade-tolerant or understorey species that usually do not reach the canopy, and thus demonstrates a selective mortality feedback on floristic composition.

Tree diversity in Central Amazon forests is high, and our data agree with those of other studies conducted in the same [52,67,93] and in adjacent areas [55,57,94,95]. We observed clear effects of the blowdown mortality on community demographic patterns from low to high disturbance (Figure 3). Part of the observed changes can be attributed to the fast recruitment of species with different syndromes and growth (lateral expansion) in the available gap space, such as *Cecropia sciadophylla* Mart., *Pourouma tomentosa* Mart. ex Miq., *Inga cf. paraensis*, *Iryanthera juruensis* Warb., *Protium hebetatum* D. C. Daly, *Mabea speciosa* Müll.Arg. and *Zygia racemosa* (Ducke) Barneby & J. W. Grimes. These species improved their importance within the high disturbance sub-plots by increasing their relative density and frequency. Such patterns may indicate success of establishment and expansion of these populations [81], which in the longer-term may increase species richness and forest diversity [89]. Common tree canopy genera in adjacent areas (e.g. *Couratari*, *Eschweilera*, *Pouteria*, *Licania*, *Micropholis*, *Ocotea*, *Sloanea*, *Swartzia* and *Vantanea*) [67,90,93], also presented high importance within the sub-plots with high disturbance (i.e. high mortality). Survivorship of shade-tolerant and slower-growing species from these genera may be attributable to the relatively high wood density (~0.79 g/cm³) [71], small crown footprint, and presence of buttress and supporting roots [54,56]. Blowdowns are a major disturbance in these forests, thus the greater likelihood of survival and resprouting ability may be reasons for these genera to be of such high importance in the *terra firme* forests of this region [54–56,96].

Table 3. NMDS and linear regression relating measures of disturbance intensity to the floristic composition of a forest disturbed by a large blowdown, in Amazonas, Brazil.

NMDS Stress	Mantel-test*		NMDS [Axis1] related to disturbance measures ^y			Pearson's <i>r</i>
	Axis 1	Axis 2	Predictors	F	<i>r</i> ²	
0.286	0.442	0.367	SP	18.15	0.129	0.370
			NG	21.81	0.159	0.400
			GS	25.56	0.175	0.427

Legend: SP-sub-plot mortality; NG-neighboring mortality; GS-gap size.

*Related to species distance matrix and NMDS axis scores.

^yLinear regressions with NMDS (Axis1) as dependent variable and disturbance intensity measures as predictors.
doi:10.1371/journal.pone.0103711.t003

Blowdown mortality, which directly affected species richness by reducing tree density at a local scale, resulted in the negative correlations between species richness and Shannon diversity with sub-plot mortality (Figure 4a and b). Nevertheless, the rarefaction curve indicate that a slightly higher number of species would be observed for any smaller subsample of individuals taken from low to intermediate disturbance areas, under the assumption of random mixing of individuals (Figure 4c). Interestingly, despite differences in species richness driven by disturbance intensity, the higher number of rare species at low and intermediate disturbance levels indicates that a short-term feedback of blowdown mortality is to promote species richness at the landscape scale, with apparent lower impacts on valleys.

Disturbance gradient effects and vegetation responses

So far we have focused on the importance of wind disturbance for providing niche space for light-demanding species requiring large canopy gaps for regeneration as a mechanism for promoting species coexistence and thus diversity at the landscape scale. Concomitantly, our data and tests related to the third and fourth questions support that the studied gaps also provide adequate niches for species with different requirements.

Disturbance and selective mortality patterns promoted immediate effects on forest structure and species composition, as evidenced by changes in tree size distribution (Figure 2), species importance between levels of disturbance (Figure 3) and species diversity along the mortality gradient (Figure 4). Nonetheless, blowdown gaps seem to produce long-term effects at the community level. The observed landscape mortality gradient also changed diversity patterns by promoting compositional changes with respect to the fraction of resprouters (Figure 5) and with light-demanding/fast-growing species (Figure 6).

Thus, a second potentially important niche axis is the ability to survive wind disturbance, which may provide a selective advantage to species that are less susceptible to wind damage either because they possess specific morphological and anatomical adaptations lending stability or because they are of small stature and are typically not exposed to wind. Both characteristics may represent a competitive disadvantage in the absence of wind disturbances. In the first case, stability conferred by e.g. high wood density is associated with high construction costs and reduced growth rates – a typical growth-defense tradeoff reported in the literature [8,71,97]. In the second case, staying short or retaining a low height/diameter ratio is certainly a disadvantage in the race for light [62].

The positive correlations between disturbance intensity measures and density of resprouters in the disturbed forest (Figure 5) confirms the importance of this regeneration mechanism in gaps created by wind disturbances [31,47,48,86,98,99]. The similarities in mean wood density between resprouters and non-resprouters (usually undamaged trees) indicate that resprouting is a regeneration pathway adopted by species with different traits and light requirements, predominantly by smaller trees ($DBH \leq 20$ cm). A similar pattern was found in a Caribbean hurricane-damaged forest [45] and indicates that, although canopy trees from higher wood density species may have higher wind resistance, resprouting is not an exclusive regeneration pathway for shade-tolerant, slower-growing or climax species. As for sub-tropical hurricane-damaged forests [46], we hypothesize that in *terra firme* forests of Central Amazon, both early secondary and understory species may benefit from wind disturbances. Finally, the decrease in the mean aggregated wood density in disturbed sub-plots is a direct consequence of the higher fraction of pioneer species which are characterized by low wood densities (Figure 6). Wood density

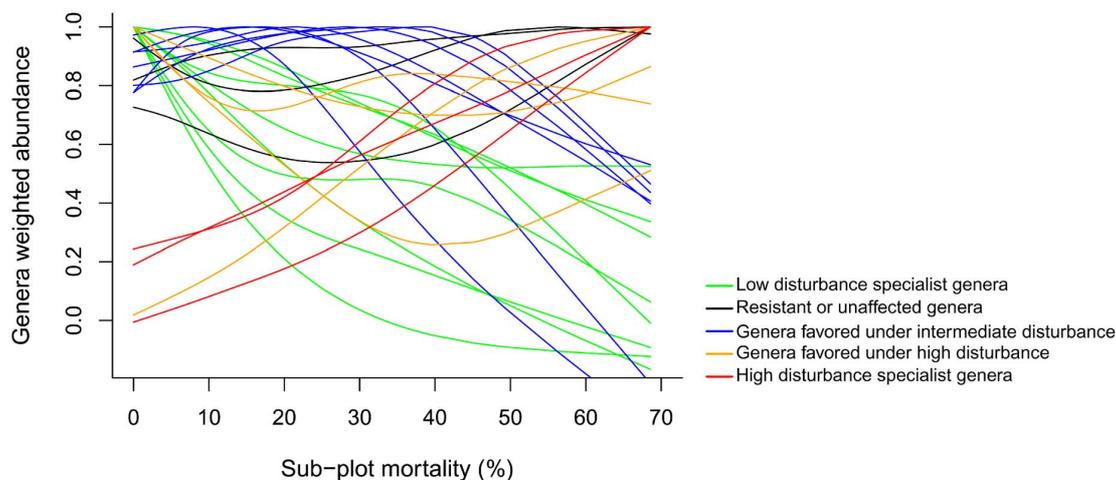


Figure 8. Genera abundance related to a mortality gradient in plateaus and slopes of a forest disturbed by a large blowdown, in Amazonas, Brazil. Legend: low disturbance specialist genera- *Brosimum*, *Eperua*, *Iryanthera*, *Micrandropsis*, *Micropholis*, *Pouteria*, *Protium* and *Unonopsis*; resistant or unaffected genera- *Couratari*, *Ocotea* and *Sloanea*; genera favored under intermediate disturbance- *Eschweilera*, *Lecythis*, *Licania*, *Naucleopsis*, *Swartzia*, *Qualea* and *Zygia*; genera favored under high disturbance- *Couepia*, *Mabea*, *Scleronema* and *Vantanea*; high disturbance specialist genera- *Cecropia*, *Inga* and *Pourouma*. doi:10.1371/journal.pone.0103711.g008

variation among sub-plots was partially explained by sub-plot mortality, which is significant when low wood density pioneers are observed (Figure 6a and b). This greater importance of pioneers in heavily damaged areas corroborates demographic patterns found by assessing species IVI (Figure 3b) and patterns in species composition, which was indicated by the NMDS-test and regressions (Figure 7).

Our data show that species turnover in the 20 most important genera (as quantified by IVI in Figure 3) is due to the increasing importance of both non-pioneer and pioneer species. Indirect evidence for this mechanism is provided by fact that the floristic dissimilarity between undisturbed and disturbed sub-plots seems to be driven by the admixture of light-demanding species (Figure 7a and Figure 8). There was a significant correlation between sub-plot mortality and the position of sub-plots along the first NMDS axis, the latter explaining significant part of the total variation in species composition (Figure 7b). This relationship was higher when considering neighboring-mortality and gap size values (Table 3). However, even in the plots with highest mortality rates (40–70%) there was no complete takeover by classical pioneer local genera (e.g. *Cecropia*, *Conceveiba*, *Croton*, *Goupia*, *Inga*, *Laetia*, *Miconia*, *Pourouma*, *Tachigali* and *Vismia*) or shade-tolerant common genera in undisturbed forests (e.g. *Couratari*, *Eschweilera*, *Licania*, *Pouteria*, *Scleronema*, *Sloanea* and *Swartzia*). These last, maintained up a large fraction of the IVI as indicated by their high proportion in the largest diameter class. Some of the fast growth species we have recorded, especially from the genus *Cecropia*, *Inga*, *Pourouma* and *Tachigali* were also reported as important species during early succession stages of secondary *terra-firme* forests around Manaus [40,90,100] and in the upper Rio Negro [41]. In anthropic secondary forests, under non-intensive use and without fire regimes, areas dominated by species from the genus *Cecropia* and *Pourouma* present relatively higher species richness, which hence more rapid plant succession [40,100].

The variations of genera importance in respect to mortality intensity support classical studies [2,5,6,34] that attempt to classify species into a simplified conception of pioneer species in gaps

versus intermediate or late-succession species under undisturbed forest patches. These classical opposing strategies were observed within the 25 most important genera of the disturbed forest (Figure 8), as characterized as high (light-demanding and faster-growing - red lines) and low disturbance specialists (shade-tolerant and slower-growing - green lines). Additionally, our data highlighted alternative successional trajectories related to survival (resistant or unaffected - black lines), resprouting and fast-recruitment (favored under intermediate and high disturbance - blue and orange, respectively).

These alternative successional trajectories have not been observed as important regeneration mechanisms in smaller treefall events. In larger gaps (>2000 m²), the canopy emergence of specialized guilds with an optimum at specific levels of disturbance, indicate a smooth occupation of the entire gap space and light conditions. The similar pattern within genera belonging to the same guilds may indicate similar regeneration strategies and historical life. A possible explanation for the success of species from these different genera may be the higher plasticity of traits and alternative resilience mechanisms (such as survival, resprouting and recruitment). As blowdowns are common in these forests [10,12,14], these results show that a simplified classification system is not enough to describe successional trajectories of large gaps.

Surprisingly, all the 25 most important genera in the disturbed forest (Figure 3) also figured within the 121 most abundant genera of the main portion of the Amazon [96]. *Protium*, *Pouteria* and *Eperua* characterized the low disturbance specialist guild in the disturbed forest (Figure 8) and took the second, third and seventh position in the Amazonian genera abundance ranking, respectively [96]. *Ocotea*, *Sloanea* and *Couratari* characterized the resistant or unaffected guild in the disturbed forest and took the 14th, 22nd and 106th position in the Amazonian ranking, respectively. *Eschweilera*, *Licania*, *Lecythis* and *Swartzia* characterized the intermediate disturbance intensity at the disturbed forest and took the first, fourth, 10th and 17th position in the Amazonian ranking, respectively. *Inga*, *Pourouma* and *Cecropia* characterized the high disturbance specialist guild in the disturbed forest and figured at the sixth, 18th and 30th position in the Amazonian ranking.

The co-occurrence of species with a broad range of life history strategies at intermediate disturbance levels (evidentiated as higher confluence of lines - Figure 8) shows that this blowdown promoted species richness probably by amplifying niches and/or resources. We assume that large gaps ($>2000 \text{ m}^2$) produced by blowdowns can be partly associated to increased diversity and the contrasting dominance of some species in these forests [54,55,57,67,94,96]. Variations in genera importance and species composition along the disturbance gradient indicate that gap recovery in large gaps is influenced by mortality patterns, most pronounced in plateaus and slopes. Additionally, selective mortality and fast-recruitment highlight genera specialization along the mortality gradient, and indicate that large gaps contain environmental variability that together with species responses and resistance, allow high tree species diversity. In this study, intermediate-disturbance levels had higher species richness suggesting that there was a selective mortality and resulting species turnover in response to the disturbance gradient. This pattern provides evidence that blowdowns allow species richness and diversity through an interaction of wind-damage with species-resistance and resilience. Although classical successional guilds may dominate small treefall gaps, the observed pattern indicate that in large gaps ($>2000 \text{ m}^2$) there are specialists for a wider range of disturbance and light. Thus, we assume that a diverse set of species differing widely in light requirements and recruitment strategies forms the pioneer cohort, thus lending a high resilience towards wind disturbances at the community level.

Our results add new and complementary information about succession and turnover of Western and Central Amazon forests and reinforce that recovery processes for large gaps differ from the trajectory observed in gaps formed by smaller treefall events [2,6,15,31,86] and secondary forests from anthropic activities, where fire and logging may increase biomass losses [41,90] and limit species regeneration [40,100]. Moreover, we revealed a gradient in demographic responses along the entire gradient of disturbance levels. Mortality intensity and gap size seem to influence community composition by filtering shade-tolerant survivors with resprouting ability and favoring more light-demanding and fast-growing species. As already observed in tropical and subtropical regions [26,29,32,47,98,101] wind damage depends on species composition and successional stage, which suggest that secondary forests in the Amazon might be more vulnerable and less resilient to windstorms than forests in more advanced successional stage. Thus, for better understanding the blowdown effects on species distribution, forest vulnerability, ecosystem functioning, and the ecological importance of large gaps on species maintenance it is necessary that future studies include

dynamic and long-term succession data. In addition, the proliferation of lianas and pioneer tree species in severely disturbed areas may represent an important impediment to seedling establishment [102]. Previous studies in this region showed that it takes an average of ~ 18 years for dead trees ($>10 \text{ cm DBB}$) to completely decay, although some can take considerably longer [103], so that coarse woody debris and greater surface litter accumulation can have a persistent effect on forest regeneration by covering the soil and acting as a physical barrier, which can favor or exclude species [104,105]. The persistence of decomposing debris may also alter nutrient and even perhaps water availability to seedlings and regenerating species, all of which will serve as filters that help determine which species recolonize large gaps.

Conclusion

Blowdown gaps larger than 2000 m^2 initiate secondary succession providing niches to establish a canopy position for species with a broad range of life history strategies and requirements. Smooth gradients in demographic responses and the existence of specialists for different levels of disturbance can perhaps help explain carbon cycle, maintenance of biodiversity and the recently reported hyperdominance of some tree and palm species in these forests [96]. If forest structure and species composition depend on the intensity and frequency of large disturbance regimes, the intensification of more extreme climate events such as convective storms, may alter forest vulnerability and resilience depending on the successional trajectories. Considering size, vegetation heterogeneity and local logistical limitations, permanent forest monitoring in Amazon must combine remote sensing methods allowing the inclusion of large natural disturbances.

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Author Contributions

Conceived and designed the experiments: DMM JQC NH SET JS GHPMR RIN. Performed the experiments: DMM GHPMR. Analyzed the data: DMM CW BR GHPMR RIN JQC. Contributed reagents/materials/analysis tools: SET NH JS JQC CW DMM. Wrote the paper: DMM CW SET GHPMR RIN BR JQC NH.

References

- Clements F (1936) Nature and structure of the climax. *J Ecol* 24: 252–284.
- Denslow J (1980) Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia* 46: 18–21.
- Sousa W (1984) The Role of Disturbance in Natural Communities. *Annu Rev Ecol Syst* 15: 353–391.
- Turner M, Baker W, Peterson C, Peet R (1998) Factors Influencing Succession: Lessons from Large, Infrequent Natural Disturbances. *Ecosystems* 1: 511–523.
- Grubb P (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol Rev* 52: 107–145.
- Brokaw N (1985) Gap-phase regeneration in a tropical forest. *Ecology* 66: 682–687.
- Uhl C, Clark K, Dezzio N, Maquirino P (1988) Vegetation dynamics in Amazonian treefall gaps. *Ecology* 69: 751–763.
- Coley P, Kursar T (2014) On tropical forests and their pests. *Science* 343: 35–36.
- Negrón-Juárez R, Chambers J, Guimarães G, Zeng H, Raupp C, et al. (2010) Widespread Amazon forest tree mortality from a single cross-basin squall line event. *Geophys Res Lett* 37: 1–5.
- Chambers JQ, Negrón-Juárez RI, Marra DM, Di Vittorio A, Tews J, et al. (2013) The steady-state mosaic of disturbance and succession across an old-growth Central Amazon forest landscape. *Proc Natl Acad Sci U S A* 110: 3949–3954.
- Chambers J, Negrón-Juárez R, Hurr G, Marra D, Higuchi N (2009) Lack of intermediate-scale disturbance data prevents robust extrapolation of plot-level tree mortality rates for old-growth tropical forests. *Ecol Lett* 12: E22–E25.
- Nelson B, Kapos V, Adams J, Oliveira W (1994) Forest disturbance by large blowdowns in the Brazilian Amazon. *Ecology* 75: 853–858.
- Espirito-Santo F, Keller M, Braswell B, Nelson B, Frolking S, et al. (2010) Storm intensity and old-growth forest disturbances in the Amazon region. *Geophys Res Lett* 37: 1–6.
- Espirito-Santo F, Gloor M, Keller M, Malhi Y, Saatchi S, et al. (2014) Size and frequency of natural forest disturbances and the Amazon forest carbon balance. *Nat Commun* 5: 1–6.
- Denslow J (1987) Tropical rainforest gaps and tree species diversity. *Annu Rev Ecol Syst* 18: 431–451.

16. Hubbell S, Foster R, O'Brien S, Harms K, Condit R, et al. (1999) Light-Gap Disturbances, Recruitment Limitation, and Tree Diversity in a Neotropical Forest. *Science* 283: 554–557.
17. Gloor M, Phillips OL, Lloyd JJ, Lewis SL, Malhi Y, et al. (2009) Does the disturbance hypothesis explain the biomass increase in basin-wide Amazon forest plot data? *Glob Chang Biol* 15: 2418–2430.
18. Chave J, Condit R, Muller-Landau HC, Thomas SC, Ashton PS, et al. (2008) Assessing evidence for a pervasive alteration in tropical tree communities. *PLoS Biol* 6: e45.
19. Kellner JR, Asner GP (2009) Convergent structural responses of tropical forests to diverse disturbance regimes. *Ecol Lett* 12: 887–897.
20. Di Vittorio A, Negrón-Juárez R, Higuchi N, Chambers J (2014) Tropical forest carbon balance: effects of field-and satellite-based mortality regimes on the dynamics and the spatial structure of Central Amazon forest biomass. *Environ Res Lett* 9: 1–10.
21. Fisher J, Hurtt G, Thomas R, Chambers J (2008) Clustered disturbances lead to bias in large-scale estimates based on forest sample plots. *Ecol Lett* 11: 554–563.
22. Hjelmfelt M (2007) Microbursts and macrobursts: windstorms and blowdowns. In: Johnson E, Miyanishi K, editors. *Plant Disturbance Ecology: The Process and the Response*. Burlington, MA: Elsevier, Academic Press. 59–95.
23. Brokaw N, Grear J (1991) Forest structure before and after the hurricane Hugo at three elevations in the Luquillo Mountains, Puerto Rico. *Biotropica* 23: 386–392.
24. Boose E, Serrano M, Foster D (2004) Landscape and regional impacts of hurricanes in Puerto Rico. *Ecol Monogr* 74: 335–352.
25. Negrón-Juárez R, Chambers J, Marra D, Ribeiro G, Rifai S, et al. (2011) Detection of subpixel treefall gaps with Landsat imagery in Central Amazon forests. *Remote Sens Environ* 115: 3322–3328.
26. Putz F (1983) Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. *Ecology* 64: 1069–1074.
27. Denslow J, Ellison A, Sanford R (1998) Treefall gap size effects on above- and below-ground processes in a tropical wet forest. *J Ecol* 86: 597–609.
28. Vitousek P, Denslow J (1986) Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. *J Ecol* 74: 1167–1178.
29. Negrón-Juárez R, Baker D, Chambers J, Hurtt G, Goosem S (2014) Multi-scale sensitivity of Landsat and MODIS to forest disturbance associated with tropical cyclones. *Remote Sens Environ* 140: 679–689.
30. Bellingham P, Tanner E, Healey J (1995) Damage and responsiveness of Jamaican montane tree species after disturbance by a hurricane. *Ecology* 76: 2562–2580.
31. Vandermeer J, la Cerda I de, Boucher D, Perfecto I, Ruiz J (2000) Hurricane Disturbance and Tropical Tree Species Diversity. *Science* 290: 788–791.
32. Canham C, Thompson J, Zimmerman J, Uriarte M (2010) Variation in susceptibility to hurricane damage as a function of storm intensity in Puerto Rican tree species. *Biotropica* 42: 87–94.
33. Uriarte M, Canham C, Thompson J, Zimmerman J, Brokaw N (2005) Seedling recruitment in a hurricane-driven tropical forest: light limitation, density-dependence and the spatial distribution of parent trees. *J Ecol* 93: 291–304.
34. Swaine M, Whitmore T (1988) On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75: 81–86.
35. Dalling JW, Winter K, Hubbell SP (2004) Variation in growth responses of neotropical pioneers to simulated forest gaps. *Funct Ecol* 18: 725–736.
36. Clark D, Clark D (2001) Getting to the canopy: tree height growth in a neotropical rain forest. *Ecology* 82: 1460–1472.
37. Wright J, Muller-Landau H, Condit R, Hubbell S (2003) Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. *Ecology* 84: 3174–3185.
38. Schupp E, Howe H, Augspurger C, Levey D (1989) Arrival and survival in tropical treefall gaps. *Ecology* 70: 562–564.
39. Poorter L, Bongers F (2006) Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* 87: 1733–1743.
40. Mesquita R, Ickes K, Ganade G, Williamson G (2001) Alternative successional pathways in the Amazon Basin. *J Ecol* 89: 528–537.
41. Saldarriaga J, West D, Tharp M, Uhl C (1998) Long-Term Chronosequence of Forest Succession in the Upper Rio Negro of Colombia and Venezuela. *J Ecol* 76: 938–958.
42. Rüger N, Berger U, Hubbell SP, Vieilledent G, Condit R (2011) Growth strategies of tropical tree species: disentangling light and size effects. *PLoS One* 6: e25330.
43. Gravel D, Canham C, Beaudet M, Messier C (2006) Reconciling niche and neutrality: the continuum hypothesis. *Ecol Lett* 9: 399–409.
44. Violle C, Jiang L (2009) Towards a trait-based quantification of species niche. *J Plant Ecol* 2: 87–93.
45. Vandecar K, Lawrence D, Richards D, Schneider L, Rogan J, et al. (2011) High mortality for rare species following hurricane disturbance in the Southern Yucatan. *Biotropica* 43: 676–684.
46. Putz F, Brokaw N (1989) Sprouting of broken trees on Barro Colorado Island, Panama. *Ecology* 70: 508–512.
47. Zimmerman J, III Everham E, Waide R, Lodge D, Taylor C, et al. (1994) Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. *J Ecol* 82: 911–922.
48. Lugo A (2008) Visible and invisible effects of hurricanes on forest ecosystems: an international review. *Austral Ecol* 33: 368–398.
49. Foster D, Knight D, Franklin J (1998) Landscape Patterns and Legacies Resulting from Large, Infrequent Forest Disturbances. *Ecosystems* 1: 497–510.
50. Ranzani G (1980) Identificação e caracterização de alguns solos da Estação Experimental de Silvicultura Tropical. *Acta Amaz* 10: 7–41.
51. Sombroek W (2001) Spatial and temporal patterns of Amazon rainfall: consequences for the planning of agricultural occupation and the protection of primary forests. *Ambio* 30: 388–396.
52. Silva R da, Santos J dos, Tribuzy E, Chambers J, Nakamura S, et al. (2002) Diameter increment and growth patterns for individual tree growing in Central Amazon, Brazil. *For Ecol Manage* 166: 295–301.
53. Higuchi N, Santos J dos, Lima A, Higuchi F, Chambers J (2011) A floresta amazônica e a água da chuva. *FLORESTA* 41: 427–434.
54. Ribeiro J da S, Hopkins M, Vicentini A, Sothers C, Costa M da S, et al. (1999) Flora da Reserva Ducke: Guia de Identificação das Plantas Vasculares de uma Floresta de Terra-firme na Amazônia Central. Manaus: INPA.
55. Oliveira A de, Mori S (1999) A central Amazonian terra firme forest. I. High tree species richness on poor soils. *Biodivers Conserv* 8: 1219–1244.
56. Braga P (1979) Subdivisão fitogeográfica, tipos de vegetação, conservação e inventário florístico da floresta amazônica. *Acta Amaz* 9: 53–80.
57. Guillaumet J (1987) Some structural and floristic aspects of the forest. *Experientia* 43: 241–251.
58. Kahn F (1986) Life forms of Amazonian palms in relation to forest structure and dynamics. *Biotropica* 18: 214–218.
59. Chauvel A, Lucas Y, Boulet R (1987) On the genesis of the soil mantle of the region of Manaus, Central Amazonia, Brazil. *Experientia* 43: 234–241.
60. Castilho C, Magnusson W, Araújo R, Luizão R, Luizão F, et al. (2006) Variation in aboveground tree live biomass in a central Amazonian Forest: Effects of soil and topography. *For Ecol Manage* 234: 85–96.
61. Costa F, Guillaumet J, Lima A, Pereira O (2009) Gradients within gradients: the mesoscale distribution patterns of palms in a central Amazonian forest. *J Veg Sci* 20: 69–78.
62. Ribeiro G, Suwa R, Marra D, Kajimoto T, Ishizuka M, et al. (2014) Allometry for juvenile trees in an Amazonian forest after wind disturbance. *JARQ* 48: 213–219.
63. APGIII (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot J Linn Soc* 161: 105–121.
64. APG II TAPG (2003) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Bot J Linn Soc London* 141: 399–436.
65. Stevens P (2012) Angiosperm Phylogeny Website: version 12. Available: <http://www.mobot.org/MOBOT/research/APweb/>.
66. Higuchi N, Santos J dos, Vieira G, Ribeiro R, Sakurai S, et al. (1998) Análise Estrutural da Floresta Primária da Bacia do Rio Cuieiras, ZF-2, Manaus-AM, Brasil. In: Higuchi N, Campos M, Sampaio P, Santos J dos, editors. *Pesquisas Florestais para Conservação da Floresta e Reabilitação de Áreas Degradadas da Amazônia*. Manaus, Amazonas, Brazil: INPA. 51–81.
67. Vieira S, Camargo P de, Selhorst D, Silva R da, Hutrya L, et al. (2004) Forest structure and carbon dynamics in Amazonian tropical rain forests. *Oecologia* 140: 468–479.
68. Phillips OL, Aragão LEOC, Lewis SL, Fisher JB, Lloyd J, et al. (2009) Drought sensitivity of the Amazon rainforest. *Science* 323: 1344–1347.
69. Marengo J, Nobre C, Tomasella J, Oyama M, Oliveira G de, et al. (2008) The drought of Amazonia in 2005. *J Clim* 21: 495–517.
70. Fearnside P (1997) Wood density for estimating forest biomass in Brazilian Amazonia. *For Ecol Manage* 90: 59–87.
71. Chave J, Muller-Landau H, Baker T, Easdale T, ter Steege H, et al. (2006) Regional and phylogenetic variation of wood density across 2456 neotropical tree species. *Ecol Appl* 16: 2356–2367.
72. Nogueira EM, Nelson BW, Fearnside PM (2005) Wood density in dense forest in central Amazonia, Brazil. *For Ecol Manage* 208: 261–286.
73. Nogueira EM, Fearnside PM, Nelson BW, França MB (2007) Wood density in forests of Brazil's "arc of deforestation": Implications for biomass and flux of carbon from land-use change in Amazonia. *For Ecol Manage* 248: 119–135.
74. Carlotto M (1999) Reducing the effects of space-varying, wavelength-dependent scattering in multispectral imagery. *Int J Remote Sens* 20: 3333–3344.
75. Adams J, Sabol D, Kapos V, Filho R, Roberts D, et al. (1995) Classification of multispectral images based on fractions of endmembers: Application to land-cover change in the Brazilian Amazon. *Remote Sens Environ* 52: 137–154.
76. Adams J, Gillespie A (2006) Remote sensing of landscapes with spectral images. A physical modeling approach. Cambridge University Press.
77. Higuchi N, Chambers J, Santos J dos, Ribeiro R, Pinto A, et al. (2004) Dinâmica e balanço do carbono da vegetação primária da Amazônia Central. *Floresta* 34: 295–304.
78. Hijmans R, van Etten J (2012) raster: Geographic data analysis and modeling. R package. Available: <http://cran.r-project.org/>.
79. Lewin-Koh N, Bivand R (2013) mapproj: Tools for reading and handling spatial objects. R package. Available: <http://cran.r-project.org/>.
80. R Core Team (2013) R: A language and environment for statistical computing. Available: <http://www.r-project.org>.

81. Curtis J, McIntosh R (1950) The interrelations of certain analytic and synthetic phytosociological characters. *Ecology* 31: 434–455.
82. Anderson M, Crist T, Chase J, Vellend M, Inouye B, et al. (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecol Lett* 14: 19–28.
83. Legendre P, Legendre L (2012) *Numerical ecology*. 3rd ed. Amsterdam: Elsevier.
84. Oksanen J, Blanchet F, Kindt R, Legendre P, Minchin P, et al. (2013) *vegan: Community Ecology Package*. Available: <http://cran.r-project.org/>.
85. Lewis S, Phillips O, Sheil D, Vinceti B, Baker T, et al. (2004) Tropical forest tree mortality, recruitment and turnover rates: calculation, interpretation and comparison when census intervals vary. *J Ecol* 92: 929–944.
86. Walker L (1991) Tree damage and recovery from Hurricane Hugo in Luquillo experimental forest, Puerto Rico. *Biotropica* 23: 379–385.
87. Xi W, Peet RK, Decoster JK, Urban DL (2008) Tree damage risk factors associated with large, infrequent wind disturbances of Carolina forests. *Forestry* 81: 317–334.
88. Garstang M, White S, Shugart H, Halverson J (1998) Convective cloud downdrafts as the cause of large blowdowns in the Amazon rainforest. *Meteorol Atmos Phys* 67: 199–212.
89. Chambers J, Robertson A, Carneiro V, Lima A, Smith M, et al. (2009) Hyperspectral remote detection of niche partitioning among canopy trees driven by blowdown gap disturbances in the Central Amazon. *Oecologia* 160: 107–117.
90. Lima A, Teixeira L, Carneiro V, Santos J dos, Higuchi N (2007) Análise da estrutura e do estoque de fitomassa de uma floresta secundária da região de Manaus AM, dez anos após corte raso seguido de fogo. *Acta Amaz* 37: 49–54.
91. Toledo J de, Magnusson W, Castilho C, Nascimento H (2012) Tree mode of death in Central Amazonia: Effects of soil and topography on tree mortality associated with storm disturbances. *For Ecol Manage* 263: 253–261.
92. Toledo J de, Magnusson W, Castilho C (2013) Competition, exogenous disturbances and senescence shape tree size distribution in tropical forest: evidence from tree mode of death in Central Amazonia. *J Veg Sci* 24: 651–663.
93. Carneiro V, Higuchi N, Santos J dos, Pinto A, Teixeira L, et al. (2005) Composição Florística e Análise Estrutural da Floresta de Terra Firme na Região de Manaus, Estado do Amazonas, Brasil. *Actas das Comunicações - Inventário, Modelação e Gestão. Viso, Portugal: V Congresso Florestal Nacional A Floresta e as Gentes*. Available: <http://www.esac.pt/cernas/cfn5/docs/T2-40.pdf>.
94. Prance G, Rodrigues W, Silva M da (1976) Inventário florestal de um hectare de mata de terra firme km 30 da Estrada Manaus-Itacoatira. *Acta Amaz* 6: 9–35.
95. Oliveira A, Nelson B (2001) Floristic relationships of terra firme forests in the Brazilian Amazon. *For Ecol Manage* 146: 169–179.
96. Ter Steege H, Pitman NC a, Sabatier D, Baraloto C, Salomão RP, et al. (2013) Hyperdominance in the Amazonian tree flora. *Science* 342: 1243092.
97. Muller-Landau H (2004) Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica* 36: 20–32.
98. Brokaw N, Walker L (1991) Summary of the effects of Caribbean hurricanes on vegetation. *Biotropica* 23: 442–447.
99. Burslem D, Whitmore T, Brown G (2000) Short-term effects of cyclone impact and long-term recovery of tropical rain forest on Kolombangara, Solomon Islands. *J Ecol* 88: 1063–1078.
100. Massoca P, Jakovac A, Bento T, Williamson G, Mesquita R (2012) Dynamics and trajectories of secondary succession in Central Amazonia. *Bol Mus Para Emilio Goeldi* 7: 235–250.
101. Thompson J, Brokaw N, Zimmerman J, Waide RB, Everham EM III, et al. (2002) Land use history, environment, and tree composition in a tropical forest. *Ecol Appl* 12: 1344–1363.
102. Schnitzer S, Dalling J, Carson W (2001) The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. *J Ecol* 88: 655–666.
103. Chambers J, Higuchi N, Teixeira L, Santos J dos, Laurance S, et al. (2004) Response of tree biomass and wood litter to disturbance in a Central Amazon forest. *Oecologia* 141: 596–611.
104. Clark D, Clark D (1991) The impact of physical damage on canopy tree regeneration in tropical rain forest. *J Ecol* 79: 447–457.
105. Scariot A (2006) Seedling Mortality by Litterfall in Amazonian Forest Fragments1. *Biotropica* 32: 662–669.

3. ORIGINAL CONTRIBUTIONS

3.2. Paper 2

Santos LT dos, **Magnabosco Marra D**, Trumbore S, Camargo PB de, Negrón-Juárez RI, Lima AJN, Ribeiro GHPM, Santos J dos, Higuchi N (2016): Windthrows increase soil carbon stocks in a central Amazon forest. *Biogeosciences* 13:1299-1308. doi: 10.5194/bg-13-1299-2016



Windthrows increase soil carbon stocks in a central Amazon forest

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Abstract. Windthrows change forest structure and species composition in central Amazon forests. However, the effects of widespread tree mortality associated with wind disturbances on soil properties have not yet been described in this vast region. We investigated short-term effects (7 years after disturbance) of widespread tree mortality caused by a squall line event from mid-January of 2005 on soil carbon stocks and concentrations in a central Amazon terra firme forest. The soil carbon stock (averaged over a 0–30 cm depth profile) in disturbed plots ($61.4 \pm 8.2 \text{ Mg ha}^{-1}$, mean $\pm 95\%$ confidence interval) was marginally higher ($p = 0.09$) than that from undisturbed plots ($47.7 \pm 13.6 \text{ Mg ha}^{-1}$). The soil organic carbon concentration in disturbed plots ($2.0 \pm 0.17\%$) was significantly higher ($p < 0.001$) than that from undisturbed plots ($1.36 \pm 0.24\%$). Moreover, soil carbon stocks were positively correlated with soil clay content ($r^2 = 0.332$, $r = 0.575$ and $p = 0.019$) and with tree mortality intensity ($r^2 = 0.257$, $r = 0.506$ and $p = 0.045$). Our results indicate that large inputs of plant litter associated with large windthrow events cause a short-term increase in soil carbon content, and the degree of increase is related to soil clay content and tree mortality intensity. The higher carbon content and potentially higher nutrient availability in soils from areas recovering from windthrows may favor forest regrowth and increase vegetation resilience.

1 Introduction

Tropical forests contain about 44 % (383 Pg C) of the approximately 860 PgC stored in forests worldwide, with soils accounting for 32 % of the total carbon stocks (Queré et al., 2009; Lal, 2004). Global emissions due to changes in land use and soil cultivation are estimated to be 136 PgC since the industrial revolution (Lal, 2004; Houghton, 1999). However, there are few estimates of emissions by the decomposition and mineralization of organic carbon in soils following natural disturbances (Lal, 2004), presumably because we assume there is a balance between rapid losses that follow disturbance and recovery between disturbances at the larger spatial scales.

The effects of large-scale natural disturbances (i.e., wind disturbances) on carbon stocks and cycling due to the increase of litter inputs promoted by widespread tree mortality, the fraction of this carbon that persists in soil organic matter, and how long it is stabilized are poorly known in both in tropical and temperate forests (Foster et al., 1998; Turner et al., 1998). In temperate forests, newly exposed soil due to wind disturbance can cover from ca. 10 % (Peterson et al., 1990) up to 60 % of the surface (Beatty, 1980; Putz, 1983). In a three-species temperate forest in Slovakia, no organic carbon was lost at two windthrow sites within 3.5 years after disturbance, but shifts occurred within organic layers and mineral soil toward decomposed organic matter (Don et al., 2012). In Amazonian forests, where windthrows are a ma-

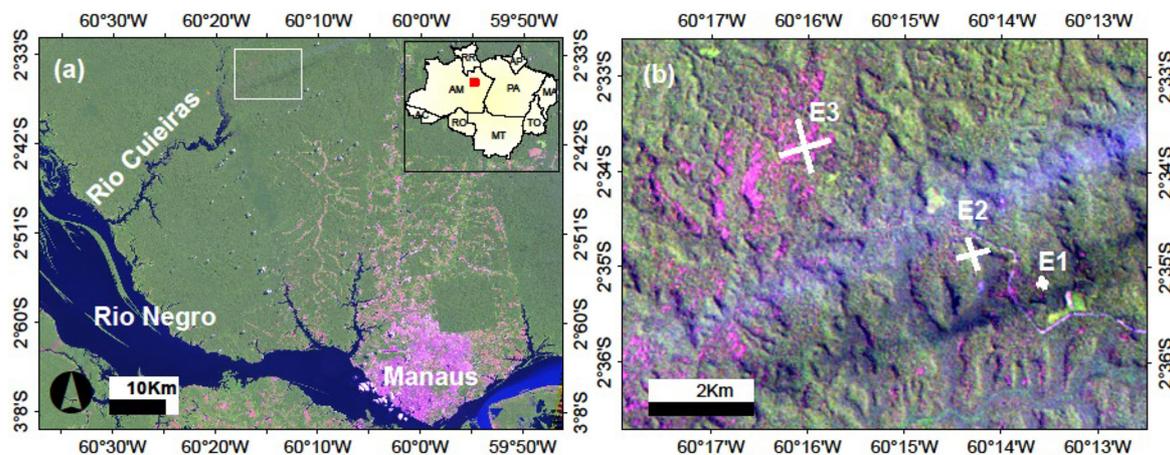


Figure 1. Study area (white inset) on the left side of the Rio Cuieiras, Amazonas, Brazil (a). Sampled transects (white inset) set along wind-disturbed terra firme forest at the Estação Experimental de Silvicultura Tropical (EEST/INPA) and a contiguous forest (SUFRAMA; b). The reddish color in (b) indicates the high middle-infrared reflectance (dead wood and litter) of wind-disturbed areas. Image: RGB composition (bands 3, 4, and 5) from Landsat 5 TM (p231, r062, from 29 July 2005). Image source: <http://earthexplorer.usgs.gov/>.

major natural disturbance (Nelson et al., 1994; Chambers et al., 2013), such effects have not yet been investigated.

Wind disturbances are frequent in the western and central Amazon, (Nelson et al., 1994; Espírito Santo et al., 2010; Negrón-Juárez et al., 2010). In this large region, windthrows are associated with torrential rains and very strong winds (16 m s^{-1}) known as downbursts (Nelson et al., 1994; Garstang et al., 1998). The widespread tree mortality creates canopy gaps with a wide range of sizes (from few square meters up to thousands of hectares; Nelson et al., 1994; Negrón-Juárez et al., 2010, 2011) and affects forests at the landscape level (Marra et al., 2014). It has been reported that these large gaps have a potential effect on carbon cycling (Chambers et al., 2013) and can promote tree species diversity by allowing a diverse cohort of species with a broad range of life history strategies (Chambers et al., 2009; Marra et al., 2014) and allometry (Ribeiro et al., 2014).

In the tropics, winds break and uproot trees causing strong soil disturbances (e.g., increasing leaves and wood debris and changing morphology and nutrient availability; Schaetzl et al., 1989; Lugo, 2008). Treefall gaps can also change microclimate conditions such as light intensity and create a variety of microsites, which can be separated into canopy, trunk, and root/uprooted sites (Putz, 1983). These microsites have important features that drive soil and vegetation recovery after disturbance (Putz, 1983; Schaetzl et al., 1989; Vitousek and Denslow, 1986). They can differ in microbial activity (Batjes, 1996) and enhance the colonization of fast-growing species that help in the assimilation of nutrients and soil carbon, which in turn can contribute to quickly restore the forest canopy through succession (Putz, 1983). This rapid recycling of nutrients potentially enhances the resilience of tropical forests to natural disturbances (Schaetzl et al., 1989; Ostertag

et al., 2003; Lugo, 2008). However, how complex and hyperdiverse tropical forests such as the Amazon will respond in a scenario of higher frequency of extreme weather events (Coumou and Rahmstorf, 2012; Cai et al., 2014) is still not clear.

We assessed the effects of wind disturbances on soils of a large terra firme forest in central Amazon. We hypothesized that windthrows forming large canopy gaps ($\geq 2000 \text{ m}^2$) affect the soil carbon content via litter and wood debris deposition and decomposition, and that the soil carbon content is controlled by the interaction of tree mortality intensity, clay content, and depth. To test our hypothesis we addressed the following questions:

1. Are there differences in soil carbon stocks between disturbed and undisturbed areas, and how do possible variations compare to other tropical and temperate forests worldwide?
2. What is the importance of soil texture (clay content) on soil organic carbon content in wind disturbed areas?
3. Does tree mortality intensity influence soil carbon stocks?

2 Methods

2.1 Study site

This study was conducted in a large terra firme forest, ca. 100 km from Manaus, Amazonas, Brazil (Fig. 1). We sampled soils from the Estação Experimental de Silvicultura Tropical (EEST) of the Instituto Nacional de Pesquisas da Amazônia (INPA) and from a contiguous forest, adjacent to

Table 1. Average concentrations of soil organic carbon content (SOC), soil carbon stocks (SCSs), bulk density (BD), and clay, silt, and sand average concentrations in transect 1 (E1), transect 2 (E2), and transect 3 (E3). Values in brackets represent the standard error of the mean.

Transect	Depth profile (cm)	Disturbed forest		Undisturbed forest		Soil texture			
		SOC (%)	SCS (Mg ha ⁻¹)	SOC (%)	SCS (Mg ha ⁻¹)	BD (g cm ⁻³)	Clay (%)	Silt (%)	Sand (%)
E1	0–10	3.72 (0.28)	31.00 (5.07)	2.48 (0.24)	20.18 (0.75)	0.74	69.42	21.97	8.56
	10–20	2.31 (0.13)	22.82 (1.97)	2.05 (0.22)	19.24 (0.74)	0.97	69.04	22.42	8.54
	20–30	1.79 (0.13)	16.61 (1.76)	1.71 (0.17)	13.06 (0.44)	0.98	68.69	22.78	8.53
E2	0–10	3.27 (0.19)	25.50 (1.42)	–	–	0.89	57.41	19.31	22.25
	10–20	1.79 (0.09)	19.87 (0.84)	–	–	1.15	67.59	22.42	8.54
	20–30	1.36 (0.07)	15.11 (1.59)	–	–	1.31	60.23	19.41	19.34
E3	0–10	2.11 (0.14)	21.52 (1.80)	1.17 (0.14)	11.36 (3.44)	1.24	22.63	10.33	67.04
	10–20	1.31 (0.08)	17.48 (3.08)	0.82 (0.09)	10.69 (2.63)	1.36	57.8	19.1	23.1
	20–30	1.13 (0.10)	16.50 (2.90)	0.75 (0.07)	10.14 (2.63)	1.41	24.78	10.94	63.93
Average	0–10	2.89 (0.13)	25.90 (2.06)	1.58 (0.19)	14.90 (3.18)	0.95	50.55	17.30	32.15
	10–20	1.71 (0.07)	20.05 (1.34)	1.13 (0.13)	14.11 (2.76)	1.16	50.45	17.90	31.65
	20–30	1.37 (0.06)	16.01 (1.27)	0.98 (0.10)	11.31 (1.91)	1.19	51.95	17.51	30.54

the Ramal-ZF2 road. The forest adjacent to the Ramal-ZF2 road is owned and administered by the Superintendência da Zona Franca de Manaus (SUFRAMA). Mean annual temperature in this region was 26.7 °C (1910–1983; Chambers et al., 2004), and rainfall ca. 50 km east of our study site averaged to 2610 mm yr⁻¹ (1980–2000; Silva et al., 2003). From July to September there is a distinct dry season with usually less than 100 mm of rain per month. The forest at the studied region has a closed canopy, high tree species diversity, and a dense understory (Braga, 1979).

The soils of the Amazon region are old and complex, with type and texture influenced by local topographical variations. At the studied region, the relief is undulating with altitude ranging from 40 to 180 m a.s.l. Soils on upland plateaus and the upper portions of slopes have high clay content (Oxisols), while soils on slope bottoms and valleys have high sand content (Spodosols; Telles et al., 2003) and are subject to sporadic inundations (Junk et al., 2011). The yellow Oxisols are found primarily on plateaus and slopes. In general, the soils are well drained and have low fertility, low pH, low cation exchange capacity, high aluminum concentration, and low organic carbon (Ferraz et al., 1998; Telles et al., 2003).

2.2 Tree mortality estimates

In January of 2005, a single squall line event propagating across the Amazon caused widespread tree mortality over large areas (Negrón-Juárez et al., 2010), including ca. 250 ha of terra firme forest in the study area (Fig. 1). Tree mortality directly caused by this event was quantified at landscape level through the correlation of plot-based measurements and changes on the fractions of green vegetation (GV) and non-photosynthetic vegetation (NPV) calculated from Landsat images – see Negrón-Juárez et al. (2010) for a detailed method description. This metric, validated by Negrón-

Juárez et al. (2011), allowed us to sample soils across an extent tree mortality gradient 0–70 %, including from small- to large-sized gaps and patches of old-growth forest not affected by the 2005 windthrows (Marra et al., 2014).

2.3 Soil sampling

We sampled soils during the dry season (July–September) of 2012 (7 years after disturbance) according to the degree of disturbance intensity measured as tree mortality (%). In total, 16 plots with dimensions of 25 m × 10 m were selected along three pairs of transects, with 200 (E1), 600 (E2), and 1000 m (E3) length (Fig. 1). The transects cross several toposequences and include local variations of soils and forest structure among plateaus, slopes, and valleys. In this study, we only considered plots established on plateaus, which were more severely affected by the 2005 windthrows (Marra et al., 2014). Although our samples covered soils types from Oxisols to Spodosols, we reduced strong soil attribute variations related to topography by excluding slope and valley areas.

In each of our 16 selected plots, we sampled six soil profiles 5 m from each other. We took samples from three depths (0–10, 10–20, and 20–30 cm) using an auger. For soil bulk density, samples were also collected in the three depths in one or two profiles per plot using 5 cm tall cylinders with a volume of 98 cm³. Altogether we collected 288 soil samples for carbon analysis (16 plots × 6 depth profiles × 3 depths) and 63 samples for density (21 depth profiles × 3 depths; Fig. 1).

2.4 Soil analysis

Before performing soil analyses, we removed leaves, twigs, and roots from our samples. Samples were then sieved, dried, and homogenized by grinding (< 2 mm). The soil carbon con-

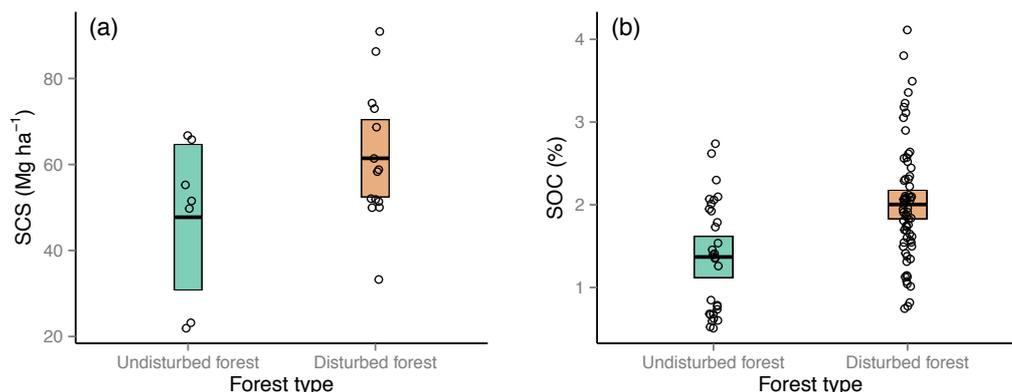


Figure 2. Comparison of the entire 0–30 cm depth profile for (a) soil carbon stock (SCS) and (b) soil organic carbon (SOC) between the disturbed and the undisturbed forest (mean \pm 95 % confidence interval) at 0–30 cm depth profile.

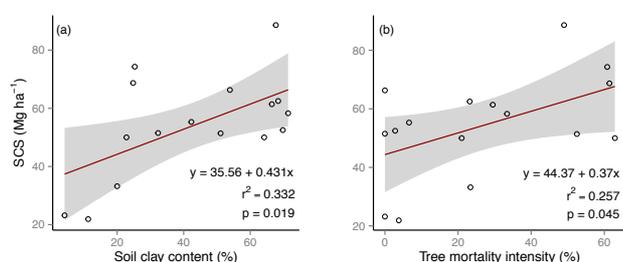


Figure 3. Soil carbon stock (SCS) as a linear function of (a) clay content (b) and tree mortality intensity (%) at 0–30 cm depth profile.

tent was determined in a combustion analyzer at the Centro de Energia Nuclear na Agricultura (CENA-USP), Piracicaba, Brazil. Bulk density samples were dried at 105 °C to constant weight. The soil carbon stock (SCS; Mg ha^{-1}) for each depth was calculated by the formula:

$$\text{SCS} = (\text{SOC} \times \text{BD} \times D)/10, \quad (1)$$

where SOC is the soil organic carbon content (g kg^{-1}), BD is bulk density (g cm^{-3}), and D is soil depth (cm). The soil clay content was determined by texture analysis using the pipetting method, with data from two profiles sampled in each plot.

2.5 Statistical analysis

Before performing statistical tests, we tested our data set for normality and homoscedasticity. To address our first question we use factorial ANOVA and compared undisturbed/low-disturbance plots (tree mortality $< 5\%$, hereafter referred as undisturbed forest) with those that experienced higher disturbance intensities (tree mortality $\geq 5\%$, hereafter referred as disturbed forest). In total we sampled 5 plots in undisturbed forest and 11 plots in disturbed forest. In the disturbed forest plots were set in disturbed patches varying from 900 m^2

(Landsat pixel size (30 \times 30 m) (Negrón-Juárez et al., 2011) to ca. 17 ha in area (Marra et al., 2014). To address our second question, we compared the SCS values from our study with those from different tropical and temperate forests. We addressed our third question using linear regression to correlate SCS to soil clay content and tree mortality intensity. We performed all analysis in R 3.0.1 platform (R Core Team, 2014) and produced Figs. 2–5 using the ggplot2 package (Wickham, 2009). We produced the Fig. 1 using the ArcMap GIS extension of the ArcGIS 10 software (ESRI, 2011).

3 Results

Soils from the disturbed forest had higher mean values of SCS and SOC than those from the undisturbed forest. This was true for all three depths we sampled (Table 1). SCS values averaged over 0–30 cm were $61.4 \pm 8.2 \text{ Mg ha}^{-1}$ (mean \pm 95 % confidence interval) for disturbed and $47.7 \pm 13.6 \text{ Mg ha}^{-1}$ for undisturbed forest ($p = 0.09$ and $F = 3.191$; Fig. 2a). For the same depth profile, SOC values were $2.0 \pm 0.17\%$ for the disturbed and $1.36 \pm 0.24\%$ for the undisturbed forest ($F = 16.74$ and $p < 0.001$; Fig. 2b).

The soil clay content in the entire study area ranged from 2.0 to 71.5 % averaged over 0–30 cm depth. This large variation in soil texture led to a large variation in the concentration of soil organic carbon (SOC) and soil carbon stocks (SCSs). The SOC in the upper samples (0–10 cm) had values ranging from 0.29 to 6.62 % and mean of $2.57 \pm 0.13\%$. For the same depth interval, values of SCS ranged from 3.79 to 48.53 Mg ha^{-1} with a mean value of $23.34 \pm 2.01 \text{ Mg ha}^{-1}$. Overall, bulk density increased with depth, while SOC and SCS decreased (Table 1). We found no difference comparing soil clay content between the disturbed and the undisturbed forest ($F = 2.648$ and $p = 0.108$). The fact that there was no difference between the two types of forest confirms

Table 2. Estimates of soil carbon stock (SCS) from this and other studies conducted in different tropical, subtropical, and temperate forests.

Author	Region	Forest type	Successional stage/management	SCS (Mg ha ⁻¹)		Soil type/description
				0–10 cm	0–30 cm	
dos Santos et al. (2016)	Manaus, AM, Brazil	Amazon terra firme forest (closed canopy) ^a	Undisturbed/old-growth forest	14.9	47.7	Oxisols ^b /Spodosols ^b
		Amazon terra firme forest (closed canopy)	Disturbed (windthrow) forest	25.9	61.4	Oxisols/Spodosols
Telles et al. (2003)	Manaus, AM, Brazil	Amazon terra firme forest (closed canopy)	Old-growth forest	19.2		Oxisols
		Amazon terra firme forest (closed canopy)	Old-growth forest	12.5		Spodosols
Trumbore et al. (1995)	Floresta Nacional do Tapajós, PA, Brazil	Amazon terra firme forest (closed canopy)	Old-growth forest	24.6		Oxisols
		Amazon terra firme forest (closed canopy)	Old-growth forest	8.7		Ultisols ^b
Camargo et al. (1999)	Paragominas, PA, Brazil	Amazon terra firme forest (closed canopy)	Old-growth forest	26		Oxisols
		Amazon terra firme forest (closed canopy)	Old-growth forest	26		Oxisols
Neil et al. (1996)	Ariquemes, RO, Brazil	Amazon terra firme forest (open canopy) ^a	Secondary forest	25		Oxisols
		Amazon terra firme forest (open canopy)	Old-growth forest		32.3	Ultisols
Neill et al. (1997)	Ouro Preto do Oeste, RO, Brazil	Amazon terra firme forest (open canopy)	Old-growth forest		27.4	Ultisols
		Amazon terra firme forest (open canopy)	Old-growth forest		29.7	Ultisols
Feigl et al. (1995)	Porto Velho, RO, Brazil	Amazon terra firme forest (open canopy)	Old-growth forest		48.1	Ultisols
		Amazon terra firme forest (open canopy)	Old-growth forest		62	Ultisols
Maia et al. (2009)	Cacaulândia, RO, Brazil	Amazon terra firme forest (open canopy)	Old-growth forest		39.3	Ultisols
		Amazon terra firme forest (open canopy)	Old-growth forest		50.4	Ultisols
Maia et al. (2009)	Vilhena, RO, Brazil	Amazon terra firme forest (open canopy)	Old-growth forest		15.9	Ultisols
		Amazon terra firme forest (open canopy)	Old-growth forest		65.3	Oxisols
Maia et al. (2009)	Conquista D'Oeste, MT, Brazil	Amazon terra firme forest (open canopy)	Old-growth forest			
		to seasonal semi-deciduous forest				
Maia et al. (2009)	Guarantã do Norte, MT, Brazil	Amazon terra firme forest (open canopy)	Old-growth forest		39.3	Ultisols
		to seasonal semi-deciduous forest				
Maia et al. (2009)	Nova Monte Verde, MT, Brazil	Amazon terra firme forest (open canopy)	Old-growth forest		35.4	Oxisols
		to seasonal semi-deciduous forest				
Maia et al. (2009)	Pimenteiras do Oeste, RO, Brazil	Amazon terra firme forest (open canopy)	Old-growth forest		46.5	Oxisols
		Amazon terra firme forest (open canopy)	Old-growth forest		33.4	Oxisols
Maia et al. (2009)	São José do Xingu, MT, Brazil	Amazon terra firme forest (open canopy)	Old-growth forest		36.1	Oxisols
		to seasonal semi-deciduous forest				
Maia et al. (2009)	Santa Luzia D'Oeste, RO, Brazil	Amazon terra firme forest (open canopy)	Old-growth forest		55.7	Oxisols
		Amazon terra firme forest (open canopy)	Old-growth forest		46.8	Oxisols
Maia et al. (2009)	Theobroma, RO, Brazil	Amazon terra firme forest (open canopy)	Old-growth forest		47.6	Oxisols
		Amazon terra firme forest (open canopy)	Old-growth forest		95.6	Andic Humitropepts
Maia et al. (2010)	Pontes e Lacerda, MT, Brazil	Amazon terra firme forest (closed canopy)	Old-growth forest		23	Orthic Ferralsol ^c
		Lower montane forest	Old-growth forest		35	Plinthic Ferralsol ^c
Rhoades et al. (2000)	Ecuador	Lower montane forest	Old-growth forest		30	Eutric Regosol ^c
		Equatorial forest	Old-growth forest		34.1	Tropohumult ^b , Dystrypept ^b and Dystrandept ^b
Batjes (2001)	Senegal	Equatorial forest	Old-growth forest		82.2	Tropohumult ^b , Dystrypept ^b and Dystrandept ^b
		Equatorial forest	Old-growth forest		64	Oxisols
Powers and Schlesinger (2002)	Costa Rica	Tropical wet forest	Old-growth forest		96	Oxisols
		Tropical wet forest	Old-growth forest		31	Oxisols
Veldkamp et al. (2003)	Costa Rica	Tropical moist forest	Old-growth forest		38.1	Oxisols, Cambisols
		Tropical moist forest	Old-growth forest (100-year-old)		34	Homogenous, silty clay and clay, pH values from 4.4 to 5.8
Marin-Spiotta et al. (2009)	Puerto Rico	Subtropical wet forest life zone	Old-growth forest		22.1	Very acidic and infertile
		Semi-deciduous moist tropical forest	Old-growth forest		ca. 47	Dystric Cambisols
Grimm et al. (2008)	Barro Colorado Island	Semi-deciduous moist tropical forest	Old-growth forest		ca. 51	
		Semi-deciduous moist tropical forest	Old-growth forest		ca. 43	
Neumann-cosel et al. (2011)	Panama	Tropical moist forest	Old-growth forest (100-year-old)		17 ^d	Heterogeneous (Spodosols, Histosols and Inceptisols)
		Tropical moist forest	Secondary forest (68-year-old)		46 ^d	
Ngo et al. (2013)	Singapore	Coastal hill dipterocarp forest	Old-growth forest		58 ^d	
		Coastal hill dipterocarp forest	Old-growth forest		32	Acidic Typic, Lithic and Aquic Haplorthods
Don et al. (2012)	Slovakia	Mixed temperate forest	Old-growth forest		ca. 47	
		Mixed temperate forest	Non-harvested windthrow (3.5-year-old)		ca. 51	
Kramer et al. (2004)	Tongass National Forest, Alaska, USA	Coastal temperate rain forest	Harvested windthrow (3.5-year-old)		ca. 43	
		Coastal temperate rain forest	Secondary forest (68-year-old)		17 ^d	
Kramer et al. (2004)	Tongass National Forest, Alaska, USA	Coastal temperate rain forest	Secondary forest (128-year-old)		46 ^d	
		Coastal temperate rain forest	Secondary forest (218-year-old)		58 ^d	
Huntington and Ryan (1990)	Hubbard Brook Experimental Forest, New Hampshire, USA	Northern hardwood forest	Secondary forest (65-year-old)		32	Acidic Typic, Lithic and Aquic Haplorthods
		Northern hardwood forest	Secondary harvested forest (65-year-old)		34	

^a IBGE, 2004; ^b USA Soil Taxonomy; ^c FAO, 1998; World Reference Base for Soil Resources (WRB); ^d Oa horizon.

our hypothesis that the tree mortality is the major vector of the changes we observed.

Along the entire sampled area (disturbed and undisturbed forest), the SCS was positively correlated with soil clay content (Fig. 3a) and with tree mortality intensity (Fig. 3b). When constraining the tree mortality gradient into three disturbance categories defined as tree mortality intensity (%), we found no differences in SCS ($F = 1.67$ and $p = 0.226$; Fig. 4a). However, SCS was $61.1 \pm 12 \text{ Mg ha}^{-1}$ in the disturbance category 3 (tree mortality $\geq 50\%$) vs. $43.1 \pm 17.2 \text{ Mg ha}^{-1}$ in disturbance category 1 (tree mortality $< 5\%$). The SOC in the disturbance category 2 ($5\% \leq$ tree mortality $< 50\%$) was marginally higher than that from category 1 (Tukey HSD, $p = 0.066$; Fig. 4b).

4 Discussion

4.1 Estimates of soil carbon stocks

As expected, our results were between those values found in the two soils types (Oxisols and Spodosols) evaluated in a previous study also conducted at the EEST (Telles et al., 2003), in which SCS values for 0–10 cm were reported as $14.9 \pm 3.18 \text{ Mg ha}^{-1}$ (Table 2). However, the overall SCS value ($23.3 \pm 2.01 \text{ Mg ha}^{-1}$) and that from our disturbed forest ($25.9 \pm 2.06 \text{ Mg ha}^{-1}$) were greater than those reported by Telles et al. (2003). Such differences indicate an increasing in SOC and SCS 7 years following disturbance.

The soils from our study area also had different SCS values from those reported for other regions of the Brazilian Amazon (i.e., same/similar soil types; Table 2). For the 0–10 cm profile, when comparing to old-growth forests in the Pará state, the mean SCSs of our undisturbed and disturbed forests were lower and similar, respectively (Trumbore et al.,

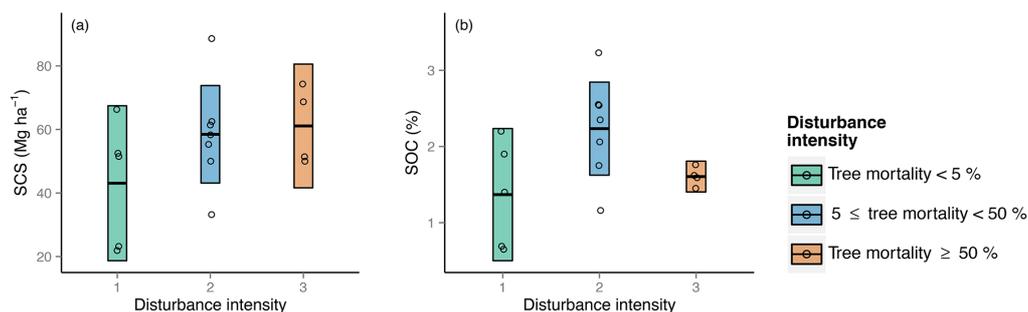


Figure 4. (a) Soil carbon stock (SCS) and (b) soil organic carbon (SOC) (mean \pm 95 % confidence interval) at 0–30 cm depth profile over disturbance intensity classes defined as tree mortality intensity (%).

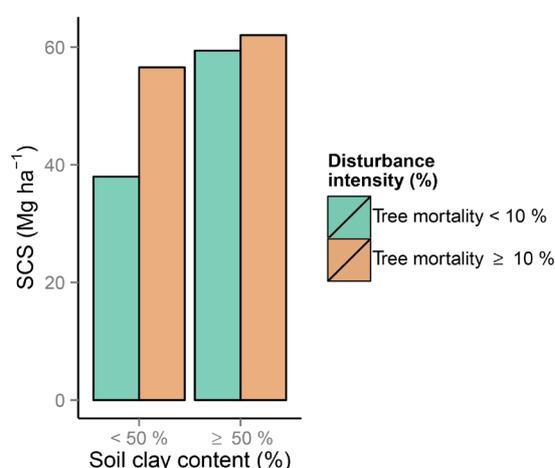


Figure 5. Soil carbon stock (SCS) at sites with different soil clay content and tree mortality intensity.

1995; Camargo et al., 1999). In the 0–30 cm depth profile, our undisturbed forest had similar SCS to that reported for other regions. When including other soil types, our disturbed forest had SCS values (61.4 Mg ha^{-1}) higher than most reported SCS values, with the exception of SCS values reported for a region in Mato Grosso (65.3 Mg ha^{-1}) and another in Rondônia (62 Mg ha^{-1} ; Maia et al., 2009). The SCS can be influenced by soil type, texture, and mineral composition (Powers and Veldkamp, 2005; López-Ulloa et al., 2005; Neumann-Cosel et al., 2011). Indeed, the different SCS rates from different soil types are related to important factors such as geology, climate, and soil formation (Adams et al., 1990; Batjes, 1996). The differences in SCS values among our undisturbed forest and other regions in the Brazilian Amazon (as shown in Table 2) might reflect a particular geology and/or landscape variations of soil type (Quesada et al., 2010, 2011).

When comparing to forests worldwide (i.e., different soil types), both our undisturbed and disturbed forest had lower SCS values (Table 2). We only found higher SCS values than

that reported for the 0–30 cm depth profile from an equatorial forest in Senegal, Africa (Batjes, 2001). For the 0–10 cm depth profile, our disturbed forest had SCS higher than that reported for an old-growth coastal hill dipterocarp forest in Singapore (Ngo et al., 2013) and a 68-year-old secondary coastal temperate rain forest in southeast Alaska (Kramer et al., 2004), both in different soil types. In contrast, our disturbed forest had lower SCSs than those reported for other temperate forests in Europe (Don et al., 2012) and North America (Huntington and Ryan 1990; Kramer et al., 2004). This was true for both non-harvested and harvested forests, in which nutrient exportation via logging has an opposite effect than that of wind disturbances (nutrient inputs).

4.2 Changes in carbon stocks and clay concentration in the soil

Soil clay content was positively correlated with the SOC (Pearson's $r = 0.907$) at 0–30 cm depth profile and consequently with SCS (Pearson's $r = 0.575$). This relationship between SOC and clay content was shown in other studies (Powers and Schlesinger, 2002; Kahle et al., 2002). The soil organic matter can form aggregates stabilizing the clay surface and the age of the soil carbon at the same depth increases with clay content (Telles et al., 2003). However, the clay content is not always a good predictor of SOC (Torn et al., 1997; Powers and Schlesinger, 2002; Telles et al., 2003). Thus, the method we applied in this study would be better applied in studies involving the same soil type and origin. In other situations, the mineralogical composition (i.e., including the type of clays) may be a better predictor of SOC than just the percentage of clay itself.

Due to the proximity of our plots, we assume climatic and geological aspects to be constant. Thus, the importance of soil texture on carbon stocks in our study site reflects a local pattern. Here we focused on assessing the effects of the existing Amazon tree mortality gradient (Espírito Santo et al., 2010; Chambers et al., 2013) on SOC and SCS, which is why we excluded valleys and selected plots along transects crossing forest patches with different disturbance inten-

sity. Nonetheless, apart from indicating significant increase of SCS due to inputs of organic matter from tree mortality, our data show that clay-richer soils originally had higher SCS (0–30 cm depth profile) compared to soils with lower clay content (Fig. 5). Soils from areas where tree mortality was <10 % and clay content ≥ 50 % had SCS ca. 36 % higher than those under the same tree mortality intensity but clay content <50 % (59.4 Mg ha^{-1} vs. 37.9 Mg ha^{-1} , respectively). In contrast, where disturbance intensity was higher (tree mortality ≥ 10 %), this difference was smaller. Soils with clay content ≥ 50 % had SCS only ca. 8 % higher than those with clay content <50 % (62 Mg ha^{-1} vs. 56.5 Mg ha^{-1} , respectively).

This comparison confirms that the widespread tree mortality caused by the 2005 windthrows increased the SCS in our study area. A higher frequency and intensity of wind disturbances in plateau areas also suggests that the higher SCS in these portions of the relief, apart from those related to abiotic factors (e.g., soil texture, topography and erosion), might also reflect differences of vegetation dynamics. Although the soil clay content is an important aspect and greater inputs of carbon can be expected in more clayey sites, significant inputs can also occur in more sandy sites, for instance, when strong wind gusts reach lower parts of slopes and valleys.

4.3 Intensity of disturbance and soil carbon stocks

Although we observed an increase of SCS in areas affected by the storm, it is notable that the fresh necromass produced by widespread tree mortality events is not fully incorporated into the soil. Under this assumption, the fast decomposition of carbon stored in roots and other woody material probably contributes most to the observed increases in SCS. Carbon inputs from belowground material, which is already incorporated to the soil, might be specially related to the increase of SCS in the 10–20 and 20–30 cm depth profiles.

Seven years after the windthrow event, the SCS at 30 cm depth was approximately 13.7 Mg ha^{-1} greater in the disturbed forest compared to the undisturbed forest. This number is equivalent to 8.3 % of the total carbon stored in the aboveground tree biomass (ca. 164 Mg ha^{-1}) of the studied forest (Higuchi et al., 2004), which indicates an average rate of soil carbon accumulation of $1.8 \text{ Mg ha}^{-1} \text{ yr}^{-1}$. Still, the amount of SCS in our disturbed forest is probably underestimated due to the large amount of carbon stored in belowground (roots) from coarse wood > 2 mm, not included in our samples. Part of this coarse material is not incorporated into the soil. Instead, it is decomposed at the surface (Chambers et al., 2000, 2004), though some is leached into the soil or carried out by detritivores.

Amazon soils typically have a great variation in texture and nutrient availability related to physical and chemical properties (Quesada et al., 2010, 2011), which can influence basin-wide variations in forest structure and function (Quesada et al., 2012). Our results indicate that in central Amazon terra firme forests, vegetation dynamics can also influence

soil attributes at the landscape level. In this region, the observed organic carbon enrichment derived from widespread tree mortality might also be related to the fast establishment and growth of pioneer species in heavily disturbed areas (Chambers et al., 2009; Marra et al., 2014).

In contrast, according to Lin et al. (2003), the Fushan Experimental Forest, which has experienced frequent windstorms, did not regain any nutrients following disturbance. This, in turn, has limited local tree growth (shown as lower canopy height) and, consequently, decreased carbon input into the soil. Thus, more intense mortality regime can also be expected to change forest dynamics, and eventually decrease SCS and nutrient cycling. The effects might depend on forest stature, successional stage (i.e., floristic composition and forest structure attributes such as tree density, basal area, and biomass), and tree mortality intensity, often controlled by the speed and duration of wind gusts (Lugo et al., 1983; Garstang et al., 1998). In our study area, fast vegetation regeneration could even reduce short-term losses of carbon associated with the 2005 windthrows, which had an estimated emission (assuming the carbon from all felled trees emitted to the atmosphere at once) of ca. 0.076 PgC , equivalent to 50 % of the deforestation during that same year (Higuchi et al., 2011; Negrón-Juárez et al., 2010).

The size of gaps in which we observed significant increase on soil carbon content (gaps from 0.1 up to 17 ha) indicates that windthrows – apart from influencing tree species composition, forest structure, and forest dynamics (Chambers et al., 2013; Marra et al., 2014) – also change soil attributes. The nutrients released in this process might have an important feedback on vegetation resilience and recovery following disturbance. To determine how much of the added soil carbon is stabilized in a long term, future studies should assess soil carbon stocks and soil organic carbon along a chronosequence including wind-disturbed terra firme forests with different time since disturbance. Since wind is a major disturbance agent in western and central Amazon, more precise estimates of soil carbon stocks need to consider and reflect differences in tree mortality regimes at the landscape level.

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References

- Adams, J. M., Faure, H., Faure-Denard, L., McGlade, J. M., and Woodward, F. I.: Increases in terrestrial carbon storage from the Last Glacial Maximum to the present, *Nature*, 348, 711–714, 1990.
- Batjes, N. H.: Total carbon and nitrogen in the soils of the world, *Eur. J. Soil. Sci.*, 47, 151–163, 1996.
- Batjes, N. H.: Options for increasing carbon sequestration in West African soils: an exploratory study with special focus on Senegal, *Land Degrad. Dev.*, 12, 131–142, 2001.
- Beatty, S. W.: The role of treefalls and forest micro-topography in pattern formation in understory communities, Dissertation, Cornell University, Ithaca, New York, USA, 1980.
- Braga, P. I. S.: Subdivisão fitogeográfica, tipos de vegetação, conservação e inventário florístico da floresta amazônica, *Acta Amaz.*, 9, 53–80, 1979.
- Cai, W., Borlace, S., Lengaigne, M., van Rensch, P., Collins, M., Vecchi, G., Timmermann, A., Santoso, A., McPhaden, M. J., Wu, L., England, M. H., Wang, G., Guilyardi, E., and Jin, F.: Increasing the frequency of extreme El Niño events due to greenhouse warming, *Nature Climate Change*, 4, 111–116, 2014.
- Camargo, P. B., Trumbore, S. E., Martinelli, L. A., Davidson, E. A., Nepstad, D. C., and Victoria, R. L.: Soil carbon dynamics in regrowing forest of eastern Amazonia, *Glob. Change Biol.*, 5, 693–702, 1999.
- Chambers, J. Q., Higuchi, N., Schimel, J. P., Ferreira, L. V., and Melack, J. M.: Decomposition and carbon cycling of dead trees in tropical forests on the central Amazon, *Oecologia*, 122, 380–388, 2000.
- Chambers, J. Q., Higuchi, N., Teixeira, L. M., Santos, J., Laurance, S. G., and Trumbore, S. E.: Response of tree biomass and wood litter to disturbance in a central Amazon forest, *Oecologia*, 141, 596–614, 2004.
- Chambers, J. Q., Robertson, A. L., Carneiro, V. M. C., Lima, A. N. L., Smith, M., Plourde, L. C., and Higuchi, N.: Hyperspectral remote detection of niche partitioning among canopy trees driven by blowdown gap disturbances in the Central Amazon, *Oecologia*, 160, 107–117, 2009.
- Chambers, J. Q., Negrón-Juárez, R. I., Marra, D. M., Di Vittorio, A., Tews, J., Roberts, D., Ribeiro, G. H. P. M., Trumbore, S. E., and Higuchi, N.: The steady-state mosaic of disturbance and succession across an old-growth Central Amazon forest landscape, *P. Natl. Acad. Sci. USA*, 110, 3949–54, 2013.
- Coumou, D. and Rahmstorf, S.: A decade of weather extremes, *Nature Climate Change, Perspective*, 2, 491–496, doi:10.1038/NCLIMATE1452, 2012.
- Don, A., Bärwolff, M., Kalbitz, K., Andruschewitsch, R., Jungkunst, H. F., and Schulze, E.: No rapid soil carbon loss after windthrow event in the High Tatra, *For. Ecol. Manage.*, 276, 239–246, 2012.
- Espírito Santo, F. D., Keller, M., Braswell, B., Nelson, B. W., Frolking, S., and Vicente, G.: Storm intensity and old-growth forest disturbances in the Amazon region, *Geophys. Res. Lett.*, 37, 1–6, 2010.
- ESRI: ArcGIS Desktop, Release 10, Redlands, CA, Environmental Systems Research Institute, 2011.
- FAO: World reference base for soil resources, Rome, World Soil Resources Report, 60, 1998.
- Feigl, B. J., Melillo, J., and Cerri, C. C.: Changes in the origin and quality of soil organic matter after pasture introduction in Rondônia (Brazil), *Plant Soil*, 175, 21–29, 1995.
- Ferraz, J., Oht, S., and Salles, P. C.: Distribuição dos solos ao longo de dois transectos em floresta primária ao norte de Manaus (AM), in: *Pesquisas Florestais para a Conservação da Floresta e Reabilitação de Áreas Degradadas da Amazônia*, edited by: Higuchi, N., Campos, M. A. A., Sampaio, P. T. B., and dos Santos, J., Manaus, INPA, 111–143, 1998.
- Foster, D., Knight, D., and Franklin, J.: Landscape Patterns and Legacies Resulting from Large, Infrequent Forest Disturbances, *Ecosystems*, 1, 497–510, 1998.
- Garstang, M., White, S., Shugart, H. H., and Halverson, J.: Convective clouds downdrafts as the cause of large blowdowns in the Amazon Rainforest, *Meteorol. Atmos. Phys.*, 67, 199–212, 1998.
- Grimm, R., Behrens, T., Märker, M., and Elsenbeer, H.: Soil organic carbon concentrations and stocks on Barro Colorado Island, Digital soil mapping using Random Forests analysis, *Geoderma*, 146, 102–113, 2008.
- Higuchi, N., Chambers, J. Q., Santos, J., Ribeiro, R. J., Pinto, A. C. M., Silva, R. P., Rocha, R. M., and Tribuzi, E. S.: Dinâmica e balanço do carbono da vegetação primária da Amazônia Central, *Floresta*, 34, 295–304, 2004.
- Higuchi, N., Santos, J., Lima, A. J. N., Higuchi, F. G., and Chambers, J. Q. A.: A floresta amazônica e a água da chuva, *Floresta*, 41, 427–434, 2011.
- Houghton, R. A.: The annual net flux of carbon to the atmosphere from changes in land use 1850–1990, *Tellus*, 50B, 298–313, 1999.
- Huntington, T. G. and Ryan, D. F.: Whole-tree-harvesting effects on soil nitrogen and carbon, *For. Ecol. Manage.*, 31, 193–204, 1990.
- IBGE: Mapa de vegetação do Brasil, Fundação Instituto Brasileiro de Geografia e Estatística/ Ministério da Agricultura/ Instituto Brasileiro de Desenvolvimento Florestal, IBGE, Rio de Janeiro, 2004.
- Junk, W., Piedade, M., Shongärt, J., Cohn-Haft, M., Adeney, J., and Wittmann, F.: A classification of major naturally-occurring amazonian lowland wetlands, *Wetlands*, 31, 623–640, 2011.
- Kahle, M., Kleber, M., Torn, M. S., and Jahn, R.: Carbon storage in coarse and fine clay fractions of illitic soils, *Soil Sci. Soc. Am. J.*, 67, 1732–1739, 2002.

- Kramer, M. G., Sollins, P., and Sletten, R. S.: Soil carbon dynamics across a windthrow disturbance sequence in southeast Alaska, *Ecology*, 85, 2230–2244, 2004.
- Lal, R.: Soil carbon sequestration to mitigate climate change, *Geoderma*, 123, 1–22, 2004.
- Lin, K., Hamburg, S. P., Tang, S., Hsia, Y., and Lin, T.: Typhoon effects on litterfall in a subtropical forest, *Can. J. Forest. Res.*, 33, 2184–2192, 2003.
- López-Ulloa, M., Veldkamp, E., and de Koning, G. H. J.: Soil carbon stabilization in converted tropical pastures and forests depends on soil type, *Soil Sci. Soc. Am. J.*, 69, 1110–1117, 2005.
- Lugo, A. E., Applefield, M., Pool, D., and McDonald, R.: The impact of Hurricane David on the forests of Dominica. *Can. J. Forest. Res.*, 13, 201–211, 1983.
- Lugo, A. E.: Visible and invisible effects of hurricanes on forest ecosystems: an international review, *Austral Ecol.*, 33, 368–398, 2008.
- Maia, S. M. F., Ogle, S. M., Cerri, C. E. P., and Cerri, C. C.: Effect of grassland management on soil carbon sequestration in Rondônia and Mato Grosso states, Brazil, *Geoderma*, 149, 84–91, 2009.
- Maia, S. M. F., Ogle, S. M., Cerri, C. C., and Cerri, C. E. P.: Changes in soil organic carbon storage under different agricultural management systems in the Southwest Amazon Region of Brazil, *Soil Till. Res.*, 106, 177–184, 2010.
- Marin-Spiotta, E., Silver, W. L., Swanston, C. W., and Ostertag, R.: Soil organic matter dynamics during 80 years of reforestation of tropical pastures, *Glob. Change Biol.*, 15, 1584–1597, 2009.
- Marra, D. M., Chambers, J. Q., Higuchi, N., Trumbore, S. E., Ribeiro, G. H. P. M., Santos, J. dos, Negrón-Juarez, R. I., Reu, B., and Wirth, C.: Large-Scale Wind Disturbances Promote Tree Diversity in a Central Amazon Forest, *PLoS ONE* 9, e103711, doi:10.1371/journal.pone.0103711, 2014.
- Negrón-Juarez, R. I., Chambers, J. Q., Guimarães, G., Zeng, H., Raupp, C. F. M., Marra, D. M., Ribeiro, G. H. P. M., Saatchi, S., Nelson, B. W., and Higuchi, N.: Widespread Amazon forest tree mortality from a single cross-basin squall line event, *Geophys. Res. Lett.*, 37, 1–5, 2010.
- Negrón-Juárez, R. I., Chambers, J. Q., Marra, D. M., Ribeiro, G. H. P. M., Rifai, S. W., Higuchi, N., and Roberts, D.: Detection of subpixel treefall gaps with Landsat imagery in Central Amazon forests, *Remote Sens. Environ.*, 115, 3322–3328, 2011.
- Neil, C., Fry, B., Melillo, J. M., Steudler, P. A., Moraes, J. F. L., and Cerri, C. C.: Forest- and pasture-derived carbon contributions to carbon stocks and microbial respiration on tropical pasture soils, *Oecologia*, 107, 113–119, 1996.
- Neill, C., Melillo, J. M., Steudler, P. A., Cerri, C. C., de Moraes, J. F. L., Piccolo, M. C., and Brito, M.: Soil carbon and nitrogen stocks following forest clearing for pasture in the southwestern Brazilian Amazon, *Ecol. Appl.*, 7, 1216–1225, 1997.
- Nelson, B. W., Kapos, V., Adams, J. B., Oliveira, W. J., and Oscar, P. G. B.: Forest Disturbance by Large Blowdowns in the Brazilian Amazon, *Ecol. Soc. Am.*, 75, 853–858, 1994.
- Neumann-Cosel, L., Zimmermann, B., Jefferson, S., van Breugel, M., and Helmut, E.: Soil carbon dynamics under young tropical secondary forests on former pastures – A case study from Panama, *Forest Ecol. Manag.*, 261, 1625–1633, 2011.
- Ngo, K. M., Turner, B. L., Muller-Landau, H. C., Davies, S. J., Larjavaara, M., Hassan, N. F. bin N., Lum, S.: Carbon stocks in primary and secondary tropical forests in Singapore, *Forest Ecol. Manag.*, 296, 81–89, 2013.
- Ostertag, R., Scatena, F. N., and Silver, W. L.: Forest floor decomposition following hurricane litter inputs in several Puerto Rican forests, *Ecosystems*, 6, 261–273, 2003.
- Peterson, C. J., Carson, W. P., McCarthy, B. C., and Pickett, S. T. A.: Microsite variation in soil dynamics within newly created treefall pits and mounds, *OIKOS*, 58, 39–46, 1990.
- Powers, J. S. and Schlesinger, W. H.: Relationships among soil carbon distributions and biophysical factors at nested spatial scales in rain forests of northeastern Costa Rica, *Geoderma*, 109, 165–190, 2002.
- Powers, J. S. and Veldkamp, E.: Regional variation in soil carbon and $\delta^{13}\text{C}$ in forests and pastures of northeastern Costa Rica, *Biogeochemistry*, 72, 315–336, 2005.
- Putz, F. E.: Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama, *Ecology*, 64, 1069–1074, 1983.
- Queré, C. L., Raupach, M. R., Canadell, J. G., and Marland, G.: Trends in the sources and sinks of carbon dioxide, *Nat. Geosci.*, 2, 831–836, 2009.
- Quesada, C. A., Lloyd, J., Schwarz, M., Patiño, S., Baker, T. R., Czimczik, C., Fyllas, N. M., Martinelli, L., Nardoto, G. B., Schmerler, J., Santos, A. J. B., Hodnett, M. G., Herrera, R., Luizão, F. J., Arneith, A., Lloyd, G., Dezzio, N., Hilke, I., Kuhlmann, I., Raessler, M., Brand, W. A., Geilmann, H., Moraes Filho, J. O., Carvalho, F. P., Araujo Filho, R. N., Chaves, J. E., Cruz Junior, O. F., Pimentel, T. P., and Paiva, R.: Variations in chemical and physical properties of Amazon forest soils in relation to their genesis, *Biogeosciences*, 7, 1515–1541, doi:10.5194/bg-7-1515-2010, 2010.
- Quesada, C. A., Lloyd, J., Anderson, L. O., Fyllas, N. M., Schwarz, M., and Czimczik, C. I.: Soils of Amazonia with particular reference to the RAINFOR sites, *Biogeosciences*, 8, 1415–1440, doi:10.5194/bg-8-1415-2011, 2011.
- Quesada, C. A., Phillips, O. L., Schwarz, M., Czimczik, C. I., Baker, T. R., Patiño, S., Fyllas, N. M., Hodnett, M. G., Herrera, R., Almeida, S., Alvarez Dávila, E., Arneith, A., Arroyo, L., Chao, K. J., Dezzio, N., Erwin, T., di Fiore, A., Higuchi, N., Honorio Coronado, E., Jimenez, E. M., Killeen, T., Lezama, A. T., Lloyd, G., López-González, G., Luizão, F. J., Malhi, Y., Monteagudo, A., Neill, D. A., Núñez Vargas, P., Paiva, R., Peacock, J., Peñuela, M. C., Peña Cruz, A., Pitman, N., Priante Filho, N., Prieto, A., Ramírez, H., Rudas, A., Salomão, R., Santos, A. J. B., Schmerler, J., Silva, N., Silveira, M., Vásquez, R., Vieira, I., Terborgh, J., and Lloyd, J.: Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate, *Biogeosciences*, 9, 2203–2246, doi:10.5194/bg-9-2203-2012, 2012.
- R Core Team: R: A language and environment for statistical computing, available at: <http://www.r-project.org> (last access: 1 October 2015), 2014.
- Rhoades, C. C., Eckert, G. E., and Coleman, D. C.: Soil carbon differences among forest, agriculture, and secondary vegetation in lower montane Ecuador, *Ecol. Appl.*, 10, 497–505, 2000.
- Ribeiro, G. H. P. M., Suwa, R., Marra, D. M., Lima, A. J. N., Kajimoto, T., Ishizuka, M., and Higuchi, N.: Allometry for Juvenile Trees in an Amazonian Forest after Wind Disturbance, *JARQ-Jpn. Agr. Res. Q.*, 48, 213–219, 2014.

- Schaetzl, R. J., Burns, S. F., Johnson, D. L., and Small, T. W.: Tree uprooting: review of impacts on forest ecology, *Vegetatio*, 79, 165–176, 1989.
- Silva, R. P. da, Nakamura, S., Azevedo, C. de, Chambers, J., Rocha, R. de M., Pinto, C., dos Santos, J., and Higuchi, N.: Use of metallic dendrometers for individual diameter growth patterns of trees at Cuieiras river basin, *Acta Amaz.*, 33, 67–84, 2003.
- Telles, E. de C. C., Camargo, P. B. de, Martinelli, L. A., Trumbore, S. E., Costa, E. S. da, Santos, J. dos, Higuchi, N., and Oliveira Jr., R. C.: Influence of soil texture on carbon dynamics and storage potential in tropical forest soils of Amazonia, *Global Biogeochem. Cy.*, 17, 1040, doi:10.1029/2002GB001953, 2003.
- Torn, M. S., Trumbore, S. E., Chadwick, O. A., Vitousek, P. M., and Hendricks, D. M.: Mineral control of soil organic carbon storage and turnover, *Nature*, 389, 3601–3603, 1997.
- Trumbore, S. E., Davidson, E. A., De Camargo, P. B., Nepstad, D. C., and Martinelli, L. A.: Belowground cycling of carbon in forests and pastures of Eastern Amazonia, *Global Biogeochem. Cy.*, 9, 515–528, 1995.
- Turner, M., Baker, W., Peterson, C., and Peet, R.: Factors influencing succession: lessons from large, infrequent natural disturbances, *Ecosystems*, 1, 511–523, 1998.
- Veldkamp, E., Becker, A., Schwendenmann, L., Clark, D. A., and Schulte-Bisping, H.: Substantial labile carbon stocks and microbial activity in deeply weathered soils below a tropical wet forest, *Glob. Change Biol.*, 9, 1171–1184, 2003.
- Vitousek, P. M. and Denslow, J. S.: Nitrogen and phosphorous availability in treefall gaps of a lowland tropical rainforest, *J. Ecol.*, 74, 1167–1178, 1986.
- Wickham, H.: *ggplot2: elegant graphics for data analysis*, Springer New York., 2009.

3. ORIGINAL CONTRIBUTIONS

3.3. Paper 3

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Predicting biomass of hyperdiverse and structurally complex central Amazonian forests – a virtual approach using extensive field data

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Abstract. Old-growth forests are subject to substantial changes in structure and species composition due to the intensification of human activities, gradual climate change and extreme weather events. Trees store ca. 90 % of the total aboveground biomass (AGB) in tropical forests and precise tree biomass estimation models are crucial for management and conservation. In the central Amazon, predicting AGB at large spatial scales is a challenging task due to the heterogeneity of successional stages, high tree species diversity and inherent variations in tree allometry and architecture. We parameterized generic AGB estimation models applicable across species and a wide range of structural and compositional variation related to species sorting into height layers as well as frequent natural disturbances. We used 727 trees (diameter at breast height ≥ 5 cm) from 101 genera and at least 135 species harvested in a contiguous forest near Manaus, Brazil. Sampling from this data set we assembled six scenarios designed to span existing gradients in floristic composition and size distribution in order to select models that best predict AGB at the landscape level across successional gradients. We found that good individual tree model fits do not necessarily translate into reliable predictions of AGB at the landscape level. When predicting AGB (dry mass) over scenarios using our different mod-

els and an available pantropical model, we observed systematic biases ranging from -31 % (pantropical) to $+39$ %, with root-mean-square error (RMSE) values of up to 130 Mg ha^{-1} (pantropical). Our first and second best models had both low mean biases (0.8 and 3.9 %, respectively) and RMSE (9.4 and 18.6 Mg ha^{-1}) when applied over scenarios. Predicting biomass correctly at the landscape level in hyperdiverse and structurally complex tropical forests, especially allowing good performance at the margins of data availability for model construction/calibration, requires the inclusion of predictors that express inherent variations in species architecture. The model of interest should comprise the floristic composition and size-distribution variability of the target forest, implying that even generic global or pantropical biomass estimation models can lead to strong biases. Reliable biomass assessments for the Amazon basin (i.e., secondary forests) still depend on the collection of allometric data at the local/regional scale and forest inventories including species-specific attributes, which are often unavailable or estimated imprecisely in most regions.

1 Introduction

Allometries describe how relationships between different dimensions (e.g., length, surface area and weight) of organisms change non-proportionally as they grow (Huxley and Teissier, 1936). The lack of proportionality arises from the fact that organisms change their shape while they grow (i.e., the dimensions differ in their relative growth rates). As one important application, allometric relationships can be used to relate simple dimensions of trees (e.g., diameter at breast height, DBH, or tree total height, H) to dimensions more relevant for forest managers and basic ecological research, such as wood volume or whole tree biomass (Brown et al., 1989; Higuchi et al., 1998; Saldarriaga et al., 1998).

Allometric relationships and biomass estimation models can differ substantially between different tree species, especially in species-rich regions with a high variation in tree sizes and architectures such as in the tropical rainforests (Banin et al., 2012; Nelson et al., 1999; Poorter et al., 2003). This variation reflects differences in growth strategy and life history, such as tree species occupying different strata when mature (e.g., understory, canopy or emergent species), successional groups (SGs) (e.g., pioneer or light-demanding species, such as *Cecropia* spp. and *Pourouma* spp., in contrast to late-successional or shade-tolerant species, such as *Cariniana* spp. and *Dipteryx* spp.) or environmental microsites (Clark and Clark, 1992; King, 1996; Swaine and Whitmore, 1988).

Important and highly variable architectural attributes of tropical tree species include stem shape (e.g., slender to stout form), branch form and branching intensity (e.g., plagiotropic, orthotropic and unbranched), crown contour (e.g., round, elongated and irregular), crown position (e.g., understory, canopy and emergent), maximum DBH and H (Hallé, 1974; Hallé et al., 1978). In addition, there is large variation in growth rate (the speed at which a certain tree volume is filled) and consequently in wood anatomy among species (Bowman et al., 2013; da Silva et al., 2002; Worbes et al., 2003). Wood density (WD), which is particularly important for biomass estimation, varies significantly across regions (Muller-Landau, 2004) and can differ between species by more than an order of magnitude (Chave et al., 2006). Given these sources of variation, it is not surprising that different allometries were reported when comparing species (Nelson et al., 1999), successional stages (Ribeiro et al., 2014), ontogenies (Sterck and Bongers, 1998) and regions (Lima et al., 2012). Unfortunately, transferring such estimation models to other contexts – other species, size ranges, life stages, sites or successional stages – typically leads to predictions that deviate strongly from observations, especially when the sampling design does not allow the selection of relevant data for proper estimation of the parameters of interest (Gregoire et al., 2016) or when predictor ranges are limited or neglected (Clark and Kellner, 2012; Sileshi, 2014).

In temperate and boreal forests, the size, ontogeny and site variations have been captured by the development of generic species-specific biomass estimation models (Wirth et al., 2004; Wutzler et al., 2008) based on data from hundreds of individuals from a single tree species. However, this approach is prohibitive in the tropics where thousands of tree species coexist (Slik et al., 2015; ter Steege et al., 2013). Instead, the challenge is to develop generic local or regional formulations that also generalize across species (Higuchi et al., 1998; Lima et al., 2012; Nelson et al., 1999; Saldarriaga et al., 1998). Ideally, they contain predictor variables that (1) jointly capture a large fraction of the variation induced by the underlying morphological and anatomical gradients and (2) are still easy enough to obtain or measure.

The development and application of such generic models pose a number of challenges. Finding the appropriate model structure and estimating the model parameters requires a data set with a large number of individual measurements containing the variable of interest (here aboveground biomass, or AGB) and the predictor variables (i.e., DBH, H , species' SGs and WD). Importantly, the data set should ideally cover all possible real-world combinations of predictor values in order to avoid error-prone extrapolations and unreliable predictions. However, in multiple regression models, this pre-condition is rarely met, not even by large design matrices.

The ultimate prediction is typically at the landscape level, which requires summing up individual predictions for several thousands of trees varying in size and species assignment. The larger the variation of predictor values within a stand, the higher is the likelihood that extrapolation errors occur. This calls for a validation at the landscape level, which requires a plot-based harvest method. For obvious reasons, this has rarely been attempted (Carvalho Jr. et al., 1995; Chambers et al., 2001; Higuchi et al., 1998; Lima et al., 2012).

Notable effort has already been made to parameterize global/pantropical AGB estimation models (Brown et al., 1989; Chave et al., 2005, 2014). Commonly, these models are derived using several different data sets, each of which is comprised of relatively few trees and species. Although few opportunities exist to evaluate these models at the landscape level, they are used worldwide in different contexts, sites and across successional stages. For instance, the pantropical model from Chave et al. (2005) (DBH + WD as predictors) overestimated biomass when tested against trees in Gabon (Ngomanda et al., 2014), Peru (Goodman et al., 2014), Colombia (Alvarez et al., 2012) and Brazil (Lima et al., 2012), but it also underestimated the AGB in mixed-species Atlantic Forest stands in Brazil (Nogueira Jr. et al., 2014).

The availability of such generic AGB estimation models applicable to many species and contexts is particularly important for management, ecological and biogeochemical research in tropical forest landscapes that encompass a particularly wide spectrum of floristic and structural variation. For example, in the central Amazonian terra firme forests, 1 ha

of old-growth forest can hold more than 280 tree species ($\text{DBH} \geq 10$ cm) (de Oliveira and Mori, 1999) with a wide range of architectures and anatomies (Braga, 1979; Muller-Landau, 2004; Ribeiro et al., 1999). At the landscape scale, this region encompasses a mosaic of successional stages promoted by windthrows (Asner, 2013; Chambers et al., 2013; Negrón-Juárez et al., 2010; Nelson et al., 1994). Disturbed areas include a diverse set of species representing the range from new regrowth to adult survivors, thereby including different SGs (pioneers, mid- and late-successional species), tree sizes and with a broader range of architectures than old-growth forests (Chambers et al., 2009; Marra et al., 2014; Ribeiro et al., 2014). Once floristic composition changes and structural gradients increase to this extent, allometry becomes more complex and reliable landscape-level biomass estimates rely on well-designed and well-tested generic biomass models.

We report here a novel data set of 727 trees harvested in a contiguous terra firme forest near Manaus, Brazil. This data set includes biomass measurements from 101 genera and at least 135 tree species that vary in architecture and are from different SGs (pioneers, mid- and late successional). These trees span a wide range of DBH (from 5 to 85 cm), H (from 3.9 to 34.5 m) and WD (from 0.348 to 1.000 g cm^{-3}). We used this data set to parameterize generic AGB estimation models for central Amazonian terra firme forests applicable across species and a wide range of structural and compositional variation (i.e., secondary forests), using various subsets of the available predictors; i.e., size (DBH and H), SGs and WD.

We next evaluated our models, as well as the pantropical model from Chave et al. (2014) at the landscape level using a virtual approach. We created scenarios of simulated 100 1 ha forest plots by assembling subsets of the 727 known-biomass trees in our data set. These scenarios were designed to span gradients in (1) floristic composition, by assembling stands with specific proportions of pioneer, mid- and late-successional species, and (2) size distributions of trees. We compared the known biomass of these forest assemblage scenarios to predictions based on the generic models, with the goal of answering the following questions.

1. Which variance modeling approach and combinations of predictors produced the best individual tree biomass estimation model?
2. Which model most reliably predicted AGB at landscape level, i.e., across successional gradients?

We expected that the best model, the one reducing both mean deviation and error of single and landscape-level biomass prediction, would require species-specific variables as well as an additional parameter allowing the modeling of heteroscedastic variance. Our approach and the independence of our data set allowed us to evaluate whether it is still important to build local/regional models or whether available

pantropical/global models are suitable for landscape biomass assessments – under the assumption that they predict biomass satisfactorily over all sorts of tropical forest types and successional stages.

2 Material and methods

2.1 Study site

Our study site is located at the Estação Experimental de Silvicultura Tropical (EEST), a 21 000 ha research reserve (Fig. 1) managed by the Laboratório de Manejo Florestal (LMF) of the Brazilian Institute for Amazon Research (INPA), Manaus, Amazonas, Brazil ($2^{\circ}56' \text{ S}$, $60^{\circ}26' \text{ W}$). Averaged annual temperature in Manaus was 26.7°C for the 1910–1983 period (Chambers et al., 2004). Averaged annual precipitation ca. 50 km east of our study site was 2610 mm for the 1980–2000 period (da Silva et al., 2003) with annual peaks of up to 3450 mm (da Silva et al., 2002). From July to September there is a distinct dry season with usually less than 100 mm of rain per month. Topography is undulating with elevation ranging from ca. 50 to 140 m a.s.l. Soils on upland plateaus and the upper portions of slopes have high clay content (Oxisols), while soils on slope bottoms and valleys have high sand content (Spodosols) and are subject to seasonal flooding (Telles et al., 2003). In contrast to floodplains (i.e., igapó and várzea) associated with large Amazonian rivers (e.g., Rio Negro and Rio Amazonas), valleys associated with streams and low-order rivers can be affected by local rain events and thus have a polymodal and unpredictable flood-pulse pattern with many short and sporadic inundations mainly during the rainy season (Junk et al., 2011).

The EEST is mainly covered by a contiguous closed canopy old-growth terra firme forest with high tree species diversity and dense understory (Braga, 1979; Marra et al., 2014). The terra firme forests are among the predominant forest types in the Brazilian Amazon (Braga, 1979; Higuchi et al., 2004) and ca. 93 % of the total plant biomass is stored in trees with $\text{DBH} \geq 5$ cm (Lima et al., 2012; da Silva, 2007). The tree density ($\text{DBH} \geq 10$ cm) in the EEST is 593 ± 28 trees ha^{-1} (mean ± 99 % confidence interval) (Marra et al., 2014). Trees larger than 100 cm in DBH are rare (< 1 individual ha^{-1}) and those with $\text{DBH} > 60$ cm accounted for only 16.7 % of the AGB (Vieira et al., 2004). In the study region, tree mortality rates can be influenced by variations in topography (Marra et al., 2014; Toledo et al., 2012). Floristic composition and species demography can also vary with the vertical distance from drainage (Schiatti et al., 2013).

2.2 Allometric data

We used data from 727 trees harvested in this region (dos Santos, 1996; da Silva, 2007), each with measured biomass and predictor variables. This data set comprised 101 genera and at least 135 species with $\text{DBH} \geq 5.0$ cm (Table 1; all data

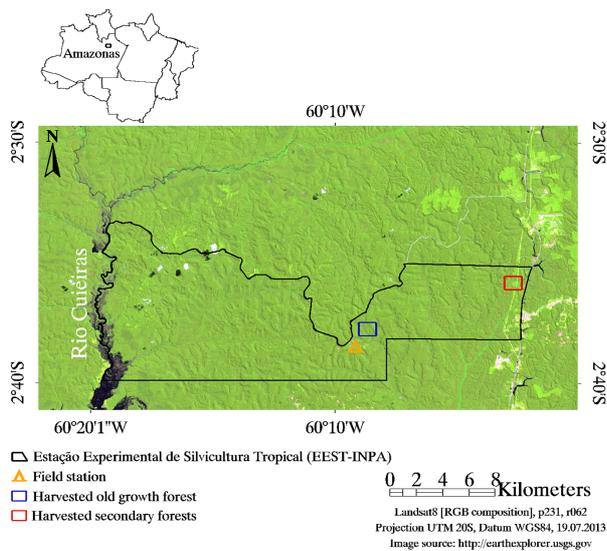


Figure 1. Study site of terra firme forest near Manaus, Amazonas, Brazil.

are given in Table S1 in the Supplement). The trees were harvested through the plot-based harvest method in an old-growth forest and in two contiguous secondary forests (14-year-old regrowth following slash and burn and 23-year-old regrowth following a clear cut) (Fig. 1). Rather than an individual selection, our plot-based method relies on the harvesting of all trees found in selected plots. This method allows for a valid/faithful representation of the DBH distribution of the target forests and a landscape validation of the fitted models (Higuchi et al., 1998; Lima et al., 2012).

Before selecting plots, we surveyed both the old-growth and secondary forests to assure that no strong differences in structure and floristic composition existed and that the selected patches were representative of our different successional stages. In the old-growth forest the trees were harvested in eight plateau and three valley plots ($10\text{ m} \times 10\text{ m}$) randomly selected within an area of 3.6 ha (da Silva, 2007). In each of the secondary forests the trees were harvested in five plots ($20\text{ m} \times 20\text{ m}$), each randomly selected within a 1 ha plateau area (dos Santos, 1996; da Silva, 2007). By including trees from secondary forests we were able to increase the variation in floristic composition and consequently the range of species-related variation in architecture and allometry (Table 1 and Table S1). Since our secondary forests were inserted in the contiguous matrix from which old-growth plots were sampled, we also controlled for the effects of important drivers of tree allometry and architecture, such as variations in environmental conditions (e.g., soil, precipitation rates and distribution), forest structure and wood density (Banin et al., 2012); the last is intrinsically related to variation in floristic composition.

Table 1. Summary of the data set applied in this study. Trees were harvested in the Estação Experimental de Silvicultura Tropical, a contiguous terra firme forest reserve near Manaus, Amazonas, Brazil.

Variables	Old-growth forest	Secondary forest (23 years old)	Secondary forest (14 years old)
NT	131	346	250
SR	82	63	51
DBH	5.0–85.0	5.0–37.2	5.0–33.1
H	5.9–34.5	3.9–27.0	9.0–15.5
WD	0.348–0.940	0.389–1.000	0.395–1.000
AGB	8.3–7509.1	5.4–1690.2	7.5–1562.8

Variables: number of trees (NT), species richness (SR), diameter at breast height (DBH) (cm), tree total height (H) (m), wood density (WD) (g cm^{-3}) and aboveground biomass (AGB) (dry mass in kilograms).

Trees were harvested at ground level. For each tree, the DBH (cm), H (m) and fresh mass (kg) were recorded in the field by using a diameter tape, a meter tape and a mechanical metal scale ($300\text{ kg} \times 200\text{ g}$), respectively. The DBH was measured before, while H was measured after harvesting. For trees with buttresses or irregular trunk shape, the diameter was measured above these parts. Each tree component (i.e., stem, branches and leaves) was weighted separately. For large trees, stems were cut into smaller sections before weighing. The mass of sawdust was collected and weighted together with its respective stem section. Leaves and reproductive material, when available, were collected to allow species identification according to the APGIII system (Stevens, 2012). Botanical samples were incorporated in the EEST collection. The water content for each tree was determined from three discs (2–5 cm in thickness), collected from the top, middle and bottom of the bole, and samples (ca. 2 kg) of small branches and leaves. The samples were oven dried at $65\text{ }^\circ\text{C}$ to constant dry mass. The dry mass data were calculated by using the corresponding water content of each component (Lima et al., 2012; da Silva, 2007). Dry mass for each tree was used for subsequent model fits and comparisons.

2.3 Species' architecture attributes

Each of our tree species or genera was assigned to one of three SGs known to vary in their architecture, namely pioneer, mid- and late-successional groups. To make this assignment, we considered several attributes related to species' architecture (i.e., shape and life history), growth position (i.e., stratum), morphology, wood density and ecology (Table S1 and Table S2). We validated this approach by checking our assignments against those of classic studies (Clark and Clark, 1992; Denslow, 1980; Saldarriaga et al., 1998; Shugart and West, 1980; Swaine and Whitmore, 1988), local/regional studies conducted in the Amazon (Amaral et al., 2009; Chambers et al., 2009; Kammesheidt, 2000; Marra

et al., 2014) and species descriptions available in the Missouri Botanical Garden (<http://www.tropicos.org>), species-Link (<http://www.splink.cria.org.br>) and Lista de Espécies da Flora do Brasil (<http://www.floradobrasil.jbrj.gov.br/>). More importantly, we considered empirical field observations, architectural information from our data set and data for species presence/absence from a network of permanent plots representing a wide range of successional stages in central Amazon (Table S2). This network includes plots in old-growth forests (LMF unpublished data (census from 1996 to 2012); da Silva et al., 2002), secondary forests (Carvalho Jr. et al., 1995; dos Santos, 1996), and small and large canopy gaps (\geq ca. 2000 m²) created by windthrows that are 4, 7, 14, 17, 24 and 27 years old (LMF unpublished data; Marra et al., 2014).

Since reported WD values for the same species or genera can vary strongly among different studies (Chave et al., 2006) and sites (Muller-Landau, 2004), we compiled WD values mainly from studies carried out in the Brazilian Amazon (Chave et al., 2009; Fearnside, 1997; Laurance et al., 2006; Nogueira et al., 2005, 2007). For species where WD data were not available for the Brazilian Amazon, we considered studies from other Amazonian regions (Chave et al., 2009). For species where no published WD was available, or where the identification was carried out to the genus level (63 in total), we used the mean value for all species from the same genus occurring in central Amazon. For trees identified only to the family level (seven in total), we used the mean value of genera from that family excluding those not reported in the study region (Table S1).

2.4 Statistical analyses

2.4.1 Individual tree biomass estimation model fits

The AGB estimation models we applied varied in the number and combination of our predictor variables (eight combinations/series) as well as the strategy of modeling the variance (three model types – see below), yielding a set of 24 candidate models (Table 2). We used DBH (cm), WD (g cm⁻³) and H (m) as predictors. Furthermore, we used the species' SG assignment as a “categorical predictor” (factor 1 is pioneer, 2 is mid-successional and 3 is late-successional species), thereby representing functional diversity along a main axis of tree successional strategies, functional and architectural variation. Depending on the model-type parameters, the continuous variables were allowed to vary for capturing the successional aspects of functional diversity. We consider the SG grouping factor as integral part of the model. Fitting all SGs in one model in an Markov chain Monte Carlo context is different than fitting separate models because the joint model also absorbs the covariance structure of the parameters across groups, especially in models where not all parameters are allowed to vary among SGs.

We tested variables for collinearity by calculating the variance inflation factor (VIF). A conservative VIF > 2.0 in-

dicates significant collinearity among variables (Graham, 2003; Petraitis et al., 1996). Model series 1–4 had VIF < 1.5 (Table 2), which indicated no significant collinearity among predictors. For model series 5–8, we found VIF > 2.0 for DBH and H , which indicates significant collinearity between these two variables. This pattern was previously reported for other data sets from Amazon and other tropical regions (Lima et al., 2012; Ribeiro et al., 2014; Sileshi, 2014).

We fit models representing the eight different predictor combinations to our entire data set of 727 trees using three variance modeling approaches: nonlinear least square (NLS), ordinary least square with log-linear regression (OLS) and a nonlinear approach in which we modeled the heteroscedastic variance of the data set (MOV). In the MOV approach we modeled the variance as a function of DBH with a normally distributed residual error:

$$\varepsilon_i = N(\hat{y}_i, \sigma_i), \quad (1)$$

where i is the subscript for individuals ($i = 1, \dots, n$) and σ_i is modeled with a heteroscedastic variance according to

$$\sigma_i = c_i \cdot \text{DBH}_i^{c_2}. \quad (2)$$

Model series 1 (M11, M12 and M13) used DBH as the sole predictor (Table 2). For model series 2 (M21, M22 and M23), we allowed the b regression parameters and c heteroscedastic variance to vary according to the SG assignment (1, 2 or 3). This approach allowed us to account for differences among the SGs without splitting the data set into three different groups. This method has increased analytical power and allowed us to assess the relationships between tree allometry and architecture.

For model series 3 (M31, M32 and M33), we ignored the SG assignment but introduced WD (which did not correlate strongly with SG). For model series 4 (M41, M42 and M43) we allowed each SG to have its own wood density effect. For model series 5 and 6, we replaced the WD with H . In model series 5 (M51, M52 and M53), we restricted the SG variation of b and c , while in series 6 (M61, M62 and M63) we allowed these parameters to vary according to SG. For model series 7 (M71, M72 and M73), we combined DBH, H and WD but restricted the SG variation of b and c . Finally, for model series 8 (M81, M82 and M83), we combined DBH, H and WD and allowed b and c to vary with SG (Table 2).

In contrast to prior approaches, we did not test models based on compound (e.g., $\log[\text{AGB}] \sim \log[b1] + b2[\log\text{DBH}^2\text{HWD}]$) or quadratic/cubic derivatives (e.g., $\log[\text{AGB}] \sim \log[b1] + b2[\log\text{DBH}] + b3[\log\text{DBH}^2] + b4[\log\text{DBH}^3]$) (Brown et al., 1989; Chave et al., 2005, 2014; Ngomanda et al., 2014). These structures would have limited our ability to include biological variation by defining SG-specific parameters for DBH, H and WD separately.

We fit the AGB estimation models with non-informative uniform priors using WinBUGS 1.4.3 (Lunn et al., 2000; Spiegelhalter et al., 2002). For each model, three chains were

Table 2. Tested equations for estimating aboveground tree biomass (AGB) in a terra firme forest near Manaus, Amazonas, Brazil.

Series	Model	Equation	Variance modeling (range) approach	VIF
1	M11	$AGB \sim b1DBH^{b2}$	NLS	1
	M12	$\log(AGB) \sim \log(b1) + b2(\log DBH)$	OLS	1
	M13	$AGB \sim b1DBH^{b2}$	MOV	
2	M21	$AGB \sim b1[SG]DBH^{b2[SG]}$	NLS	1.001
	M22	$\log(AGB) \sim \log(b1[SG]) + b2(\log DBH[SG])$	OLS	1.005
	M23	$AGB \sim b1[SG]DBH^{b2[SG]}$	MOV	
3	M31	$AGB \sim b1DBH^{b2}WD^{b3}$	NLS	1.007
	M32	$\log(AGB) \sim \log(b1) + b2(\log DBH) + b3(\log WD)$	OLS	1.017
	M33	$AGB \sim b1DBH^{b2}WD^{b3}$	MOV	
4	M41	$AGB \sim b1[SG]DBH^{b2[SG]}WD^{b3[SG]}$	NLS	1.016–1.468
	M42	$\log(AGB) \sim \log(b1[SG]) + b2(\log DBH[SG]) + b3(\log WD[SG])$	OLS	1.017–1.395
	M43	$AGB \sim b1[SG]DBH^{b2[SG]}WD^{b3[SG]}$	MOV	
5	M51	$AGB \sim b1DBH^{b2}H^{b3}$	NLS	3.382
	M52	$\log(AGB) \sim \log(b1) + b2(\log DBH) + b3(\log H)$	OLS	3.342
	M53	$AGB \sim b1DBH^{b2}H^{b3}$	MOV	
6	M61	$AGB \sim b1[SG]DBH^{b2[SG]}H^{b3[SG]}$	NLS	1.019–3.439
	M62	$\log(AGB) \sim \log(b1[SG]) + b2(\log DBH[SG]) + b3(\log H[SG])$	OLS	1.010–3.360
	M63	$AGB \sim b1[SG]DBH^{b2[SG]}H^{b3[SG]}$	MOV	
7	M71	$AGB \sim b1DBH^{b2}H^{b3}WD^{b4}$	NLS	1.014–3.428
	M72	$\log(AGB) \sim \log(b1) + b2(\log DBH) + b3(\log H) + b4(\log WD)$	OLS	1.038–3.469
	M73	$AGB \sim b1DBH^{b2}H^{b3}WD^{b4}$	MOV	
8	M81	$AGB \sim b1[SG]DBH^{b2[SG]}H^{b3[SG]}WD^{b4[SG]}$	NLS	1.523–3.624
	M82	$\log(AGB) \sim \log(b1[SG]) + b2(\log DBH[SG]) + b3(\log H[SG]) + b4(\log WD[SG])$	OLS	1.422–3.547
	M83	$AGB \sim b1[SG]DBH^{b2[SG]}H^{b3[SG]}WD^{b4[SG]}$	MOV	

Predictors: diameter at breast height (DBH) (cm), species' successional group (SG) (pioneers, mid- and late successional), tree total height (H) (m) and wood density (WD) (g cm^{-3}). Variance modeling approach: nonlinear least square (NLS), ordinary least square with log-linear regression (OLS) and nonlinear with modeled variance (MOV). Since NLS and MOV rely on the same equation, they have analogue variation inflation factor values (VIF).

run in parallel, and convergence of the posterior distribution for each parameter was assessed by convergence of the ratio of pooled to mean within-chain central 80 % intervals to 1 or by the stability of both intervals (Brooks and Gelman, 1998; Brooks and Roberts, 1998).

To select the best model we calculated the deviance information criterion (DIC). The DIC is a generalization of Akaike's information criterion and consists of a cross-validatory term that expresses both the goodness of the fit and the models' complexity. The lower the value the higher the predictive ability and parsimony (Spiegelhalter et al., 2002). We also checked whether the 95 % credible intervals of the parameter's posterior distributions excluded 0. However, we did not attempt to test the null hypothesis that a particular parameter is 0 (Bolker et al., 2013; Bolker, 2008). Contrasts were evaluated by monitoring differences between parameters or predictions based on their posterior distribution. For communicating the results we consider two parameters significantly different if the 95 % credible interval of the posterior distribution of their difference does not include 0.

To allow for comparisons of different model structures and approaches with the available literature, we calculated the coefficient of determination (R^2), the adjusted coefficient of

determination (R^2_{adj}) and the relative standard error ($S_{yx\%}$). The $S_{yx\%}$ was calculated as follows:

$$S_{yx\%} = \left(\frac{2s}{\hat{y}\sqrt{N}} \right), \quad (3)$$

where s , \hat{y} and N are the standard deviation of the regression, the mean of the focal independent variable and the number of observations, respectively. As in all allometric data sets relating linear to volume-proportional data, there is indeed heteroscedasticity in our data, which restricts the use of the $S_{yx\%}$ for model selection. Nonetheless, this measure is prescribed for assessing models' uncertainty (IPCC, 2006) and is commonly used (Chave et al., 2014; Lima et al., 2012; Ribeiro et al., 2014; Sileshi, 2014).

For the OLS approach including log-transformed variables, we calculated the $S_{yx\%}$ using untransformed data. To correct for the bias introduced by the log-transformed data, a correction factor (CF) was calculated as follows:

$$CF = \exp\left(\frac{SSE^2}{2}\right), \quad (4)$$

where SSE is the standard error of the estimate (Sprugel, 1983).

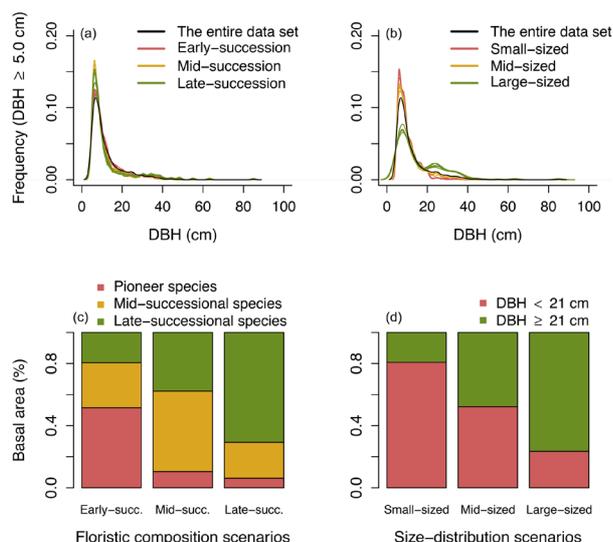


Figure 2. Sampling schemes applied to assemble the six forest scenarios designed to reflect changes in floristic composition and size distribution of trees, typical of central Amazonian terra firme forests.

2.5 Landscape-level biomass predictions across scenarios

To evaluate the models outlined in Table 2, we predicted AGB at the landscape level for six forest scenarios assembled by a stratified random selection of individual trees from our data set of 727 trees. Our scenarios were designed to span a successional gradient created by natural disturbances in which the interaction of tree mortality intensity and species vulnerability and resilience produce complex communities varying in species composition and size distribution of trees (Chambers et al., 2009, 2013; Marra et al., 2014). We assembled three scenarios to reflect variations in floristic composition and three scenarios to reflect variations in size distribution. Each scenario was sampled 100 times, resulting in 100 1 ha plots per scenario with different combination of trees randomly (with replacement) assembled according to the scenario-specific design principles.

To address the effect of variations in floristic composition on estimated AGB, we created scenarios where we varied the proportion of pioneer, mid- and late-successional species. The early-successional scenario comprised 50 % from trees sampled randomly from the species classified as pioneer, 40 % from mid- and 10 % from late-successional species (as survivors of disturbances). The mid-successional scenario comprised 10 % from trees sampled randomly from the species classified as pioneer, 70 % from mid- and 20 % from late-successional species. The late-successional scenario comprised 10 % from trees sampled randomly from the species classified as pioneer, 40 % from mid- and 50 % from late-successional species (Fig. 2a and c). We con-

strained our floristic composition scenarios to a stem density of 1255 trees ha^{-1} ($\text{DBH} \geq 5$ cm) typical for the old-growth terra firme forests at the EEST (Lima et al., 2007; Marra et al., 2014; Suwa et al., 2012).

To address variations in size distribution, we varied the proportion of small and big trees fixing a threshold value of 21 cm, which represents the mean DBH (trees with $\text{DBH} \geq 10$ cm) of our studied forest (Marra et al., 2014). Our size-distribution scenarios included a small-sized stand, with 90 % from small ($\text{DBH} < 21$ cm) and 10 % from big trees ($\text{DBH} \geq 21$ cm); a mid-sized stand with equal numbers of trees smaller and greater than or equal to 21 cm in DBH; and a large-sized stand, with 10 % small and 90 % big trees (Fig. 2b and d). As for our floristic composition scenarios, in order to produce reliable size-distributions, we constrained our sampling effort to a basal area value of $30.3 \text{ m}^2 \text{ ha}^{-1}$ also typical of our studied old-growth forest (trees with $\text{DBH} \geq 5$ cm) (Marra et al., 2014; Suwa et al., 2012). Both our floristic and size-distribution scenarios produced the J -inverse distribution pattern, typical of tropical forests (Clark and Clark, 1992; Denslow, 1980).

AGB at the landscape level was determined by adding up the measured AGB for “sampled” trees in each scenario. To test how well our biomass estimation models predicted the AGB at the stand level, we related biases and root-mean-square error (RMSE). In order to assess the accuracy of different predictions in the context of models’ uncertainty, we additionally reported the overall performance of the tested models along all forest scenarios. When doing so, we present the bias and RMSE in the same unit (Mg), which allow for assessing the magnitudes of deviations in model predictions (Gregoire et al., 2016; McRoberts and Westfall, 2014). Because data on tree height are normally unavailable or estimated imprecisely in Amazonian forest inventories, we focused on models including only DBH, WD and SG as predictors (model series 1–4). In addition to the “internal evaluation” of our models, we tested the pantropical model from Chave et al. (2014):

$$\widehat{\log \text{AGB}} \sim -1.803 - 0.976E + 0.976[\log \text{WD}] + 2.673[\log \text{DBH}] - 0.0299[\log \text{DBH}]^2, \quad (5)$$

which was parameterized with data from 4004 trees ($\text{DBH} \geq 5$ cm) harvested in 53 old-growth and five secondary forests. This model has DBH, H (estimated from a $\text{DBH} : H$ relationship), WD and a variable E (environmental stress) as predictors and was suggested for estimating tree AGB in the absence of height measurements.

We performed all analysis using the R 3.2.1 software platform (R Core Team, 2014). We use the R2WinBUGS (Sturtz et al., 2005) package for running WinBUGS from R and the ggplot2 package (Wickham, 2009) for producing figures, with the exception of Fig. 1, which was produced in the Environment for Visualizing Images software (ENVI, ITT Indus-

Table 3. Statistics of aboveground biomass (AGB) estimation models fit in a terra firme forest near Manaus, Amazonas, Brazil. See Table 2 for predictors and applied variance modeling approaches and Table A3 for the models' parameters.

Series	Model	Dev	pD	DIC	R^2	R^2 adj	$S_{yx\%}$	CF
1	M11	9694.5	2.919	9697.4	0.894	0.894	3.130	1.066
	M12	6808.0	2.990	6811.3	0.865	0.865	3.542	
	M13	6821.0	3.856	6825.2	0.864	0.864	3.544	
2	M21	9216.0	3.773	9219.9	0.946	0.945	2.259	1.061
	M22	6751.0	6.943	6758.3	0.557	0.540	6.458	
	M23	6739.0	10.465	6749.5	0.558	0.554	6.381	
3	M31	9291.0	4.052	9294.7	0.949	0.939	2.373	1.056
	M32	6683.0	4.062	6687.0	0.885	0.884	3.280	
	M33	6698.0	4.918	6702.5	0.865	0.865	3.527	
4	M41	9057.0	2.303	9059.8	0.957	0.956	2.030	1.054
	M42	6657.0	10.006	6667.5	0.701	0.699	5.215	
	M43	6649.0	13.059	6661.6	0.701	0.699	5.239	
5	M51	9479.0	0.023	9479.3	0.921	0.921	2.702	1.055
	M52	6680.0	4.017	6684.3	0.899	0.898	3.060	
	M53	6720.0	4.674	6724.7	0.897	0.896	3.103	
6	M61	9183.9	-71.746	9112.2	0.948	0.947	2.214	1.050
	M62	6614.0	10.078	6624.1	0.754	0.750	4.845	
	M63	6631.0	11.754	6642.9	0.740	0.737	4.896	
7	M71	8998.0	0.951	8999.1	0.959	0.959	1.942	1.047
	M72	6570.0	5.023	6574.9	0.934	0.933	2.480	
	M73	6610.0	5.697	6615.4	0.922	0.920	2.707	
8	M81	8812.0	-42.073	8770.3	0.968	0.967	1.719	1.046
	M82	6548.0	13.031	6561.3	0.811	0.804	4.200	
	M83	6566.0	13.778	6580.0	0.801	0.800	4.262	

Parameters: models' deviance (Dev), effective number of parameters (pD), deviance information criterion (DIC), coefficient of determination (R^2), adjusted coefficient of determination (R^2 adj), relative standard error ($S_{yx\%}$) and correction factor (CF) for models fit from ordinary least square with log-linear regressions.

tries, Inc, Boulder CO, USA). All codes used in this study were written by the authors.

3 Results

3.1 Individual tree biomass estimation model fits

Although the NLS approach produced models with overall higher values of R^2 and R^2 adj and lower values of $S_{yx\%}$, the DIC values indicated that the MOV and the OLS approaches produced the best models. The models M33 (DBH and WD as predictors) and M43 (DBH, SG and WD) were the two best fitting models across all tree individuals (high R^2 and R^2 adj and low $S_{yx\%}$ and DIC values compared to other models). These two models also produced more reliable landscape predictions (see Sect. 3.2). The statistics for the goodness of fit for the 24 models are given in Table 3. For the models fit with OLS, which rely on log-transformed variables, the addition of other predictors together with DBH systematically decreased the CF values. This pattern suggests a reduction in the biases resulting from back transformation.

As expected, the addition of other predictors to a model containing only DBH systematically increased the models'

parsimony, as indicated by the lower DIC values (Table 3). The inclusion of the SG assignment resulted in models with slightly lower R^2 adj and higher $S_{yx\%}$ compared to the same model structure without SG.

We observed differences with respect to the parameters b and c among pioneer, mid- and late-successional species in most of the models that included the SG assignment (Table S3 and Fig. S1). The late-successional species tended to have higher intercepts and steeper slopes. Pioneer and mid-successional species had lower differences in intercepts but still strong differences in the slopes.

Evaluations of AGB predictions for individual trees from our two best models (as described in the Sect. 3.2) as well from the pantropical model (Chave et al., 2014) are presented in the Supplement of this study (Fig. S1). The models M33 and M43 had lower biases (overestimation of 0.6 and 3.5 %, respectively) than the tested pantropical model (underestimation of 30 %).

3.2 Landscape-level biomass predictions across scenarios

To search for the model that best predicts AGB at the landscape level, we tested our models (excluding those with H as

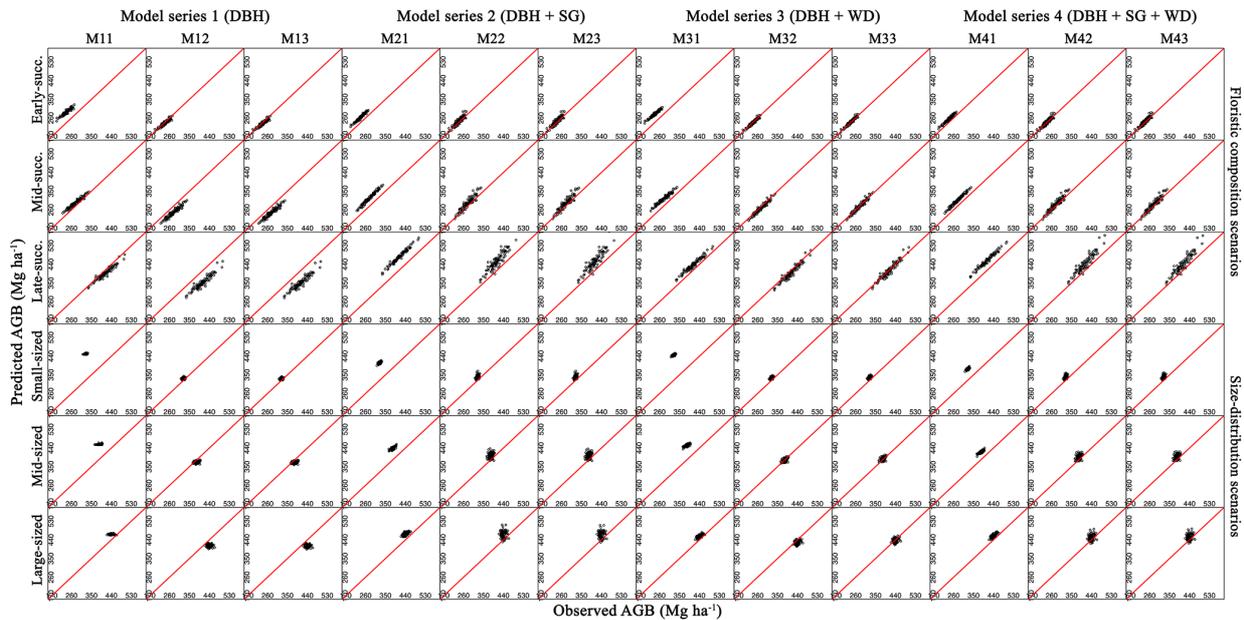


Figure 3. Predicted vs. observed aboveground biomass (AGB) along six forest scenarios composed of 100 1 ha plots. The line of equality (1 : 1 line) is shown as a red/straight line. Forest scenarios were designed to reflect landscape-level variations in floristic composition and size distribution of trees, typical of central Amazonian terra firme forests. Floristic composition and size-distribution scenarios followed the sampling scheme described in Sect. 2.4.2 (Fig. 2) of this study. Models' predictors: diameter at breast height (DBH) (cm), species' successional group (SG) (pioneers, mid- and late successional) and wood density (WD) (g cm^{-3}). See Table 2 for the variance modeling approach of different equations. Note that models containing tree total height (H) as predictor were excluded here.

a predictor; Table 2) across the 100 1 ha plots assembled for each of our six forest scenarios (Figs. 3–5) as well as jointly for all of them (Fig. 6).

The “true” AGB in our 1 ha plots (from the summed mass of trees used to assemble the forest scenarios) varied from 198.1 to 314.3 (early- to late-successional scenarios) and 101.4 to 391.8 Mg ha^{-1} (small- to large-sized scenarios). The ability of the various biomass estimation models to predict the “true” virtual biomass values generally reflected the goodness of fit of the models for predicting individual tree data (Table 3 and Figs. 3–6). The same pattern was observed when evaluating the tested pantropical model, which underestimated both the AGB of individual trees (Fig. S1) and in all of our scenarios (Table S4 and Fig. S2).

While some models produced accurate and satisfactory predictions across all scenarios, others systematically under- or overestimated the observed AGB (Fig. 3 and Fig. S2). The agreement between models and observations was influenced not only by the different combinations of predictors but also by the different methods to model the variance. Interestingly, despite producing the best fits to the individual tree data, models fit with NLS produced the least reliable landscape-level predictions, with model M11 (only DBH as predictor) being the unique exception for the mid- and late-successional scenarios (Fig. 3).

We observed systematic biases ranging from -14% (underestimation) to 38.8% (overestimation) in estimated landscape-level AGB (Fig. 4). The models fit with NLS tended to overestimate landscape-level AGB, with biases ranging from -3.6 up to 38.8% , both extreme values from model series 1 (only DBH as predictor). Overall, the models fit with NLS tended to capture changes in floristic composition better than in tree size distribution. The tested pantropical model systematically underestimated landscape-level biomass, with a mean bias of -29.7% (Table S4 and Fig. S2).

The models fit with the OLS and particularly with the MOV approaches were clearly more efficient at capturing the variation in floristic composition and size distribution of trees. Consequently, these models produced the most reliable landscape-level predictions within the scenarios (Fig. 3). As also indicated by the individual tree model fits, the MOV approach produced more reliable AGB predictions, especially with model series 2 and 4.

In general, the models fit with the OLS and MOV approaches did not show systematic trends in under- or overestimation. The models fit with the OLS approach had biases ranging from -13.8 to 11.1% , with extreme values from model series 1 and 2, respectively. The models fit with the MOV approach had biases ranging from -14 to 10.5% , also

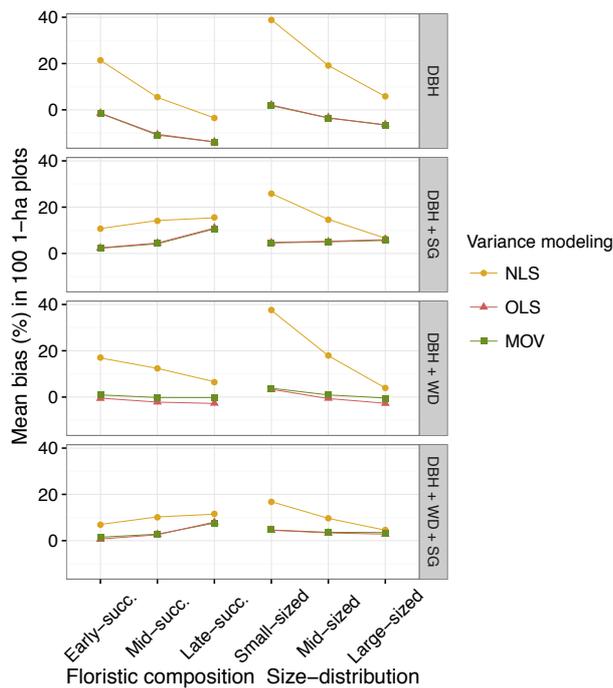


Figure 4. Profiles relating the bias of 12 aboveground tree biomass estimation models tested along six forest scenarios composed of 100 1 ha plots. Forest scenarios were designed to reflect landscape-level variations in floristic composition and size distribution of trees, typical of central Amazonian terra firme forests. Models' predictors: diameter at breast height (DBH) (cm), species' successional group (SG) (pioneers, mid- and late successional) and wood density (WD) (g cm^{-3}). Variance modeling approaches: nonlinear least square (NLS), ordinary least square with log-linear regression (OLS) and nonlinear with modeled variance (MOV). Note that models containing tree total height (H) as predictor were excluded here.

with extreme values from model series 1 and 2, respectively (Fig. 4).

The reported systematic biases led to strong differences between the predicted and the observed AGB (Fig. 5). The models fit with NLS resulted in RMSE values ranging from 16.8 up to 125.8 Mg ha^{-1} . For the models fit with OLS, the RMSE values ranged from 5.1 to 57.6 Mg ha^{-1} . The MOV models had RMSE ranging from 5.5 to 58.7 Mg ha^{-1} . The pantropical model's predictions had a mean RMSE of 102.6 Mg ha^{-1} (Table S4).

By combining the bias and RMSE values, we could observe the overall models' performance in predicting AGB across scenarios (Fig. 6). When challenged to predict biomass across all scenarios, the models fit with the MOV approach produced more reliable predictions (smaller range of biases and RMSE), except for model series 1 (only DBH as a predictor), for which the OLS approach performed better. Independently of applied predictors, the NLS approach had the highest mean and range of values for bias and RMSE.

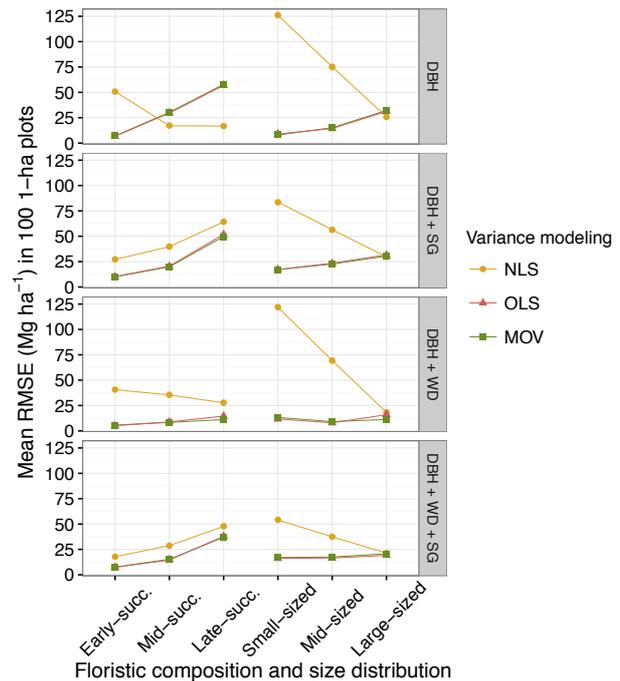


Figure 5. Profiles relating the root-mean-square error of 12 aboveground tree biomass estimation models tested along six forest scenarios composed of 100 1 ha plots. Forest scenarios were designed to reflect landscape-level variations in floristic composition and size distribution of trees, typical of central Amazonian terra firme forests. Models' predictors: diameter at breast height (DBH) (cm), species' successional group (SG) (pioneers, mid- and late successional) and wood density (WD) (g cm^{-3}). Variance modeling approaches: nonlinear least square (NLS), ordinary least square with log-linear regression (OLS) and nonlinear with modeled variance (MOV). Note that models containing tree total height (H) as predictor were excluded here.

As we expected, the addition of SG and WD improved the quality of the joint prediction. This was evidenced by the systematic reduction of models' bias and RMSE. Notably for the NLS approach, the inclusion of SG led to strong reduction of the bias and RMSE (Fig. 6). Interestingly, for this approach the addition of WD alone did not improve the estimations accuracy.

4 Discussion

4.1 Individual tree biomass estimation model fits

The best-performing allometry model structures for predicting the biomass of individual trees included species-specific predictors and either the OLS or MOV fitting approaches (Fig. 3, Fig. 6 and Table S3). As we hypothesized, including both the SG and WD as predictors greatly increased the models' performance. When taken alone, adding either

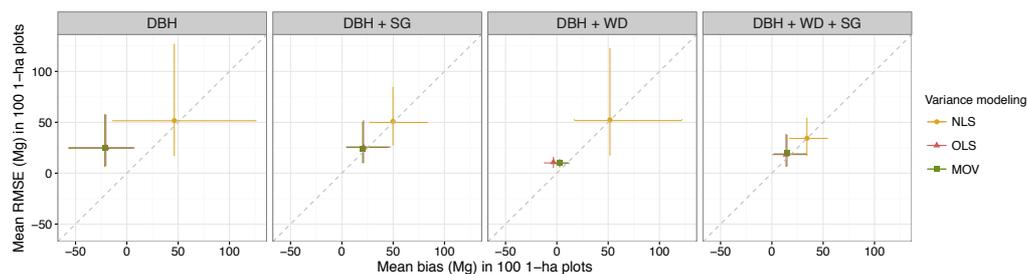


Figure 6. Overall performance of 12 aboveground tree estimation models along six forest scenarios composed of 100 1 ha plots. Forest scenarios were designed to reflect landscape-level variations in floristic composition and size distribution of trees, typical of central Amazonian terra firme forests. Models are rated by the absolute mean bias and root-mean-square error (RMSE), both in Mg. Solid points and bars represent absolute mean and range values, respectively. Models' predictors: diameter at breast height (DBH) (cm), species' successional group (SG) (pioneers, mid- and late successional) and wood density (WD) (g cm^{-3}). Variance modeling approaches: nonlinear least square (NLS), ordinary least square with log-linear regression (OLS) and nonlinear with modeled variance (MOV). Note that models containing tree total height (H) as predictor were excluded here.

of these two predictors to the basic DBH model yielded a more consistent model than adding H (Table S3). This pattern was true for all the three variance modeling approaches and supports having the species' identification (i.e., further assignment into SGs) and/or coherent wood density values, which is crucial when aiming for precise tree AGB predictions. Since old-growth forests comprise a mosaic of different successional stages, with trees of various architectures and sorted into different forest layers/strata, these variables are especially important when aiming for reliable AGB predictions at the landscape level (see Sect. 4.2).

Although the NLS approach fits our data set better (higher R^2_{adj} and lower $S_{yx\%}$), the assumption of a constant variance violates the natural heteroscedasticity of allometric data sets. With the log transformation of the OLS approach, homoscedasticity is reached but in a way that does not exactly reflect how variance actually changes. As previously reported for Amazon terra firme forests (Chambers et al., 2001; Lima et al., 2012), models fit with the OLS approach tend to overestimate the biomass of large-sized trees.

Indeed, the best models are obtained using the MOV and OLS approaches, in which we explicitly modeled variance depending on the main predictor (DBH). This explains why the models fit with these approaches produced more reliable (i.e., smaller differences between predictions and observations) AGB estimates as compared to those fit with the NLS approach. The NLS approach is still frequently found in the literature (Sileshi, 2014), despite the fact that assuming constant variance is not an appropriate choice for allometric data sets. We included the latter approach mainly for illustrative purposes.

Despite the highly heterogeneous nature of our data set (Table 1 and Table S1), DBH alone still captures a large fraction of the variation in AGB. This could be confirmed by lower $S_{yx\%}$ values within model series 1 in comparison to the other model series (Table 2). This result illustrates that

ignoring selection criteria that capture a model's capacity to make predictions for new predictor combinations (e.g., different region or successional stage), such as the DIC or our landscape-level evaluation (see Sect. 4.2), can lead to the wrong choice. The basic models containing only DBH had a higher DIC in comparison to other model series and consequently did poorly in predicting the AGB of our different landscape scenarios (Fig. 6).

Our data set contains a large number of species, which allowed for the maximum expression of architectural attributes. In comparison to species-specific biomass estimation models (Nelson et al., 1999) or models fit from data collected in undisturbed and homogenous forests (Higuchi et al., 1998; Lima et al., 2012), we expected the addition of predictors reflecting architectural and anatomical variation to improve model parsimony. This pattern was observed when adding both SG and WD (Fig. 6 and Table S3).

The differences related to the parameters b and c we found among our successional groups highlighted the importance of using SG as a predictor of the architectural attributes that influence allometry, especially in disturbed or secondary forests where WD is not available (Table S3). In the models containing SG, the significant variation of the parameters b and c between pioneers, mid- and late-successional species highlights the importance of architectural attributes on defining allometries (Nelson et al., 1999). Often, these differences were neglected in previous studies that dealt with heterogeneous data sets and aimed at parameterizing global/pantropical biomass estimation models.

Interestingly, when compared to our two best models, the tested pantropical model from Chave et al. (2014) produced the largest bias (overestimation) for individual tree biomass prediction (Fig. S1 and Sect. 3.1). As previously mentioned, underestimation was also reported when applying the Chave et al. (2005) biomass estimation model in Atlantic Forest stands in Brazil (Nogueira Jr. et al., 2014). For our study,

we attribute part of this pattern to strong differences in forest structure and tree allometry/architecture between our central Amazon data set and that used to parameterize the pantropical model from Chave et al. (2014). Although the DBH and H range of the trees used in our study is well represented by the pantropical data set, the two data sets vary strongly with respect to the DBH and H distribution of trees (Fig. S3). Our data set clearly has a much higher density of small-sized trees and a much lower density of large-sized trees. The pantropical data set comprises ca. 8 % ($n = 329$) of trees with $\text{DBH} \geq 60$ cm and mean H of 39.3 m (and even a tree with 212 cm DBH and another one with 70.7 m H). Interestingly, none of these 329 large-sized trees were found in terra firme forests in the region of Manaus. Note that the largest tree in our data set has 85 cm DBH and 33 m H (Table 1 and Table S1) and, as previously reported, trees with $\text{DBH} \geq 60$ cm account for less than 17 % of the total AGB in central Amazonian terra firme forests (Vieira et al., 2004). Thus the structure and biomass of these central Amazonian forests is not well predicted from the “improved” pantropical biomass estimation model from Chave et al., 2014.

Observed differences on the relationship between predictor variables (DBH and WD) and AGB of trees from our data set and that used in the pantropical model highlight part of the variation in tree allometry and architecture that was not represented in the pantropical data set (Fig. S4). As for the differences in forest structure, these differences in tree allometry and architecture reflect typical differences in species composition among successional stages (Clark and Clark, 1992; Denslow, 1980; Marra et al., 2014). By including our two secondary forests, we added a greater proportion of allometric variation in our models compared to the Chave et al. (2014) data set (Fig. S5). Our results indicate that neglecting variations in tree allometry and architecture related to floristic composition can lead to strong bias when predicting individual tree AGB, especially when complex old-growth and secondary forests (Asner, 2013; Chambers et al., 2013; Norden et al., 2015) are not accounted for in the model parameterization.

4.2 Landscape-level biomass predictions across scenarios

The different combinations of floristic composition and structure (i.e., tree density and basal area) used in our virtual approach reflected forest changes along succession (Chambers et al., 2009; Marra et al., 2014; Norden et al., 2015), including realistic variations in AGB reported for central Amazon stands differing in successional stage (from early successional to old growth) (Carvalho Jr. et al., 1995; Higuchi et al., 2004; Lima et al., 2007). When taking into account the accuracy of landscape-level predictions across scenarios, the best models were those fit by using the MOV and the OLS approaches. From the MOV approach, the models M33, M43

and M23 were the first, second and third best models, respectively (Fig. 6).

Modeling the variance properly as in the MOV approach is particularly important when both small and large trees – at the respective endpoints of the size predictors DBH and H – are to be estimated precisely. Assuming homoscedastic variance in allometric data gives a stronger weight to the information of large trees (which have large residuals) and reduces the “strength” of the small trees (with small residuals) on the estimation of the parameters. This almost invariably leads to models that overestimate the biomass of small trees (i.e., large trees pulling the “line” upwards). This effect can be clearly seen in Fig. 4 where the NLS models dramatically overestimated the biomass, particularly in the small-sized and the early-successional scenario. The OLS approach tends to produce the opposite effect. The log transformation shrinks the size of the residuals of the large-sized trees and inflates it for the small-sized trees. The influence of positive residuals or large-sized trees that often have a strong lever is reduced, and the lever of very small trees is increased. This may (although not as extremely as in the NLS case) lead to an underestimation of the biomass of big trees. A slight tendency of this effect is also visible in Fig. 4 when the OLS and MOV models are compared in the model series 2 and 3. The model evaluation with our virtual forests thus clearly illustrates that a balanced modeling of the variance, i.e., giving the small and large trees equal weight, is very important when (1) the design matrices are very heterogeneous or unbalanced with respect to size and when (2) predictions are made at landscape level across stands that vary in the mean size/shape of trees.

Models containing only size predictors (such as DBH) are particularly sensitive to this problem. Including SG and WD as predictors captured part of the interspecific variation in architecture and anatomy and partly alleviated the above-mentioned problems of the NLS and OLS models. Thus, although a simple allometric model (e.g., $\text{AGB} \sim b1\text{DBH}^{b2}$) can accurately describe the DBH : AGB relationship at the individual level (Table 3 and Table S3), our results demonstrate that reliable estimates of biomass in heterogeneous landscapes (i.e., mixtures of successional stages and tree sizes) requires correct modeling of the size-related variance (Sileshi, 2014; Todeschini et al., 2004) and including suitable predictors of species-specific attributes reflecting ecological, architectural and anatomical variation.

Our model evaluation using “virtual forests” was used to test what level of model complexity and appropriateness of variance modeling is needed to avoid “distortions” and make satisfying predictions at the fringes of our predictor space. This approach also allowed us to assess the magnitude of RMSE in model predictions in relation to the bias of these predictions. Our best performance models produced predictions with RMSE similar (i.e., M33, M43, and M23) to the bias associated to these prediction, which indicates that model deviations can be attributed to random variation

and possibly be ignored (Gregoire et al., 2016; McRoberts and Westfall, 2014). However, since we constructed the forest scenarios with trees from our data set, this is an “internal evaluation” and not a test of model behavior in the face of new predictor combinations. Furthermore, we used DIC as parsimony-based model selection criterion, which was designed to exactly approximate this capacity and typically yields similar results as cross-validation (Wirth et al., 2004). The DIC is therefore particularly important for judging the quality of the model, especially for application in other regions or for other species. Unlike the virtual forest approach, where the DBH + WD with modeled variance (M33) appeared to be the best model (lowest bias and RMSE at the same time) (Fig. 6), the DIC invariably requires the full model complexity irrespective of whether H is considered or not (Table 3).

As reported in other studies (Alvarez et al., 2012; Lima et al., 2012; Ngomanda et al., 2014; Nogueira Jr. et al., 2014), using the pantropical biomass estimation model by Chave et al. (2014) for landscape-level predictions led to strong biases in the case of our central Amazonian forest scenarios. Thus, our recommendation is not to assume that their model is equally applicable across all tropical forests, especially for secondary or hyperdiverse tropical forests. In this context, we alert researchers and managers about the importance of applying local or regional generic models when estimating biomass and the importance of species composition information in plot studies.

4.3 Suitability of the chosen predictors for practical application

As we have seen, predicting biomass correctly at the landscape level and in particular improving performance at the fringes or outside the predictor space requires the inclusion of predictors related to species architecture (DBH in combination with H (when available), WD and/or SG). Knowledge of these last two variables depends on the identification of species, further assignment into successional groups and measurement or compilation of species-specific WD values. For the purposes of our study, these variables were successfully addressed.

However, we understand that reliable biomass estimation models also require variables that can be easily and confidently acquired or measured. As we discuss below, this is not the case for the species identification, H and, consequently, in many cases for WD and SG.

The tree species diversity in the Amazon is high (de Oliveira and Mori, 1999; ter Steege et al., 2013). Species identification requires extensive field work (i.e., collection of botanical samples) and joint effort of parobotanists, botanists and taxonomists. In many cases, this task might pose a major problem.

For WD, values can vary widely not only between species (Chave et al., 2006) – which we exploit in our modeling ap-

proach – but also between different sites/regions (Muller-Landau, 2004), within individuals of the same species or even in an individual tree (density varying along the tree bole) (Higuchi et al., 1998; Nogueira et al., 2005). Ideally, WD measures should be carried out in situ following a method that allows for sampling both heart- and sapwood. Measuring WD from nonrepresentative samples and applying measures from studies in which samples were oven dried at different temperatures can produce complication. At temperatures below 100 °C, the wood bound water content cannot be removed (Williamson and Wiemann, 2010). This requires improvement of available methods and tools (e.g., resistography, X-ray, ultrasonic tomography, near-infrared spectroscopy, acoustic/ultrasonic wave propagation and high-frequency densitometry) (Isik and Li, 2003; Lin et al., 2008; Schinker et al., 2003) that in the future may allow the measurement of WD in live trees from hyperdiverse tropical forests (thousands of species). However, the acquisition of WD data is still expensive and is not easily conducted simultaneously with forest inventories.

In the Amazon, information on WD is not available at the species level for most regions, and the available WD data have been acquired using a wide range of methods. Thus, the compilation of WD data from different sources without filtering criteria may introduce an unpredictable source of error. As a result, researchers and managers need to establish robust criteria and test whether including WD information compiled from the available literature can really increase the quality of biomass predictions (as shown in our study). These limitations become critical when adjusting biomass estimation models both from small or even large/combined data sets collected without a plot-based harvest method that allows for a landscape-level evaluation of models derived using individual trees (Carvalho Jr. et al., 1995; Higuchi et al., 1998; Lima et al., 2012; da Silva, 2007). One important result of our study is that correct assignment of species into successional groups can satisfactorily replace the use of WD despite the fact that WD and SG were not trivially correlated (Table 2).

Most of the available biomass estimation models include H as a predictor. Indeed, we expected the inclusion of H to substantially improve our individual tree fits and landscape-level predictions. Although H is a powerful predictor of AGB, because together with DBH it defines the slenderness of trees and also indicates the lifetime light availability (suppressed trees with typically short crowns have a high H : DBH ratio), acquiring these data is still costly and difficult in tall and complex tropical forest canopies. As a consequence, H is often measured imprecisely or not at all in most existing forest inventories across the Amazon. H varies with plant ontogeny and can be affected by environmental and neighbor effects (Henry and Aarssen, 1999; Sterck and Bongers, 1998). Consequently, the error of AGB estimates can increase when applying H values estimated from regional or global models (Feldpausch et al., 2011, 2012; Hunter et al., 2013; Santos Jr. et al., 2006). As observed in

our (Table 2) and other data sets (Sileshi, 2014), the high collinearity between DBH and H can distort coefficient values, inflate standard errors and lead to unreliable estimates. The increased availability of new tools such as Lidar can improve the resolution of data on tree height and thus biomass (Marvin et al., 2014; Sawada et al., 2015), but currently the areas where such data are available are limited. The calibration of remote-sensing-based biomass models for diverse tropical forest still relies on the degree of uncertainty associated to plot-level AGB estimates (Chen et al., 2015).

Despite uncertainties associated with global estimates of carbon stocks, tropical forests store ca. 25 % of the terrestrial carbon (Bonan, 2008; Saatchi et al., 2011) and provide resources (e.g., food, fuel, timber and water) essential for humankind (Trumbore et al., 2015). Nonetheless, old-growth tropical forests are rapidly changing and degrading due to the intensification of human activities, gradual climate change and extreme weather events (FAO, 2010; IPCC, 2014). The Reducing Emissions from Deforestation and Forest Degradation (REDD+) program from the United Nations Framework Convention on Climate Change (UNFCCC) establishes rewards for actions that mitigate carbon emission through prevention of forest loss and degradation. For countries with large forest cover (e.g., Brazil and other Amazonian countries), such programs emerge as an economical alternative to historically more lucrative land uses resulting in forest degradation or suppression. However, we showed that reliable estimates of forest biomass are complex to obtain and prone to large uncertainty. Reliable predictions of biomass/carbon stocks over large regions of structurally complex and hyperdiverse tropical forests such as the Amazon still depend on the collection of plot-based allometric data and forest inventories including information on species composition, tree height and wood density, which are often unavailable or estimated imprecisely in most regions.

Natural and anthropogenic tropical secondary forests are widely distributed and account for ca. 50 % of the global forest cover (FAO, 2010). Although highly productive and resilient (Poorter et al., 2016), Neotropical forests can take unpredictable successional trajectories (Norden et al., 2015). During forest succession, once floristic composition changes and structural gradients increase, allometry becomes more complex and reliable landscape-level biomass estimates may require models that include predictors approximating species-specific architecture and anatomy. Extra care should be taken when using biomass estimation models to assess biomass dynamics (e.g., biomass recovery after disturbances). Earlier stages of recovery can have a higher proportion of small trees from pioneers species, which have lower wood density (Chambers et al., 2009; Marra et al., 2014; Saldarriaga et al., 1998) and a particular type of architecture (Hallé et al., 1978; Swaine and Whitmore, 1988).

We recommend the use of the best models fit in this study when aiming for reliable landscape AGB estimations for central Amazonian terra firme forests, especially those under

complex disturbance regimes and for which specific/local models are not available. When data on species composition and wood density are available or could be accurately compiled from the literature, we encourage the use of the model M33 or M23 (MOV approach). In case the MOV approach cannot be applied for model parameterization (i.e. technical or computational restrictions), the OLS is presumably more appropriate and efficient than the NLS.

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References

- Alvarez, E., Duque, A., Saldarriaga, J., Cabrera, K., de las Salas, G., del Valle, I., Lema, A., Moreno, F., Orrego, S., and Rodríguez, L.: Tree above-ground biomass allometries for carbon stocks estimation in the natural forests of Colombia, *Forest Ecol. Manag.*, 267, 297–308, 2012.
- Amaral, D. D., Vieira, I. C. G., Almeida, S. S., Salomão, R. P., Silva, A. S. L., and Jardim, M. A. G.: Checklist of remnant forest fragments of the metropolitan area of Belém and historical value of the fragments, State of Pará, Brazil, *Bol. Mus. Para. Emílio Goeldi*, 4, 231–289, 2009.

- Asner, G. P.: Geography of forest disturbance, *P. Natl. Acad. Sci. USA*, 110, 3711–3712, 2013.
- Banin, L., Feldpausch, T. R., Phillips, O. L., Baker, T. R., Lloyd, J., Affum-Baffoe, K., Arets, E. J. M. M., Berry, N. J., Bradford, M., Brienen, R. J. W., Davies, S., Drescher, M., Higuchi, N., Hilbert, D. W., Hladik, A., Iida, Y., Salim, K. A., Kassim, A. R., King, D. A., Lopez-Gonzalez, G., Metcalfe, D., Nilus, R., Peh, K. S. H., Reitsma, J. M., Sonké, B., Taedoumg, H., Tan, S., White, L., Wöll, H., and Lewis, S. L.: What controls tropical forest architecture? Testing environmental, structural and floristic drivers, *Glob. Ecol. Biogeogr.*, 21, 1179–1190, 2012.
- Bolker, B. M.: *Ecological Models and Data in R*, Princeton University Press, New Jersey, 2008.
- Bolker, B. M., Gardner, B., Maunder, M., Berg, C. W., Brooks, M., Comita, L., Crone, E., Cubaynes, S., Davies, T., de Valpine, P., Ford, J., Gimenez, O., Kéry, M., Kim, E. J., Lennert-Cody, C., Magnusson, A., Martell, S., Nash, J., Nielsen, A., Regetz, J., Skaug, H., and Zipkin, E.: Strategies for fitting nonlinear ecological models in R, *AD Model Builder*, and *BUGS*, *Methods Ecol. Evol.*, 4, 501–512, 2013.
- Bonan, G. B.: Forests and climate change: forcings, feedbacks, and the climate benefits of forests, *Science*, 320, 1444–1449, doi:10.1126/science.1155121, 2008.
- Bowman, D. M. J. S., Brienen, R. J. W., Gloor, E., Phillips, O. L., and Prior, L. D.: Detecting trends in tree growth: Not so simple, *Trends Plant Sci.*, 18, 11–17, 2013.
- Braga, P. I. S.: Subdivisão fitogeográfica, tipos de vegetação, conservação e inventário florístico da floresta amazônica, *Acta Amaz.*, 9, 53–80, 1979.
- Brooks, S. P. and Gelman, A.: General Methods for Monitoring Convergence of Iterative Simulations, *J. Comput. Graph. Stat.*, 7, 434–455, 1998.
- Brooks, S. P. and Roberts, G. O.: Convergence assessment techniques for Markov chain Monte Carlo, *Stat. Comput.*, 8, 319–335, 1998.
- Brown, S., Gillespie, A. J. R., and Lugo, A. E.: Biomass estimation methods for tropical forests with applications to forest inventory data, *Forest Sci.*, 35, 881–902, 1989.
- Carvalho Jr., J. A., Santos, J. M., Santos, J. C., Leitão, M. M., and Higuchi, N.: A tropical rainforest clearing experiment by biomass burning in the Manaus region, *Atmos. Environ.*, 29, 2301–2309, 1995.
- Chambers, J., Higuchi, N., Teixeira, L., Santos, J. dos, Laurance, S., and Trumbore, S.: Response of tree biomass and wood litter to disturbance in a Central Amazon forest, *Oecologia*, 141, 596–611, 2004.
- Chambers, J. Q., dos Santos, J., Ribeiro, R. J., and Higuchi, N.: Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest, *Forest Ecol. Manag.*, 152, 73–84, 2001.
- Chambers, J. Q., Robertson, A. L., Carneiro, V. M. C., Lima, A. J. N., Smith, M. L., Plourde, L. C., and Higuchi, N.: Hyperspectral remote detection of niche partitioning among canopy trees driven by blowdown gap disturbances in the Central Amazon, *Oecologia*, 160, 107–117, 2009.
- Chambers, J. Q., Negron-Juarez, R. I., Marra, D. M., Di Vittorio, A., Tews, J., Roberts, D., Ribeiro, G. H. P. M., Trumbore, S. E., and Higuchi, N.: The steady-state mosaic of disturbance and succession across an old-growth Central Amazon forest landscape, *P. Natl. Acad. Sci. USA*, 110, 3949–3954, 2013.
- Chave, J., Andalo, C., Brown, S., Cairns, M. A., Chambers, J. Q., Eamus, D., Fölster, H., Fromard, F., Higuchi, N., Kira, T., Lescur, J. P., Nelson, B. W., Ogawa, H., Puig, H., Riéra, B., and Yamakura, T.: Tree allometry and improved estimation of carbon stocks and balance in tropical forests, *Oecologia*, 145, 87–99, 2005.
- Chave, J., Muller-Landau, H. C., Baker, T. R., Easdale, T. A., Hans Steege, T. E. R., and Webb, C. O.: Regional and phylogenetic variation of wood density across 2456 neotropical tree species, *Ecol. Appl.*, 16, 2356–2367, 2006.
- Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., and Zanne, A. E.: Towards a worldwide wood economics spectrum, *Ecol. Lett.*, 12, 351–366, 2009.
- Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C., Duque, A., Eid, T., Fearnside, P. M., Goodman, R. C., Henry, M., Martínez-Yrizar, A., Mugasha, W., Muller-Landau, H. C., Mencuccini, M., Nelson, B. W., Ngomanda, A., Nogueira, E. M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C. M., Saldarriaga, J. G., and Vieilledent, G.: Improved allometric models to estimate the aboveground biomass of tropical trees, *Glob. Chang. Biol.*, 20, 3177–3190, 2014.
- Chen, Q., Vaglio Laurin, G., and Valentini, R.: Uncertainty of remotely sensed aboveground biomass over an African tropical forest: Propagating errors from trees to plots to pixels, *Remote Sens. Environ.*, 160, 134–143, doi:10.1016/j.rse.2015.01.009, 2015.
- Clark, D. A. and Clark, D. B.: Life history diversity of canopy and emergent trees in a neotropical rain forest, *Ecol. Monogr.*, 62, 315–344, 1992.
- Clark, D. B. and Kellner, J. R.: Tropical forest biomass estimation and the fallacy of misplaced concreteness, *J. Veg. Sci.*, 23, 1191–1196, 2012.
- da Silva, R.: Alometria, estoque e dinâmica da biomassa de florestas primárias e secundárias na região de Manaus (AM), PhD Thesis, Universidade Federal do Amazonas, Brazil, available at: https://www.inpa.gov.br/arquivos/Tese_Biomassa_Roseana_Silva.pdf (last access: 5 March 2015), 2007.
- da Silva, R. P., dos Santos, J., Tribuzy, E. S., Chambers, J. Q., Nakamura, S., and Higuchi, N.: Diameter increment and growth patterns for individual tree growing in Central Amazon, Brazil, *Forest Ecol. Manag.*, 166, 295–301, 2002.
- da Silva, R. P., Nakamura, S., Azevedo, C. de, Chambers, J., Rocha, R. de M., Pinto, C., dos Santos, J., and Higuchi, N.: Use of metallic dendrometers for individual diameter growth patterns of trees at Cuieiras river basin, *Acta Amaz.*, 33, 67–84, 2003.
- Denslow, J. S.: Patterns of plant species diversity during succession under different disturbance regimes, *Oecologia*, 46, 18–21, 1980.
- de Oliveira, A. A. and Mori, S. A.: A central Amazonian terra firme forest. I. High tree species richness on poor soils, *Biodivers. Conserv.*, 8, 1219–1244, 1999.
- dos Santos, J.: Análise de modelos de regressão para estimar a fitomassa da floresta tropical úmida de terra-firme da Amazônia Brasileira, Ph.D. Thesis, Universidade Federal de Viçosa, Minas Gerais, Brazil, 1996.
- FAO: Global Forest Resources Assessment, *FAO For. Pap.*, 163, 2010.

- Fearnside, P. M.: Wood density for estimating forest biomass in Brazilian Amazonia, *Forest Ecol. Manag.*, 90, 59–87, 1997.
- Feldpausch, T. R., Banin, L., Phillips, O. L., Baker, T. R., Lewis, S. L., Quesada, C. A., Affum-Baffoe, K., Arets, E. J. M. M., Berry, N. J., Bird, M., Brondizio, E. S., de Camargo, P., Chave, J., Djagbletey, G., Domingues, T. F., Drescher, M., Fearnside, P. M., França, M. B., Fyllas, N. M., Lopez-Gonzalez, G., Hladik, A., Higuchi, N., Hunter, M. O., Iida, Y., Salim, K. A., Kassim, A. R., Keller, M., Kemp, J., King, D. A., Lovett, J. C., Marimon, B. S., Marimon-Junior, B. H., Lenza, E., Marshall, A. R., Metcalfe, D. J., Mitchard, E. T. A., Moran, E. F., Nelson, B. W., Nilus, R., Nogueira, E. M., Palace, M., Patiño, S., Peh, K. S.-H., Raventos, M. T., Reitsma, J. M., Saiz, G., Schrod, F., Sonké, B., Taedoumg, H. E., Tan, S., White, L., Wöll, H., and Lloyd, J.: Height-diameter allometry of tropical forest trees, *Biogeosciences*, 8, 1081–1106, doi:10.5194/bg-8-1081-2011, 2011.
- Feldpausch, T. R., Lloyd, J., Lewis, S. L., Brienen, R. J. W., Gloor, M., Monteagudo Mendoza, A., Lopez-Gonzalez, G., Banin, L., Abu Salim, K., Affum-Baffoe, K., Alexiades, M., Almeida, S., Amaral, I., Andrade, A., Aragão, L. E. O. C., Araujo Murakami, A., Arets, E. J. M. M., Arroyo, L., Aymard, C., G. A., Baker, T. R., Bánki, O. S., Berry, N. J., Cardozo, N., Chave, J., Comiskey, J. A., Alvarez, E., de Oliveira, A., Di Fiore, A., Djagbletey, G., Domingues, T. F., Erwin, T. L., Fearnside, P. M., França, M. B., Freitas, M. A., Higuchi, N., E. Honorio C., Iida, Y., Jiménez, E., Kassim, A. R., Killeen, T. J., Laurance, W. F., Lovett, J. C., Malhi, Y., Marimon, B. S., Marimon-Junior, B. H., Lenza, E., Marshall, A. R., Mendoza, C., Metcalfe, D. J., Mitchard, E. T. A., Neill, D. A., Nelson, B. W., Nilus, R., Nogueira, E. M., Parada, A., Peh, K. S.-H., Pena Cruz, A., Peñuela, M. C., Pitman, N. C. A., Prieto, A., Quesada, C. A., Ramírez, F., Ramírez-Angulo, H., Reitsma, J. M., Rudas, A., Saiz, G., Salomão, R. P., Schwarz, M., Silva, N., Silva-Espejo, J. E., Silveira, M., Sonké, B., Stropp, J., Taedoumg, H. E., Tan, S., ter Steege, H., Terborgh, J., Torello-Raventos, M., van der Heijden, G. M. F., Vásquez, R., Vilanova, E., Vos, V. A., White, L., Willcock, S., Woell, H., and Phillips, O. L.: Tree height integrated into pantropical forest biomass estimates, *Biogeosciences*, 9, 3381–3403, doi:10.5194/bg-9-3381-2012, 2012.
- Goodman, R. C., Phillips, O. L., and Baker, T. R.: The importance of crown dimensions to improve tropical tree biomass estimates, *Ecol. Appl.*, 24, 680–698, 2014.
- Graham, M. H.: Confronting multicollinearity in ecological multiple regression, *Ecology*, 84, 2809–2815, 2003.
- Gregoire, T. G., Næsset, E., McRoberts, R. E., Ståhl, G., Andersen, H. E., Gobakken, T., Ene, L., and Nelson, R.: Statistical rigor in LiDAR-assisted estimation of above-ground forest biomass, *Remote Sens. Environ.*, 173, 98–108, doi:10.1016/j.rse.2015.11.012, 2016.
- Hallé, F.: Architecture of trees in the rain forest of Morobe District, New Guinea, *Biotropica*, 6, 43–50, 1974.
- Hallé, F., Oldeman, R. A. A., and Tomlinson, P. B.: Tropical trees and forests: an architectural analysis, Springer-Verlag, Berlin, German Federal Republic, 1978.
- Henry, H. A. L. and Aarssen, L. W.: The interpretation of stem diameter-height allometry in trees: Biomechanical constraints, neighbour effects, or biased regressions?, *Ecol. Lett.*, 2, 89–97, 1999.
- Higuchi, N., Santos, J. dos, Ribeiro, R. J., Minette, L., and Biot, Y.: Biomassa da parte aérea da vegetação da floresta tropical úmida de terra-firme da Amazônia brasileira, *Acta Amaz.*, 28, 153–166, 1998.
- Higuchi, N., Chambers, J. Q., Santos, J. dos, Ribeiro, R. J., Pinto, A. C. M., Silva, R. P. da, Rocha, R. de M., and Tribuzy, E. S.: Dinâmica e balanço do carbono da vegetação primária da Amazônia Central, *Floresta*, 34, 295–304, 2004.
- Hunter, M. O., Keller, M., Victoria, D., and Morton, D. C.: Tree height and tropical forest biomass estimation, *Biogeosciences*, 10, 8385–8399, doi:10.5194/bg-10-8385-2013, 2013.
- Huxley, J. and Teissier, G.: Terminology of relative growth, *Nature*, 137, 780–781, 1936.
- IPCC: Guidelines for National Greenhouse Gas Inventories. IGES, Japan, available at: <http://www.ipcc-nggip.iges.or.jp/public/2006gl/index.html> (last access: 5 February 2016), 2006.
- IPCC: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, Geneva, Switzerland, available at: <http://www.ipcc.ch/report/ar5/syr/> (last access: 5 February 2016), 2014.
- Isik, F. and Li, B.: Rapid assessment of wood density of live trees using the Resistograph for selection in tree improvement programs, *Can. J. Forest Res.*, 33, 2426–2435, 2003.
- Junk, W., Piedade, M., Shongärt, J., Cohn-Haft, M., Adeney, J., and Wittmann, F.: A classification of major naturally-occurring amazonian lowland wetlands, *Wetlands*, 31, 623–640, 2011.
- Kammesheid, L.: Some autecological characteristics of early to late successional tree species in Venezuela, *Acta Oecologica*, 21, 37–48, 2000.
- King, D. A.: Allometry and life history of tropical trees, *J. Trop. Ecol.*, 12, 25–44, 1996.
- Laurance, W. F., Nascimento, H. E. M., Laurance, S. G., Andrade, A., Fearnside, P. M., Ribeiro, J. E. L., and Capretz, R. L.: Rain forest fragmentation and the proliferation of successional trees, *Ecology*, 87, 469–482, 2006.
- Lima, A. J. N., Teixeira, L. M., Carneiro, V. M. C., dos Santos, J., and Higuchi, N.: Análise da estrutura e do estoque de fitomassa de uma floresta secundária da região de Manaus AM, dez anos após corte raso seguido de fogo, *Acta Amaz.*, 37, 49–54, 2007.
- Lima, A. J. N., Suwa, R., Ribeiro, G. H. P. M., Kajimoto, T., Santos, J. dos, Silva, R. P. da, Souza, C. A. S. de, Barros, P. C. de, Noguchi, H., Ishizuka, M., and Higuchi, N.: Allometric models for estimating above- and below-ground biomass in Amazonian forests at São Gabriel da Cachoeira in the upper Rio Negro, Brazil, *Forest Ecol. Manag.*, 277, 163–172, 2012.
- Lin, C. J., Kao, Y. C., Lin, T. T., Tsai, M. J., Wang, S. Y., Lin, L. D., Wang, Y. N., and Chan, M. H.: Application of an ultrasonic tomographic technique for detecting defects in standing trees, *Int. Biodeterior. Biodegrad.*, 62, 434–441, 2008.
- Lunn, D. J., Thomas, A., Best, N., and Spiegelhalter, D.: WinBUGS – a Bayesian modelling framework: concepts, structure, and extensibility, available at: <http://www.mrc-bsu.cam.ac.uk/software/bugs/> (last access: 10 September 2015), 2000.
- Marra, D. M., Chambers, J. Q., Higuchi, N., Trumbore, S. E., Ribeiro, G. H. P. M., Santos, J. dos, Negrón-Juárez, R., Reu, B., and Wirth, C.: Large-scale wind disturbances promote tree diversity in a central Amazon forest, *PLoS One*, 9, e103711, doi:10.1371/journal.pone.0103711, 2014.

- Marvin, D. C., Asner, G. P., Knapp, D. E., Anderson, C. B., Martin, R. E., Sinca, F., and Tupayachi, R.: Amazonian landscapes and the bias in field studies of forest structure and biomass, *P. Natl. Acad. Sci.*, 111, E5224–E5232, 2014.
- McRoberts, R. E. and Westfall, J. A.: The effects of uncertainty in individual tree volume model predictions on the uncertainty of large area volume estimates The method?, *Forest Sci.*, 60, 34–42, doi:10.5849/forsci.12-141, 2014.
- Muller-Landau, H. C.: Interspecific and inter-site variation in wood specific gravity of tropical trees, *Biotropica*, 36, 20–32, 2004.
- Negrón-Juárez, R. I., Chambers, J. Q., Guimaraes, G., Zeng, H., Raupp, C. F. M., Marra, D. M., Ribeiro, G. H. P. M., Saatchi, S. S., Nelson, B. W., and Higuchi, N.: Widespread Amazon forest tree mortality from a single cross-basin squall line event, *Geophys. Res. Lett.*, 37, 1–5, 2010.
- Nelson, B., Kapos, V., Adams, J., Oliveira, W., Braun, O., and do Amaral, I.: Forest disturbance by large blowdowns in the Brazilian Amazon, *Ecology*, 75, 853–858, 1994.
- Nelson, B. W., Mesquita, R. C. G., Pereira, J. L. G., de Souza, S. G. A., Batista, G. T., and Couto, L. B.: Allometric regressions for improved estimate of secondary forest biomass in the central Amazon, *Forest Ecol. Manag.*, 117, 149–167, 1999.
- Ngomanda, A., Obiang, N. L. E., Lebamba, J., Mavouroulou, Q. M., Gomat, H., Mankou, G. S., Loumeto, J., Iponga, D. M., Ditsouga, F. K., Koumba, R. Z., Bobé, K. H. B., Okouyi, C. M., Nyangadouma, R., Lépengué, N., Mbatchesi, B., and Picard, N.: Site-specific versus pantropical allometric equations: Which option to estimate the biomass of a moist central African forest?, *Forest Ecol. Manag.*, 312, 1–9, 2014.
- Nogueira, E. M., Nelson, B. W., and Fearnside, P. M.: Wood density in a dense forest in central Amazonia, Brazil, *Forest Ecol. Manag.*, 208, 261–286, 2005.
- Nogueira, E. M., Fearnside, P. M., Nelson, B. W., and França, M. B.: Wood density in forests of Brazil’s “arc of deforestation”: Implications for biomass and flux of carbon from land-use change in Amazonia, *Forest Ecol. Manag.*, 248, 119–135, 2007.
- Nogueira Jr., L. R., Engel, V. L., Parrotta, J. A., Melo, A. C. G., and Ré, D. S.: Allometric equations for estimating tree biomass in restored mixed-species Atlantic, *Biota Neotrop.*, 14, 1–9, 2014.
- Norden, N., Angarita, H. A., Bongers, F., Martínez-Ramos, M., Granzow-de la Cerda, I., van Breugelf, M., Lebrija-Trejos, E., Meave, J. A., Vandermeer, J., Williamson, G. B., Finegan, B., Mesquita, R., and Chazdon, R. L.: Successional dynamics in Neotropical forests are as uncertain as they are predictable, *P. Natl. Acad. Sci. USA*, 112, 8013–8018, 2015.
- Petraitis, P. S., Dunham, A. E., and Niewiarowski, P. H.: Inferring multiple causality: the limitations of path analysis, *Funct. Ecol.*, 10, 421–431, 1996.
- Poorter, L., Bongers, F., Sterck, F. J., and Wöll, H.: Architecture of 53 Rain Forest Tree Species Differing in Adult Stature and Shade Tolerance, *Ecology*, 84, 602–608, 2003.
- Poorter, L., Bongers, F., Aide, T. M., Almeyda Zambrano, A. M., Balvanera, P., Becknell, J. M., Boukili, V., Brancalion, P. H. S., Broadbent, E. N., Chazdon, R. L., Craven, D., de Almeida-Cortez, J. S., Cabral, G. A. L., de Jong, B. H. J., Denslow, J. S., Dent, D. H., DeWalt, S. J., Dupuy, J. M., Durán, S. M., Espírito-Santo, M. M., Fandino, M. C., César, R. G., Hall, J. S., Hernandez-Stefanoni, J. L., Jakovac, C. C., Junqueira, A. B., Kennard, D., Letcher, S. G., Licona, J.-C., Lohbeck, M., Marín-Spiotta, E., Martínez-Ramos, M., Massoca, P., Meave, J. A., Mesquita, R., Mora, F., Muñoz, R., Muscarella, R., Nunes, Y. R. F., Ochoa-Gaona, S., de Oliveira, A. A., Orihuela-Belmonte, E., Peña-Claros, M., Pérez-García, E. A., Piotta, D., Powers, J. S., Rodríguez-Velázquez, J., Romero-Pérez, I. E., Ruiz, J., Saldarriaga, J. G., Sanchez-Azofeifa, A., Schwartz, N. B., Steininger, M. K., Swenson, N. G., Toledo, M., Uriarte, M., van Breugel, M., van der Wal, H., Veloso, M. D. M., Vester, H. F. M., Vicentini, A., Vieira, I. C. G., Bentos, T. V., Williamson, G. B., and Rozendaal, D. M. A.: Biomass resilience of Neotropical secondary forests, *Nature*, 530, 211–214, doi:10.1038/nature16512, 2016.
- R Core Team: R: A language and environment for statistical computing, available at: <http://www.r-project.org> (last access: 10 February 2016), 2014.
- Ribeiro, G. H. P. M., Suwa, R., Marra, D. M., Kajimoto, T., Ishizuka, M., and Higuchi, N.: Allometry for juvenile trees in an Amazonian forest after wind disturbance, *Japan Agricultural Research Quarterly*, 48, 213–219, 2014.
- Ribeiro, J. E. L. S., Hopkins, M. J. G., Vicentini, A., Sothers, C. A., Costa, M. A. da S., Brito, J. M. de, Souza, M. A. D. de, Martins, L. H. P., Lohmann, L. G., Assunção, P. A. C. L., Pereira, E. da C., Silva, C. F. da, Mesquita, M. R., and Procópio, L. C.: Flora da Reserva Ducke: Guia de Identificação das Plantas Vasculares de uma Floresta de Terra-firme na Amazônia Central, INPA, Manaus, 1999.
- Saatchi, S., Harris, N., S. B., Lefsky, M., Mitchard, E., Salas, W., Zutta, B., Buermann, W., Lewis, S., Hagen, S., Petrova, S., White, L., and Silman, M.: Benchmark map of forest carbon stocks in tropical regions across three continents, *P. Natl. Acad. Sci. USA*, 108, 9899–9904, 2011.
- Saldarriaga, J. G., West, D. C., Tharp, M. L., and Uhl, C.: Long-Term Chronosequence of Forest Succession in the Upper Rio Negro of Colombia and Venezuela, *J. Ecol.*, 76, 938–958, 1998.
- Santos Jr., U. M., Gonçalves, J. F. de C., and Feldpausch, T. R.: Growth, leaf nutrient concentration and photosynthetic nutrient use efficiency in tropical tree species planted in degraded areas in central Amazonia, *Forest Ecol. Manag.*, 226, 299–309, 2006.
- Sawada, Y., Suwa, R., Jindo, K., Endo, T., Oki, K., Sawada, H., Arai, E., Shimabukuro, Y. E., Celes, C. H. S., Campos, M. A. A., Higuchi, F. G., Lima, A. J. N., Higuchi, N., Kajimoto, T., and Ishizuka, M.: A new 500-m resolution map of canopy height for Amazon forest using paceborne LiDAR and cloud-free MODIS imagery, *Int. J. Appl. Earth Obs. Geoinf.*, 43, 92–101, 2015.
- Schiatti, J., Emilio, T., Rennó, C. D., Drucker, D. P., Costa, F. R. C., Nogueira, A., Baccaro, F. B., Figueiredo, F., Castilho, C. V., Kinupp, V., Guillaumet, J.-L., Garcia, A. R. M., Lima, A. P., and Magnusson, W. E.: Vertical distance from drainage drives floristic composition changes in an Amazonian rainforest, *Plant Ecol. Divers.*, 7, 1–13, doi:10.1080/17550874.2013.783642, 2013.
- Schinker, M. G., Hansen, N., and Spiecker, H.: High-frequency density variations – a new method for the rapid evaluation of wood density variations, *IAWA J.*, 24, 231–239, 2003.
- Shugart, H. H. and West, D. C.: *Forest Succession Models*, Bioscience, 30, 308, 1980.
- Sileshi, G. W.: A critical review of forest biomass estimation models, common mistakes and corrective measures, *Forest Ecol. Manag.*, 329, 237–254, 2014.
- Slik, J. W. F., Arroyo-Rodríguez, V., Aiba, S., Alvarez-Loayza, P., Alves, L. F., Ashton, P., Balvanera, P., Bastian, M. L., Belling-

- ham, P. J., van den Berg, E., Bernacci, L., Bispo, P. da C., Blanc, L., Bö-Gaese, K., Boeckx, P., Bongers, F., Boyle, B., Bradford, M., Brearley, F. Q., Hockemba, M. B., Bunyavejchewin, S., Matos, D. C. L., Castillo-Santiago, M., Catharino, E. L. M., Chai, S., Chen, Y., Colwell, R. K., Chazdon, R. L., Clark, C., Clark, D. B., Clark, D. A., Culmsee, H., Damas, K., Dattaraja, H. S., Dauby, G., Davidar, P., DeWalt, S. J., Doucet, J., Duque, A., Durigan, G., Eichhorn, K. A. O., Eisenlohr, P. V., Eler, E., Ewango, C., Farwig, N., Feeley, K. J., Ferreira, L., Field, R., Oliveira Filho, A. T. de, Fletcher, C., Forshed, O., Franco, G., Fredriksson, G., Gillespie, T., Gillet, J., Amarnath, G., Griffith, D. M., Grogan, J., Gunatilleke, N., Harris, D., Harrison, R., Hector, A., Homeier, J., Imai, N., Itoh, A., Jansen, P. A., Joly, C. A., Jong, B. H. J. de, Kartawinata, K., Kearsley, E., Kelly, D. L., Kenfack, D., Kessler, M., Kitayama, K., Kooyman, R., Larney, E., Laumonier, Y., Laurance, S., Laurance, W. F., Lawes, M. J., Amaral, I. L. do, Letcher, S. G., Lindsell, J., Lu, X., Mansor, A., Marjokorpi, A., Marti, E. H., Meilby, H., Melo, F. P. L., Metcalfe, D. J., Medjibe, V. P., Metzger, J. P., Millet, J., Mohandass, D., Montero, J. C., Valeriano, M. de M., Mugerwa, B., Nagamasu, H., Nilus, R., et al.: An estimate of the number of tropical tree species, *P. Natl. Acad. Sci.*, 112, 7472–7477, 2015.
- Spiegelhalter, D. J., Best, N. G., Carlin, B. P., and van der Linde, A.: Bayesian measures of model complexity and fit, *J. R. Stat. Soc. B*, 64, 583–639, 2002.
- Sprugel, D. G.: Correcting for bias in log-transformed allometric equations, *Ecology*, 64, 209–210, 1983.
- ter Steege, H., Pitman, N. C., Sabatier, D., Baraloto, C., Salomão, R. P., Guevara, J. E., Phillips, O. L., Castilho, C. V., Magnusson, W. E., Molino, J., Monteagudo, A., Núñez Vargas, P., Montero, J. C., Feldpausch, T. R., Coronado, E. N. H., Killeen, T. J., Mostacedo, B., Vasquez, R., Assis, R. L., Terborgh, J., Wittmann, F., Andrade, A., Laurance, W. F., Laurance, S., Marimon, B. S., Marimon, B., Vieira, I. C. G., Amaral, I. L., Brien, R., Castellanos, H., López, D. C., Duivenvoorden, J. F., Mogollón, H. F., Matos, F. D. de A., Dávila, N., García-Villacorta, R., Diaz, P. R. S., Costa, F., Emilio, T., Levis, C., Schiatti, J., Souza, P., Alonso, A., Dallmeier, F., Montoya, A. J. D., Fernandez Piedade, M. T., Araujo-Murakami, A., Arroyo, L., Gribel, R., Fine, P., Peres, C., Toledo, M., Aymard, C. G., Baker, T. R., Cerón, C., Engel, J., Henkel, T. W., Maas, P., Petronelli, P., Stropp, J., Zartman, C. E., Daly, D., Neill, D., Silveira, M., Paredes, M. R., Chave, J., Lima Filho, D. de A., Jørgensen, P. M., Fuentes, A., Schöngart, J., Cornejo Valverde, F., Di Fiore, A., Jimenez, E. M., Peñuela Mora, M. C., Phillips, J. F., Rivas, G., van Andel, T. R., von Hildebrand, P., Hoffman, B., Zent, E. L., Malhi, Y., Prieto, A., Rudas, A., Ruschell, A. R., Silva, N., Vos, V., Zent, S., Oliveira, A. A., Schutz, A. C., Gonzales, T., Nascimento, M. T., Ramirez-Angulo, H., Sierra, R., Tirado, M., Medina, M. N. U., van der Heijden, G., Vela, C. I., Torre, E. V., Vriesendorp, C., et al.: Hyperdominance in the Amazonian tree flora, *Science*, 342, 1243092, doi:10.1126/science.1243092, 2013.
- Sterck, F. J. and Bongers, F.: Ontogenetic Changes in Size, Allometry, and Mechanical Design of Tropical Rain Forest Trees, *Am. J. Bot.*, 85, 266–272, 1998.
- Stevens, P. F.: Angiosperm Phylogeny Website, version 12, available at: <http://www.mobot.org/MOBOT/research/APweb/> (last access: 10 September 2015), 2012.
- Sturtz, S., Ligges, U., and Gelman, A.: R2WinBUGS: A Package for Running WinBUGS from R, *J. Stat. Softw.*, 12, 1–16, 2005.
- Suwa, R., Kajimoto, T., Ishizuka, M., Pinto, A. C. M., Trindade, A. S., Silva, R. O., and Higuchi, N.: Comparative study of forest structure between plateau and valley bottom in a central Amazonian forest, *Kanto ShinrinKenkyu*, 63, 85–88, 2012.
- Swaine, M. D. and Whitmore, T. C.: On the definition of ecological species groups in tropical rain forests, *Vegetatio*, 75, 81–86, 1988.
- Telles, E. C., Camargo, P. B., Martinelli, L. A., Trumbore, S. E., Costa, E. S., Santos, J., Higuchi, N., and Oliveira Jr., C.: Influence of soil texture on carbon dynamics and storage potential in tropical forest soils of Amazonia, *Global Biogeochem. Cy.*, 17, 1–12, 2003.
- Todeschini, R., Consonni, V., Mauri, A., and Pavan, M.: Detecting “bad” regression models: Multicriteria fitness functions in regression analysis, *Anal. Chim. Acta*, 515, 199–208, 2004.
- Toledo, J. de, Magnusson, W., Castilho, C., and Nascimento, H.: Tree mode of death in Central Amazonia: Effects of soil and topography on tree mortality associated with storm disturbances, *Forest Ecol. Manag.*, 263, 253–261, 2012.
- Trumbore, S., Brandt, P., and Hartmann, H.: Forest health and global change, *Science*, 349, 814–818, doi:10.1126/science.aac6759, 2015.
- Vieira, S., de Camargo, P. B., Selhorst, D., da Silva, R., Hutyra, L., Chambers, J. Q., Brown, I. F., Higuchi, N., Santos, J. dos, Wofsy, S. C., Trumbore, S. E., and Martinelli, L. A.: Forest structure and carbon dynamics in Amazonian tropical rain forests, *Oecologia*, 140, 468–479, 2004.
- Wickham, H.: *ggplot2: elegant graphics for data analysis*, Springer New York, 2009.
- Williamson, B. G. and Wiemann, M. C.: Measuring wood specific gravity...correctly, *Am. J. Bot.*, 97, 519–524, 2010.
- Wirth, C., Schumacher, J., and Schulze, E.: Generic biomass functions for Norway spruce in Central Europe – a meta-analysis approach toward prediction and uncertainty estimation, *Tree Physiol.*, 24, 121–139, 2004.
- Worbes, M., Staschel, R., Roloff, A., and Junk, W. J.: Tree ring analysis reveals age structure, dynamics and wood production of a natural forest stand in Cameroon, *Forest Ecol. Manag.*, 173, 105–123, 2003.
- Wutzler, T., Wirth, C., and Schumacher, J.: Generic biomass functions for common beech (*Fagus sylvatica* L.) in Central Europe – predictions and components of uncertainty, *Can. J. For. Res.*, 38, 1661–1675, 2008.

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Supplement of

Predicting biomass of hyperdiverse and structurally complex central Amazonian forests – a virtual approach using extensive field data

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Supplement

Tables

Table S1. Summary of the dataset (727 trees from 101 genera and at least 135 tree species) included in this study.

No.	Family	Species	Common name	NT	DBH range	H range	WD level	SG	AGB range
1	Anacardiaceae	<i>Asironium lecointei</i> Ducke	mutacatiara	1	8.5	11.3	0.752	lat	39.3
2	Anacardiaceae	<i>Thyrsodium guianense</i> Sagot ex Marchand	breu de leite	9	5.6-17.7	4.2-19.5	0.630	mid	8.0-245.1
3	Annonaceae	<i>Annona neoinsignis</i> H.Rainer	envira bobó	10	5.4-24.3	6.9-19.8	0.430	pio	5.4-288.2
4	Annonaceae	<i>Bocageopsis multiflora</i> (Mart.) R.E. Fr.	envira surucucu	2	6.0-21.4	9.0-28.5	0.643	mid	22.2-712.2
5	Annonaceae	<i>Duguetia</i> spp.	envira vermelha	4	6.5-13.9	12-17.5	0.787	lat	23.5-165.1
6	Annonaceae	<i>Duguetia surinamensis</i> R.E. Fr.	envira amarela	2	5.2-5.5	6.0-7.3	0.800	lat	15.2-15.8
7	Annonaceae	<i>Guatteria olivacea</i> R.E. Fr.	envira fofá, envira preta lisa	13	6.8-34.2	11-25.6	0.510	pio	26.6-1690.2
8	Annonaceae	<i>Guatteria</i> spp.	envira branca	3	5.9-16.6	10.8-17.8	0.556	pio	14.4-206.6
9	Annonaceae	ni	envira	1	12.4	18.5	0.630	mid	102.9
10	Annonaceae	<i>Unonopsis stipitata</i> Diels	envira preta cascuda	2	5.5-6.5	8.0-10.8	0.686	mid	12.7-33.9
11	Annonaceae	<i>Xylopia benthamii</i> R.E. Fr.	envira taripucu, embiriba	10	6.6-17.8	5.9-19.2	0.600	mid	20.7-210.2
12	Annonaceae	<i>Xylopia</i> spp.	envira pimenta	4	7.7-12.0	9.8-16.0	0.626	gen	31.1-137.5
13	Apocynaceae	<i>Aspidosperma desmanthum</i> Benth. ex Müll. Arg.	pequiá marfim	1	85.0	33.0	0.610	lat	7509.1
14	Apocynaceae	<i>Couma guianensis</i> Aubl.	sorvinha	1	7.0	8.9	0.560	lat	27.0
15	Apocynaceae	<i>Couma utilis</i> (Mart.) Müll. Arg.	sorva	1	8.5	14.5	0.660	lat	35.0
16	Apocynaceae	<i>Geissospermum argenteum</i> Woodson	acariquera branca	3	5.2-9.8	7.6-13.0	0.760	lat	15.6-66.3
17	Araliaceae	<i>Schefflera morototoni</i> (Aubl.) Maguire, Steyerl. & Frodin	morototó	12	5.8-33.1	9.0-27.0	0.437	pio	9.0-909.3
18	Bignoniaceae	<i>Jacaranda copaia</i> (Aubl.) D. Don	jacaranda, pará pará	1	13.5	17.8	0.348	pio	69.8
19	Boraginaceae	<i>Cordia</i> cf. <i>naidophylla</i>	freijó	2	5.6-6.4	8.6-10.3	0.520	mid	14.2-28.4
20	Burseraceae	<i>Protium decandrum</i> (Aubl.) Marchand	breu branco	5	5.8-9.3	9.9-15.4	0.560	mid	15.3-58.5
21	Burseraceae	<i>Protium hebetatum</i> D.C. Daly	breu vermelho	11	5.2-30.0	4.2-25.0	0.579	mid	7.7-1258.9
22	Burseraceae	<i>Protium</i> sp.	breu	1	10.7	15.0	0.579	gen	74.7
23	Burseraceae	<i>Protium trifoliatum</i> Engl.	breu peludo	1	6.5	12.0	0.640	mid	20.8
24	Burseraceae	<i>Tetragastris panamensis</i> (Engl.) Kuntze	breu manga	13	5.0-17.5	3.9-19.0	0.742	mid	7.9-159.1
25	Caryocaraceae	<i>Caryocar pallidum</i> A.C. Sm.	piquiarana	2	5.9-8.1	8.8-12.6	0.680	lat	21.4-75.8
26	Chrysobalanaceae	<i>Acioa longipendula</i> (Pitig.) Sothers & Prance	castanha de galinha	1	48.3	29.2	0.940	lat	3994.5
27	Chrysobalanaceae	<i>Licania coriacea</i> Benth.	marí bravo	4	5.8-10.5	10.5-12.3	0.880	lat	19.9-113.7

No.	Family	Species	Common name	NT	DBH range	H range	WD level	WD range	SG	AGB range
28	Chrysobalanaceae	<i>Licania heteromorpha</i> Benth.	macucú fofo	1	7.0	14.3	spp	0.740	lat	38.8
29	Chrysobalanaceae	<i>Licania oblongifolia</i> Standl.	macucú chiador	2	5.0-13.5	8.5-17.6	spp	0.878	lat	19.1-178.6
30	Chrysobalanaceae	<i>Licania</i> spp.	macucú	5	5.2-9.9	7.5-17.8	gen	0.822	lat	16.7-121.3
31	Clusiaceae	<i>Tovomita</i> spp.	sapateteiro	2	8.7-37.0	17.2-28.4	gen	0.799	mid	69.0-1624.7
32	Combretaceae	<i>Buchenavia</i> sp.	tanimbuca	1	33.8	17.9	gen	0.719	lat	1801.4
33	Comaraceae	<i>Comarus perrotteti</i> (DC.) Planch.	sacaca brava	28	5.2-8.9	6.2-12.3	gen	0.450	pio	15.0-69.0
34	Dichapetalaceae	<i>Tapura amazonica</i> Poepp.	tapura	2	20-21.2	18.9-21.2	gen	0.711	mid	355.8-599.8
35	Elaeocarpaceae	<i>Sloanea</i> sp.	urucurana	1	5.8	7.6	gen	0.827	lat	21.2
36	Euphorbiaceae	<i>Alchorneopsis</i> sp.	supiarana	1	19.5	23.0	gen	0.390	pio	336.5
37	Euphorbiaceae	<i>Croton draconoides</i> Müll. Arg.	sacaca	6	5.1-7.9	5.7-12.0	gen	0.626	pio	9.0-20.5
38	Euphorbiaceae	<i>Croton matourensis</i> Aubl.	dima	69	5.4-28.7	8.7-26.5	spp	0.620	pio	12.9-1066.6
39	Euphorbiaceae	<i>Hevea guianensis</i> Aubl.	seringa vermelha	1	8.0	11.6	spp	0.575	lat	39.1
40	Euphorbiaceae	<i>Mabea angularis</i> Hollander	taquari branco	4	7.0-11.8	10.0-16.2	gen	0.634	mid	20.6-105.0
41	Euphorbiaceae	<i>Mabea piriiri</i> Aubl.	taquari vermelho	21	5.3-16.5	6.4-24.2	spp	0.617	mid	13.5-321.5
42	Euphorbiaceae	<i>Mabea</i> spp.	taquari	5	6.2-9.3	11.8-15.0	gen	0.634	mid	22.6-58.2
43	Euphorbiaceae	<i>Micrandra</i> spp.	seringarana	12	5.1-35.0	7.4-27.5	gen	0.848	lat	15.9-1677.5
44	Euphorbiaceae	<i>Micrandropsis scleroxylon</i> (W.A. Rodrigues) W.A. Rodrigues	piãozinho	11	5.7-32.4	7.2-25.0	spp	0.880	lat	22.9-1235.5
45	Euphorbiaceae	<i>Pogonophora schomburgkiana</i> Miens ex Benth.	amarelinho	1	5.6	10.0	spp	0.833	lat	48.2
46	Fabaceae	<i>Andira micrantha</i> Ducke	sucupira preta	2	6.0-8.1	7.5-12.3	spp	1.000	lat	19.0-45.1
47	Fabaceae	<i>Andira</i> spp.	sucupira	3	5.2-35.0	10.0-30.0	gen	0.730	lat	15.4-2012.2
48	Fabaceae	<i>Bocoa viridiflora</i> (Ducke) R.S. Cowan	muirajiboia preta	1	22.6	20.8	spp	0.835	lat	1165.0
49	Fabaceae	<i>Cedrelina cateniformis</i> (Ducke) Ducke	cedrorana	1	55.0	34.1	spp	0.480	lat	3754.2
50	Fabaceae	<i>Dipteryx magnifica</i> Ducke	cumarana	1	7.0	16.0	gen	0.940	lat	43.3
51	Fabaceae	<i>Eperua glabriflora</i> (Ducke) R.S. Cowan	muirapiranga	3	7.5-30.5	9.4-20.5	spp	0.759	lat	23.8-1304.4
52	Fabaceae	<i>Inga cf. peizizifera</i>	ingá vermelha	14	5.5-31.3	7.0-23.0	spp	0.650	pio	14.0-1562.8
53	Fabaceae	<i>Inga</i> spp.	ingá branca	11	5.3-24.9	5.9-22.5	gen	0.614	mid	8.3-485.8
54	Fabaceae	<i>Inga thibaudiana</i> DC.	ingá peluda	5	9.231.9	15-22.7	spp	0.657	mid	62.2-1509.0
55	Fabaceae	<i>Macarolobium</i> spp.	ingarana	3	10.3-19.5	14.3-17.0	gen	0.606	mid	78.3-374.9
56	Fabaceae	<i>Ormosia</i> spp.	tento	5	8.0-37.5	12.7-25.4	gen	0.676	mid	30.5-1606.9
57	Fabaceae	<i>Parkia</i> sp.	fava parkia	2	6.5-9.5	9.0-12.5	gen	0.532	lat	10.6-85.0
58	Fabaceae	<i>Pterocarpus rohrii</i> Vahl	mutuí	2	29.8-35.5	27.3-34.5	spp	0.550	mid	1240.0-1740.6
59	Fabaceae	<i>Strychnodendron guianense</i> (Aubl.) Benth.	fava camuzé	14	5.5-32.9	9.5-27.0	spp	0.650	mid	7.5-1120.5
60	Fabaceae	<i>Swarzia ingifolia</i> Ducke	acupú amarelo, ingá ferro	1	40.4	21.6	spp	0.815	lat	1345.3
61	Fabaceae	<i>Swarzizia cf. recurva</i>	muirajiboia amarela	2	7.7-12.0	11.7-17.2	gen	0.883	lat	39.7-155.5

No.	Family	Species	Common name	NT	DBH range	H range	WD	WD level	SG	AGB range
62	Fabaceae	<i>Tachigali setifera</i> (Ducke) Zarucchi & Herend.	tachi preto	1	7.0	17.2	0.670	spp	pio	36.5
63	Fabaceae	<i>Zygia racemosa</i> (Ducke) Barneby & J.W. Grimes	angelim pedra	3	6.2-10.7	9.0-15.5	0.748	spp	lat	23.9-82.9
64	Fabaceae	<i>Zygia ramiflora</i> (F. Muell.) Kosterm.	ingá copaiba	2	7.2	8.4-11.3	0.727	gen	mid	16.8-33.0
65	Goupiaceae	<i>Goupiá glabra</i> Aubl.	cupiúba	17	5.1-14.2	7.7-17.0	0.730	spp	mid	12.9-216.4
66	Humiriaceae	<i>Endopleura</i> spp.	uchi amarelo	1	9.0	16.8	0.775	gen	lat	72.0
67	Humiriaceae	ni.2	uchi preto	1	14.0	18.5	0.819	fam	lat	281.2
68	Humiriaceae	<i>Sacoglottis ceratocarpa</i> Ducke	uchi coco	1	9.5	12.5	0.807	gen	lat	109.9
69	Humiriaceae	<i>Vantanea</i> sp.	uchirana	1	19.0	17.6	0.857	gen	lat	324.8
70	Hypericaceae	<i>Vismia guianensis</i> (Aubl.) Pers.	lacre branco	15	6.1-23.8	8.6-23.5	0.475	spp	pio	12.0-508.1
71	Lauraceae	<i>Aniba ferrea</i> Kubitzki	louro chumbo	1	29.8	26.6	0.709	gen	lat	1484.5
72	Lauraceae	ni.3	louro amarelo	1	9.2	14.5	0.656	fam	mid	58.1
73	Lauraceae	ni.4	louro fofo	1	5.2	7.8	0.656	fam	mid	21.6
74	Lauraceae	<i>Ocotea</i> spp.	louro preto	4	7.0-36.2	10.0-27.0	0.598	gen	lat	25.2-2162.6
75	Lauraceae	<i>Rhodostemonodaphne</i> spp.	louro peludo	1	6.5	12.2	0.395	gen	mid	35.6
76	Lecythidaceae	<i>Cariniana integrifolia</i> Ducke	tauari	6	5.0-7.5	6.4-10.0	0.490	spp	lat	12.2-29.1
77	Lecythidaceae	<i>Couratari</i> sp.	tauari vermelho	1	5.2	10.5	0.549	gen	lat	19.9
78	Lecythidaceae	<i>Eschweilera atropetiolata</i> S.A. Mori	castanha vermelha	1	20.4	25.5	0.753	spp	lat	715.2
79	Lecythidaceae	<i>Eschweilera collina</i> Eyma	ripeiro branco	2	7.7-15.7	11.2-17.7	0.778	spp	lat	20.5-178.0
80	Lecythidaceae	<i>Eschweilera</i> spp.	matamata	8	5.1-34.3	8.6-28.0	0.810	gen	lat	19.6-2588.0
81	Lecythidaceae	<i>Gustavia</i> cf. <i>elliptica</i>	mucurão	3	7.0-10.2	8.2-13.1	0.648	gen	mid	22.3-93.9
82	Lecythidaceae	<i>Lecythis barnebyi</i> S.A. Mori	castanha jarana	2	7.0-31.0	8.3-24.7	0.821	gen	lat	22.9-1785.8
83	Lecythidaceae	<i>Lecythis gracileana</i> S.A. Mori	castanha jarana folha miúda	1	16.5	18.0	0.830	spp	lat	348.6
84	Lecythidaceae	<i>Lecythis</i> sp.	ripeiro vermelho	1	42.4	27.6	0.821	gen	lat	3999.8
85	Lecythidaceae	ni.5		1	5.5	9.5	0.713	fam	lat	18.0
86	Malpighiaceae	<i>Byrsonima duckeana</i> W.R. Anderson	murici vermelho	23	5.6-25.7	9.0-22.1	0.671	gen	pio	21.9-1036.6
87	Malvaceae	<i>Scleronema micranthum</i> (Ducke) Ducke	cardeiro	2	11.5-38.4	13.2-27.6	0.595	spp	mid	75.2-2298.9
88	Malvaceae	<i>Theobroma sylvestre</i> Aubl. ex Mart.	cacaú	1	5.3	10.4	0.470	spp	mid	20.4
89	Melastomataceae	<i>Bellucia dichotoma</i> Cogn.	goiaba de arta	7	6.3-24.5	9.0-21.8	0.607	gen	pio	30.5-775.6
90	Melastomataceae	<i>Miconia argyrophylla</i> DC.	buxuku canela de velho	3	5.1-26.0	8.2-22.0	0.637	gen	pio	14.1-426.0
91	Melastomataceae	<i>Miconia minutiflora</i> (Bonpl.) DC.	tinteira, tintarana	4	6.0-13.3	6.3-18.2	0.637	gen	mid	32.5-219.2
92	Melastomataceae	<i>Miconia</i> spp.	buxuku	24	5.3-13.7	7.8-15.6	0.637	gen	pio	13.9-198.4
93	Melastomataceae	<i>Mauriti</i> sp.	mamãozinho	1	63.2	32.0	0.740	gen	mid	6655.1
94	Meliaceae	<i>Guarea</i> spp.	gitó vermelho	8	5.2-7.3	7.2-11.4	0.652	gen	lat	12.9-30.7
95	Meliaceae	<i>Trichilia</i> sp.	gitó branco	1	5.5	10.7	0.740	gen	lat	17.2

No.	Family	Species	Common name	NT	DBH range	H range	WD	WD level	SG	AGB range
96	Moraceae	<i>Brosimum rubescens</i> Taub.	pau rainha	1	10.5	14.8	0.878	spp	lat	101.9
97	Moraceae	<i>Brosimum</i> spp.	muitatinga	4	6.1-8.5	8.1-11.0	0.666	gen	mid	14.2-57.2
98	Moraceae	<i>Helianthostylis sprucei</i> Baill.	falsa rainha	1	9.8	10.4	0.628	spp	mid	63.1
99	Moraceae	<i>Pseudolmedia</i> sp.	muitatinga	1	13.7	19.0	0.630	gen	mid	182.9
100	Moraceae	<i>Soroea guillemintiana</i> Gaudich.	jaca brava	2	5.3-5.7	8.0	0.612	gen	mid	11.8-12.2
101	Myristicaceae	<i>Iryanthera juruensis</i> Warb.	ucutuba punã	3	10.1-22.0	12.85-22.0	0.663	spp	mid	65.1-544.5
102	Myristicaceae	<i>Iryanthera lancifolia</i> Ducke	ucutuba vermelha	1	8.5	10.9	0.634	gen	mid	38.1
103	Myristicaceae	<i>Iryanthera</i> sp.	ucutuba	1	32.0	25.0	0.634	gen	mid	1036.6
104	Myristicaceae	<i>Iriola michelii</i> Heckel	ucutuba preta	1	8.7	13.0	0.529	spp	mid	58.8
105	Myrtaceae	<i>Eugenia</i> spp.	araçã	3	5.9-6.8	8.4-9.8	0.742	gen	mid	21.3-24.7
106	Myrtaceae	ni.6	araçã bravo	3	8.0-14.1	14.1-17.0	0.788	fam	mid	64.8-230.7
107	Nyctaginaceae	<i>Nees</i> spp.	joão mole	5	5.9-9.3	6.8-9.0	0.631	gen	mid	17.3-38.4
108	Ochnaceae	<i>Oouratea</i> cf. <i>dischophora</i>	uchi de morego	2	5.3-11.1	12.3-14.8	0.743	gen	mid	35.0-123.0
109	Oleaceae	ni.7		1	27.0	24.0	0.692	fam	lat	926.3
110	Peraeae	<i>Pera schomburgkiana</i> (Klotzsch) Müll. Arg.	pera	1	6.2	11.0	0.590	spp	mid	30.4
111	Rubiaceae	<i>Amaïona guianensis</i> Aubl.	muitaximbé	1	6.0	8.3	0.670	spp	mid	19.8
112	Rubiaceae	<i>Faramea</i> spp.	taboquinha	3	6.0-15.0	7.7-17.9	0.618	gen	mid	23.9-134.7
113	Rubiaceae	<i>Psychotria</i> spp.	taboqua mata gado	2	6.2-6.9	8.5-10.6	0.564	gen	mid	29.5-39.0
114	Rutaceae	<i>Zanthoxylum</i> sp.	limãozinho	1	6.1	7.0	0.602	gen	mid	13.5
115	Salicaceae	<i>Cassaria arborea</i> (Rich.) Urb.	piabinha	4	5.5-9.5	9.4-15.0	0.535	spp	pio	37.9-93.0
116	Salicaceae	<i>Laetia procera</i> (Poepp.) Eichler	periquiteira	86	5.2-15.8	4.9-20.3	0.664	spp	pio	7.8-244.7
117	Sapindaceae	<i>Toulicia guianensis</i> Aubl.	pitomba da mata	3	7.8-9.7	13.0-14.7	0.756	spp	mid	33.5-80.0
118	Sapotaceae	<i>Chrysophyllum</i> cf. <i>prieurii</i>	abiurana sabiã, abiurana roxa	1	38.6	28.8	0.715	gen	lat	2890.4
119	Sapotaceae	<i>Micropholis guyanensis</i> subsp. <i>guyanensis</i> (Baehni) T.D. Penn.	maparajuba, balata brava	1	19.4	23.3	0.663	spp	lat	445.7
120	Sapotaceae	<i>Micropholis</i> sp.	balata rosada, chiclete bravo	1	31.0	27.0	0.676	spp	lat	1535.2
121	Sapotaceae	<i>Pouteria anomala</i> (Pires) T.D. Penn.	abiurana olho de veado	1	45.0	32.7	0.765	spp	lat	3729.8
122	Sapotaceae	<i>Pouteria manaosensis</i> (Aubrév. & Pellegr.) T.D. Penn.	abiurana roxa	1	6.2	8.3	0.640	spp	lat	21.7
123	Sapotaceae	<i>Pouteria oblanceolata</i> Pires	cucutiriba folha peluda	2	8.8-13.7	11.8-21.0	0.790	spp	lat	79.4-234.9
124	Sapotaceae	<i>Pouteria</i> spp.	abiurana	5	7.3-44.0	12.2-24.0	0.801	gen	lat	45.4-2934.2
125	Simaroubaceae	<i>Simarouba amara</i> Aubl.	marupá	1	27.5	21.5	0.404	spp	pio	555.6
126	Siparunaceae	<i>Siparuna</i> cf. <i>guyanensis</i>	caapitiú	10	5.4-9.3	4.5-13.0	0.593	gen	mid	15.9-92.2
127	Urticaceae	<i>Cecropia purpurascens</i> C.C. Berg	imbatuba roxa	3	11.8-15.5	14.8-16.5	0.430	spp	pio	63.9-106.4
128	Urticaceae	<i>Cecropia sciadophylla</i> Mart.	imbatuba gigante	33	8.4-37.2	10.9-23.0	0.412	spp	pio	21.6-1543.6
129	Urticaceae	<i>Pourouma</i> sp.	imbaubarana	1	17.3	18.0	0.389	gen	pio	125.9

No.	Family	Species	Common name	NT	DBH range	H range	WD range	WD level	SG	AGB range
130	Urticaceae	<i>Pourouma tomentosa</i> Mart. ex Miq.	imbaubarana	4	5.7-29.7	8.5-20.0	0.395	spp	pio	8.5-797.8
131	Verbenaceae	<i>Aegiphila</i> sp.	tabaco bravo	2	18.4-20.0	12.4-20.1	0.555	gen	pio	113.3-253.2
132	Violaceae	<i>Leonia cymosa</i> Mart.	mucurão	1	11.4	11.1	0.673	gen	mid	85.0
133	Violaceae	<i>Rinorea racemosa</i> (Mart.) Kuntze	branquinha, cancela de jacamim	9	5.0-10.5	8.0-18.0	0.682	spp	mid	14.6-114.8
134	Violaceae	<i>Rinorea</i> cf. <i>guyanensis</i>	falsa cupiúba	5	5.3-23.4	9.4-24.0	0.709	gen	mid	18.1-751.9
135	Voehysiaceae	<i>Erisma bracteosum</i> Ducke	quaruba	3	5.4-7.1	7.0-8.9	0.533	gen	lat	15.2-27.0

Species' attributes: botanic family (Family) and species' name (Species) according to the APGIII system (Stevens, 2012); species' common name in Central Amazon (Common name); number of trees (NT); diameter at breast height (DBH) (cm); tree total height (H) (m); wood density (WD) (g cm^{-3}); wood density assignment level (WD level) (value at species level [spp], value at genus level [gen] and value at family level [fam]); species' successional group (SG) (pioneer species [pio], mid-successional species [mid] and late-successional species [lat]); and aboveground biomass (AGB) (dry mass in kg).

Table S2. Attributes used to assign tree species into successional groups.

SG	Architecture, morphology and anatomy				Ecology and life history			DMo	
	BFo	CPo	CSi	CCo	GAs	NRe			
pio	pla, ort	can, eme	med, lar	rou, ell, irr	12.4 (5.1,37.2)	0.573 (0.348,0.671)	yes	BW4, BW7, BW14, BW17, SE14, SGa	ane, zoo
mid	ort	und, can	sma, med	elo, con, irr	9.8 (5.0,35.5)	0.656 (0.395,0.833)	yes	BW17, BW24, BW27, SE23, OG, SGa	zoo, ane
lat	unb	can, eme	med, lar	rou, ell	14.0 (5.0,85.0)	0.735 (0.480,1.000)	no	BW24, BW27, OG	aut, zoo

Attributes_[references]: species' successional group (SG) (pioneer species [pio], mid-successional species [mid] and late-successional species [lat])_[1]; predominant branch form (BFo) (plagiotropic [pla], orthotropic [ort] and unbranched [unb])_[2,3]; general vertical crown position of a mature tree (CPo) (understory/suppressed crown [und], canopy/co-dominant crown [can] and emergent crown [eme])_[2,3]; relative crown size of a mature tree (CSi)(small-sized crown [sma], medium-sized crown [med] and large-size crown [lar])_[2,3]; general crown contour of a mature tree (CCo) (round [rou], elliptic [ell], elongated [elo], conic [con] and irregular [irr])_[2,3,4]; mean diameter at breast height (DBH) (cm) (minimum and maximum) of the trees included in this study (mDBH)_[5]; mean wood density (g cm⁻³) (minimum and maximum) of the tree species included in this study (mWD)_[5]; gap-associated species (GAs)_[3]; natural regeneration niche mostly observed (NRe)_[3]; major seed dispersion mode (DMo) (anemochory [ane], autochory [aut] and zoochory [zoo])_[6]. References: [1] Amaral et al., 2009; Chambers et al., 2009; Kammesheidt, 2000; Marra et al., 2014; Saldarriaga et al., 1998; Swaine and Whitmore, 1988; [2] Hallé, 1974; Hallé et al., 1978; allometric data from this study (Table S1); [3] Network of permanent plots including an old-growth (OG) forest (LMF unpublished data [census from 1996 to 2012] and Silva et al., 2002), a four year-old blowdown (BW4) (Marra et al., 2014), a seven year-old blowdown (BW7), a 14 year-old blowdown (BW14), a 17 year-old blowdown (BW17), a 24 year-old blowdown (BW24), a 27 year-old blowdown (BW27) (LMF unpublished data), a 14 year-old slash and burn secondary forest (SE14), a 23 year-old clear cut secondary forest (SE23) (Lima et al., 2007; Silva, 2007) and small (< c. 2000 m²) canopy gaps (SGa) (LMF unpublished data [1996-2012 census]); [4] Myers, 1982; Trichon, 2001; [5] Dataset from this study (Table 1 and Table S1); [6] Camargo et al., 2008; Ferraz et al., 2004; Ribeiro et al., 1999; Saravy et al., 2003; Silva Junior and Pereira, 2009; Stefanello et al., 2009, 2010; Terborgh et al., 2008.

Table S3. Parameters (low [2.5%] and high [97.5%] confidence interval) of the 24 tree aboveground biomass estimation models fit in this study. See the Table 2 for checking the equations and variance modeling approaches, and the Table 3 for checking models' statistics.

Model series	Model	SG	b1	b2	b3	b4	c1	c2
1	M11		1.010 (0.858,1.179)	2.052 (2.012,2.093)			190.5 (180.8,200.4)	
	M12		-1.148 (-1.262,-1.031)	2.338 (2.289,2.386)			0.359 (0.341,0.378)	
	M13		0.336 (0.299,0.377)	2.339 (2.290,2.387)			0.106 (0.085,0.132)	2.374 (2.285,2.464)
2	M21	pio	0.496 (0.262,0.835)	2.191 (2.018,2.371)			148.8 (141.6,156.7)	
		mid	0.248 (0.082,0.521)	2.499 (2.243,2.795)				
		lat	4.284 (3.632,4.989)	1.714 (1.675,1.754)				
M22	pio		-0.874 (-1.049,-0.705)	2.203 (2.133,2.274)			0.345 (0.328, 0.365)	
		mid	-1.296 (-1.544,-1.053)	2.400 (2.290, 2.512)				
		lat	-1.335 (-1.535,-1.140)	2.481 (2.402,2.562)				
M23	pio		0.445 (0.375,0.522)	2.202 (2.135,2.271)			0.151 (0.107,0.209)	2.199 (2.061,2.335)
		mid	0.297 (0.235,0.377)	2.394 (2.289,2.487)			0.234 (0.138,0.372)	2.038 (1.820,2.264)
		lat	0.269 (0.228,0.314)	2.489 (2.422,2.554)			0.060 (0.037,0.092)	2.574 (2.401,2.756)
3	M31		1.714 (1.502,1.953)	2.036 (2.002,2.069)	1.035 (0.944,1.126)		144.3 (137.1,152.0)	
	M32		-0.869 (-0.986,-0.753)	2.375 (2.329,2.420)	0.749 (0.624,0.876)		0.329 (0.313,0.347)	
	M33		0.415 (0.373,0.460)	2.401 (2.361,2.439)	0.755 (0.631,0.881)		0.150 (0.119,0.186)	2.189 (2.097,2.282)
4	M41	pio	0.332 (0.181,0.548)	2.577 (2.398,2.767)	1.233 (0.981,1.492)		130.5 (124.1,137.6)	
		mid	0.244 (0.097,0.479)	2.484 (2.238,2.760)	-0.070 (-0.582,0.458)			
		lat	3.293 (2.797,3.832)	1.848 (1.804,1.893)	0.716 (0.591,0.841)			
M42	pio		-0.552 (-0.724,-0.378)	2.279 (2.211,2.346)	0.875 (0.692,1.055)		0.323 (0.307,0.341)	
		mid	-1.193 (-1.465,-0.913)	2.408 (2.306,2.510)	0.284 (-0.125,0.683)			

Model series	Model	SG	b1	b2	b3	b4	c1	c2
5		lat	-1.141 (-1.364,-0.919)	2.468 (2.394,2.544)	0.510 (0.185,0.829)			
	M43	pio	0.539 (0.454,0.640)	2.326 (2.251,2.397)	0.880 (0.687,1.079)		0.217 (0.151,0.300)	2.005 (1.868,2.150)
		mid	0.362 (0.268,0.490)	2.395 (2.285,2.494)	0.464 (0.054,0.956)		0.211 (0.205,0.329)	2.082 (1.874,2.304)
		lat	0.323 (0.270,0.386)	2.475 (2.409,2.538)	0.481 (0.222,0.750)		0.059 (0.037,0.090)	2.561 (2.389,2.744)
6	M51		0.078 (0.051,0.114)	1.561 (1.492,1.636)	1.347 (1.152,1.527)		164.3 (156.2,173.0)	
	M52		-2.098 (-2.290,-1.912)	1.928 (1.847,2.010)	0.735 (0.615,0.856)		0.329 (0.312,0.346)	
	M53		0.147 (0.117,0.179)	1.971 (1.884,2.057)	0.650 (0.523,0.781)		0.092 (0.073,0.116)	2.405 (2.310,2.501)
	M61	pio	0.029 (0.007,0.076)	1.926 (1.729,2.125)	1.252 (0.860,1.632)		134.1 (127.2,141.1)	
7		mid	0.144 (0.052,0.316)	2.173 (1.822,2.543)	0.508 (0.036,0.900)			
		lat	0.697 (0.454,1.041)	1.414 (1.343,1.482)	0.896 (0.709,1.077)			
	M62	pio	-1.946 (-2.238,-1.663)	1.820 (1.713,1.930)	0.751 (0.583,0.921)		0.314 (0.298,0.331)	
		mid	-2.101 (-2.405,-1.799)	1.900 (1.740,2.062)	0.762 (0.562,0.958)			
8		lat	-2.223 (-2.665,-1.814)	2.099 (1.914,2.271)	0.688 (0.406,1.001)			
	M63	pio	0.170 (0.118,0.234)	1.870 (1.757,1.984)	0.664 (0.471,0.863)		0.140 (0.098,0.192)	2.202 (2.067,2.341)
		mid	0.147 (0.101,0.207)	1.970 (1.796,2.149)	0.655 (0.414,0.883)		0.193 (0.112,0.309)	2.090 (1.866,2.328)
		lat	0.120 (0.083,0.169)	2.141 (2.000,2.288)	0.626 (0.379,0.861)		0.056 (0.035,0.084)	2.563 (2.388,2.742)
9	M71		0.143 (0.099,0.192)	1.577 (1.517,1.631)	1.273 (1.136,1.435)		118.0 (112.1,124.2)	
	M72		-1.733 (-1.921,-1.541)	2.010 (1.934,2.085)	0.643 (0.530,0.756)		0.305 (0.290,0.321)	
	M73		0.186 (0.149,0.227)	2.096 (2.017,2.170)	0.706 (0.584,0.831)		0.143 (0.112,0.181)	2.183 (2.083,2.285)
	M81	pio	0.062 (0.023,0.135)	2.318 (2.121,2.512)	0.802 (0.485,1.121)		108.4 (103.0,114.4)	
10		mid	0.074 (0.019,0.175)	2.078 (1.760,2.385)	0.933 (0.409,1.516)		6.58 (0.063,1.294)	
		lat	0.243 (0.168,0.345)	1.479 (1.422,1.539)	1.224 (1.061,1.368)		0.851 (0.754,0.948)	

Model series	Model	SG	b1	b2	b3	b4	c1	c2
M82	pio		-1.403 (-1.718,-1.397)	1.981 (1.873,2.092)	0.555 (0.385,0.731)	0.713 (0.534,0.886)	0.300 (0.284,0.317)	
	mid		-2.011 (-2.323,-1.685)	1.909 (1.757,2.065)	0.757 (0.566,0.948)	0.225 (-0.145,0.600)		
	lat		-1.982 (-2.447,-1.450)	2.133 (1.954,2.335)	0.609 (0.259,0.909)	0.362 (0.054,0.676)		
M83	pio		0.254 (0.175,0.344)	2.082 (1.958,2.192)	0.760 (0.570,0.954)	0.479 (0.311,0.683)	0.209 (0.145,0.295)	2.005 (1.860,2.151)
	mid		0.175 (0.113,0.255)	1.971 (1.791,2.137)	0.446 (0.074,0.872)	0.661 (0.445,0.901)	0.178 (0.103,0.286)	2.124 (1.899,2.362)
	lat		0.150 (0.116,0.214)	2.173 (2.033,2.314)	0.364 (0.117,0.617)	0.558 (0.321,0.798)	0.058 (0.035,0.088)	2.538 (2.362,2.730)

Table S4. Root-mean-square error (RMSE) and bias (absolute and relative values) from tree aboveground biomass predictions made by using the Chave et al. (2014)'s pantropical estimation model. Predictions were made for all the six different successional scenarios included in this study. The Chave et al. (2014)'s pantropical estimation model has diameter at breast height (DBH), tree total height (H) (estimated from a DBH: H relationship), wood density (WD) and environmental stress as predictors.

Scenarios	RMSE (Mg)	Bias (Mg)	Bias (%)
Early-succession	73.3	-73.2	-30.7
Mid-succession	81.7	-80.9	-29.2
Late-succession	115.0	-114.1	-27.9
Small-sized	99.5	-99.3	-30.7
Mid-sized	116.0	-115.4	-30.2
Large-sized	130.2	-130.2	-29.6
Mean	102.6	-102.2	-29.7

Figures

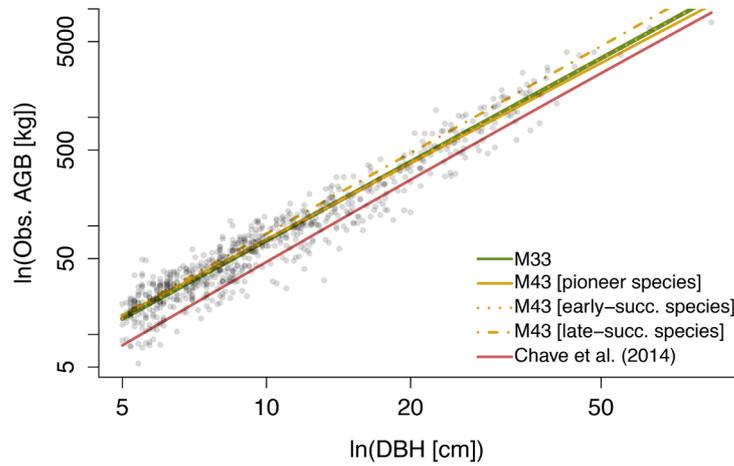


Figure S1. Fit of the two best tree aboveground estimation models parameterized in this study (M33 and M43) and that from Chave et al. (2014)'s pantropical model. Note that the pantropical model underestimates the biomass of the small-sized trees (diameter at breast height < 21 cm). This pattern was also observed at the landscape-level (Fig. S2).

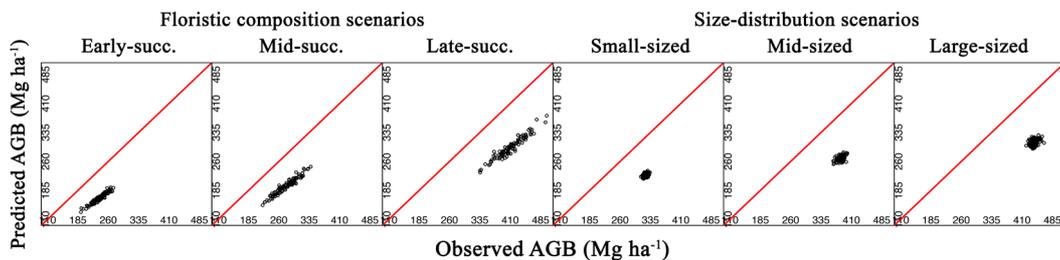


Figure S2. Predicted vs. observed aboveground biomass (AGB) along six forest-scenarios composed of 100 1-ha plots. The line of equality (1:1 line) is shown as a red/straight line. Forest scenarios were designed to reflect landscape-level variations in floristic composition and size-distribution of trees, typical of Central Amazon terra firme forests. Floristic composition and size-distribution scenarios followed the sampling scheme described in section 2.4.2 (Fig. 2) of this study. Here, the predictions were made by using the Chave et al. (2014)'s pantropical model, which has diameter at breast height (DBH), tree total height (H) (estimated from a DBH: H relationship), wood density (WD) and environmental stress as predictors.

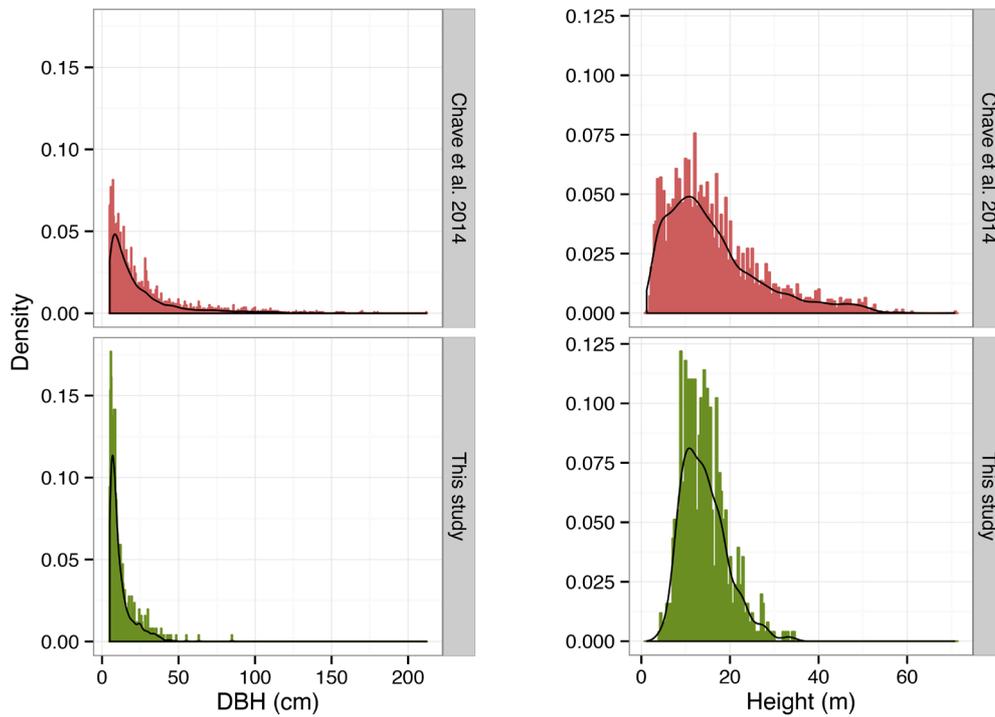


Figure S3. DBH- (diameter at breast height) and height-distribution of trees included in Chave et al. (2014)'s pantropical model ($n = 4004$) and those from this study ($n = 727$). Note the great density/probability difference for small- and large-sized trees between the two datasets.

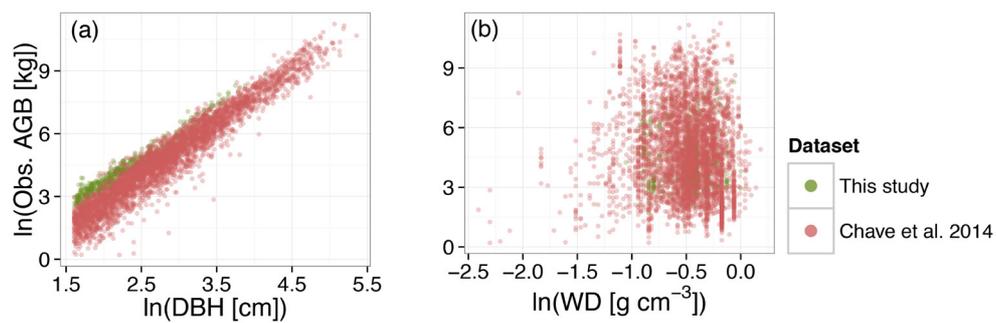


Figure S4. Relationship between predictors (diameter at breast height [DBH] and wood density [WD]) and aboveground biomass (AGB) of the trees included in this study ($n = 727$) and those included in Chave et al. (2014)'s pantropical model ($n = 4004$).

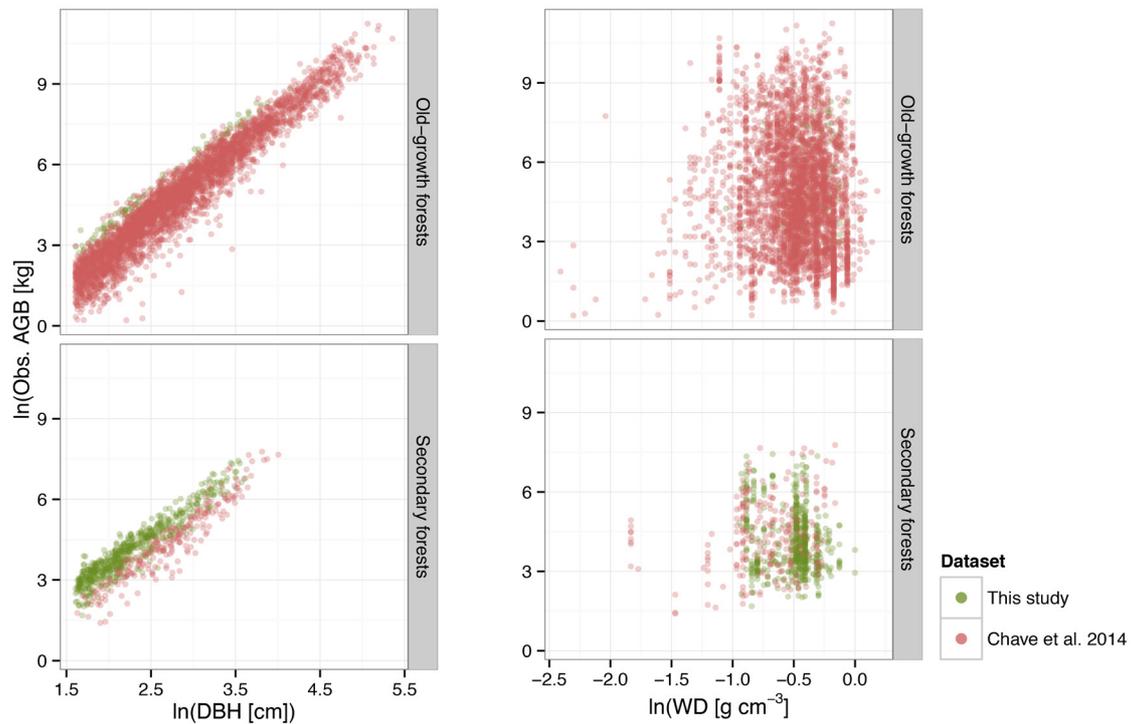


Figure S5. Relationship between predictors (diameter at breast height [DBH] and wood density [WD]) and the observed aboveground biomass (AGB) of the trees from old-growth and secondary forests used to parameterize the biomass estimation models fit in this study and Chave et al. (2014)'s pantropical model. Note that this study included 596 trees (82% of the total) harvested in secondary forests, while Chave et al. (2014) included only 220 (5% of the total). In this study, the representative amount of trees and species from different successional stages of the same forest type allowed for the inclusion of a wide range of tree architecture and thus allometries (i.e. from slender to stout trunks, from suppressed or emergent late-successional species typical of old-growth forests, up to competing or canopy/emergent pioneer species typical of large treefall gaps created by wind-disturbance).

References

- Amaral, D. D., Vieira, I. C. G., Almeida, S. S., Salomão, R. P., Silva, A. S. L. and Jardim, M. A. G.: Checklist of remnant forest fragments of the metropolitan area of Belém and historical value of the fragments, State of Pará, Brazil, *Bol. Mus. Para. Emílio Goeldi*, 4(3), 231–289, 2009.
- Camargo, J., Ferraz, I., Mesquita, M., Santos, B. and Brum, H.: *Guia de Propágulos & Plântulas da Amazônia vol.1*, 1st ed., edited by Authors, INPA, Manaus., 2008.
- Chambers, J. Q., Robertson, A. L., Carneiro, V. M. C., Lima, A. J. N., Smith, M. L., Plourde, L. C. and Higuchi, N.: Hyperspectral remote detection of niche partitioning among canopy trees driven by blowdown gap disturbances in the Central Amazon, *Oecologia*, 160(1), 107–117, 2009.
- Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C., Duque, A., Eid, T., Fearnside, P. M., Goodman, R. C., Henry, M., Martínez-Yrizar, A., Mugasha, W., Muller-Landau, H. C., Mencuccini, M., Nelson, B. W., Ngomanda, A., Nogueira, E. M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C. M., Saldarriaga, J. G. and Vieilledent, G.: Improved allometric models to estimate the aboveground biomass of tropical trees, *Glob. Chang. Biol.*, 3177–3190, 2014.
- Ferraz, I., Leal Filho, N., Imakawa, A., Varela, V. and Piña-Rodríguez, C.: Basic characteristics for a preliminary ecological ranking of timber species occurring in a non-flooded forest in Central Amazonia, *Acta Amaz.*, 34(4), 621–633, 2004.
- Hallé, F.: Architecture of trees in the rain forest of Morobe District, New Guinea, *Biotropica*, 6(1), 43–50, 1974.
- Hallé, F., Oldeman, R. A. A. and Tomlinson, P. B.: *Tropical trees and forests: an architectural analysis*, Springer-Verlag., Berlin, German Federal Republic., 1978.
- Kammesheidt, L.: Some autecological characteristics of early to late successional tree species in Venezuela, *Acta Oecologica*, 21(1), 37–48, 2000.
- Lima, A. J. N., Teixeira, L. M., Carneiro, V. M. C., Santos, J. dos and Higuchi, N.: Análise da estrutura e do estoque de fitomassa de uma floresta secundária da região de Manaus AM, dez anos após corte raso seguido de fogo, *Acta Amaz.*, 37(1), 49–54, 2007.
- Marra, D. M., Chambers, J. Q., Higuchi, N., Trumbore, S. E., Ribeiro, G. H. P. M., Santos, J. dos, Negrón-Juárez, R. ., Reu, B. and Wirth, C.: Large-scale wind disturbances promote tree diversity in a central Amazon forest., *PLoS One*, 9(8), e103711, doi:10.1371/journal.pone.0103711, 2014.
- Myers, B. J.: *Guide to the identification of some tropical rainforest species from large-scale colour aerial*

photographs, *Aust. For.*, 45(1), 28–41, 1982.

Ribeiro, J. E. L. S., Hopkins, M. J. G., Vicentini, A., Sothers, C. A., Costa, M. A. da S., Brito, J. M. de, Souza, M. A. D. de, Martins, L. H. P., Lohmann, L. G., Assunção, P. A. C. L., Pereira, E. da C., Silva, C. F. da, Mesquita, M. R. and Procópio, L. C.: *Flora da Reserva Ducke: Guia de Identificação das Plantas Vasculares de uma Floresta de Terra-firme na Amazônia Central*, INPA, Manaus., 1999.

Saldarriaga, J. G., West, D. C., Tharp, M. L. and Uhl, C.: Long-Term Chronosequence of Forest Succession in the Upper Rio Negro of Colombia and Venezuela, *J. Ecol.*, 76, 938–958, 1998.

Saravy, S., Freitas, P., Lage, M., Leite, S., Braga, L. and Souza, M.: Síndrome de dispesão em estratos arbóreos em um fragmento de floresta ombrófila aberta e densa em Alta Floresta MT, *Rev. do Programa Ciências Agro-Ambientais*, 2(1), 1–12, 2003.

Silva Junior, M. and Pereira, B.: + 100 Árvores do Cerrado -Matas de Galeria - Guia de Campo, 1st ed., Rede de Sementes do Cerrado, Brasília., 2009.

Silva, R. P. da: Alometria, estoque e dinâmica da biomassa de florestas primárias e secundárias na região de Manaus (AM), PhD Thesis, Universidade Federal do Amazonas, Brazil, available at: http://www.inpa.gov.br/arquivos/Tese_Biomassa_Roseana_Silva.pdf (last access on 20.08.2015), 2007.

Silva, R. P. da, Santos, J. dos, Tribuzy, E. S., Chambers, J. Q., Nakamura, S. and Higuchi, N.: Diameter increment and growth patterns for individual tree growing in Central Amazon, Brazil, *For. Ecol. Manage.*, 166(1-3), 295–301, 2002.

Stefanello, D., Fernandes-Bulhão, C. and Martins, S. V.: Seed dispersal syndromes in three riparian vegetation sites (source, middle and estuary) along the Pindaíba river, Mato Grosso state, Brazil, *Rev. Árvore*, 33, 1051–1061, 2009.

Stefanello, D., Ivanauskas, N. M., Martins, S. V., Silva, E. and Kunz, S. H.: Syndromes of diaspores dispersal of species of riparian vegetation of the river from Pacas, Querência - MT, *Acta Amaz.*, 40(1), 141–150, 2010.

Stevens, P. F.: Angiosperm Phylogeny Website, version 12, available in: <http://www.mobot.org/MOBOT/research/APweb/> (last access on 20.08.2015), 2012.

Swaine, M. D. and Whitmore, T. C.: On the definition of ecological species groups in tropical rain forests, *Vegetatio*, 75(1-2), 81–86, 1988.

Terborgh, J., Nuñez-Iturri, G., Pitman, N. C. a, Valverde, F. H. C., Alvarez, P., Swamy, V., Pringle, E. G. and Paine, C. E. T.: Tree recruitment in an empty forest, *Ecology*, 89(6), 1757–1768, 2008.

Trichon, V.: Crown typology and the identification of rain forest trees on large-scale aerial photographs, *Plant Ecol.*, 153(1-2), 301–312, doi:10.1023/A:1017524126999, 2001.



Corrigendum to “Predicting biomass of hyperdiverse and structurally complex central Amazonian forests – a virtual approach using extensive field data” published in Biogeosciences, 13, 1553–1570, 2016

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1 Mistake in the published paper and its impact

In our paper “Predicting biomass of hyperdiverse and structurally complex central Amazonian forests – a virtual approach using extensive field data” (Biogeosciences, 13, 1553–1570, 2016), the biomass estimation models were fit using fresh and not dry tree mass data. Thus, the models reported in our paper are valid for the estimation of fresh aboveground biomass (AGB) of trees and not dry AGB as reported. A direct implication of this mistake is that our evaluation of the pantropical biomass estimation model from Chave et al. (2014) is incorrect in the published paper. The pantropical model was fit with dry mass data. For this reason, it underestimated the biomass of the heavier fresh trees used in our paper. In this corrigendum we have redone the analyses in the paper using dry mass data, which allowed us to reassess different models’ performance across our proposed forest scenarios. The correction from wet to dry mass affected both the AGB values of trees and the models for predicting AGB. Thus, the main conclusions in our paper about which models best represent/capture the variations in AGB across our forest scenarios have not changed. However, the absolute values

of the models’ parameters are different (see Table 3, which should replace Table S3 in the Supplement). For completeness, we give the results of re-analysis here, i.e. the evaluation of our models and the pantropical model from Chave et al. (2014).

2 Obtaining dry mass data and estimating new model parameters

A detailed description of the harvesting method was provided in Sect. 2.2 of the paper. Water content was measured for 66 randomly selected trees, following the procedures also described in Sect. 2.2 of the paper and including samples representing different components (i.e., trunk, coarse branches, fine branches, leaves and flowers/fruits – when available). The weighted water content of the 66 trees was $47.4\% \pm 0.01\%$ (mean $\pm 95\%$ CI). This value is similar to those reported for other *terra firme* forests in the eastern (Araújo et al., 1999), central (Higuchi et al., 2004) and western (Brown et al., 1995; Lima et al., 2012) Amazon. For this corrigendum, we calculated a weighted mean water-content

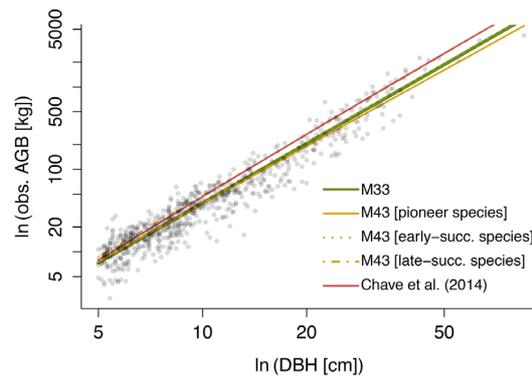


Figure 1. (Correction to Fig. S1 of the Supplement). Comparison of the two best tree aboveground estimation models (M33 and M43) – corrected now to predict dry AGB – with the prediction from the pantropical model from Chave et al. (2014). Note that the pantropical model overestimates the biomass of small and, especially, of large-sized trees (diameter at breast height ≥ 21 cm). This pattern was also observed at the landscape level (see Fig. 2).

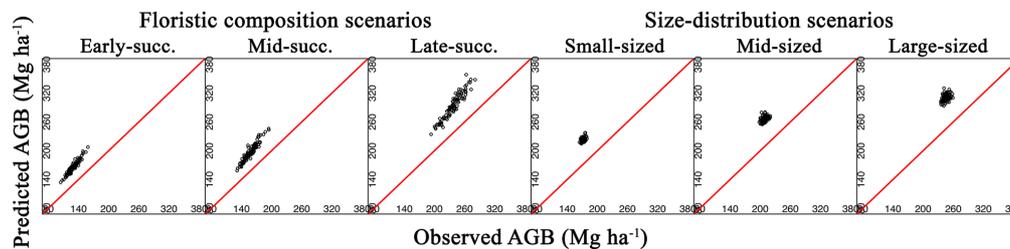


Figure 2. (Correction to Fig. S2 of the Supplement). Predicted vs. observed aboveground biomass (AGB) along six forest scenarios composed of 100 1 ha plots. The line of equality (1 : 1 line) is shown as a red/straight line. Forest scenarios were designed to reflect landscape-level variations in floristic composition and size distribution of trees, typical of central Amazon *terra firme* forests. Floristic composition and size-distribution scenarios followed the sampling scheme described in Sect. 2.4.2 (Fig. 2) of the paper. Here, the predictions were made by using the pantropical model of Chave et al. (2014), which has diameter at breast height (DBH), tree total height (H) (estimated from a DBH: H relationship), wood density (WD) and environmental stress as predictors.

value for each of our successional groups (i.e., pioneer, mid- and late-successional species). There were 49.2, 45.0 and 43.8 %, for pioneer, mid- and late-successional species, respectively (Table 1).

The mean water content of each successional group was used to convert fresh mass to dry mass for each tree and those (Table 2) were used in all subsequent re-analyses. Although water content is related to wood density (Suzuki, 1999) and thus can vary among species (Muller-Landau, 2004; Williamson and Wiemann, 2010), individuals and tree compartments (Higuchi et al., 1998; Plourde et al., 2015), our approximation reflects both the variability among sites and in community composition (i.e., from pioneer to late-successional species). Moreover, Chambers et al. (2001) reported little effect of the variation in water content (i.e., the use of mean and individual-specific water-content values) on prediction error for both individuals and groups of trees harvested in the same region as our study.

With respect to our models, since there was little variation in water content among tree species and successional groups,

and because corrections affected both the predicted variable and the models, we expected our analysis of how well the various models performed to be the same as initially. However, those interested in using biomass estimation models to estimate dry biomass need to use the new coefficients provided in Table 3 of this corrigendum, rather than those reported in Table S3 of the Supplement.

3 Evaluation of the pantropical model

We evaluated the pantropical model from Chave et al. (2014) with our corrected dry mass data. In our paper, the model understandably underestimated biomass because we were comparing estimated dry weight with our wet weight data. When we compared the estimates with our data after correction, i.e., removing the weight of water, we found that the pantropical model overestimated the biomass of individual trees on average by 29.8 % resulting in a root-mean-square error (RMSE) of 210.2 kg (Fig. 1).

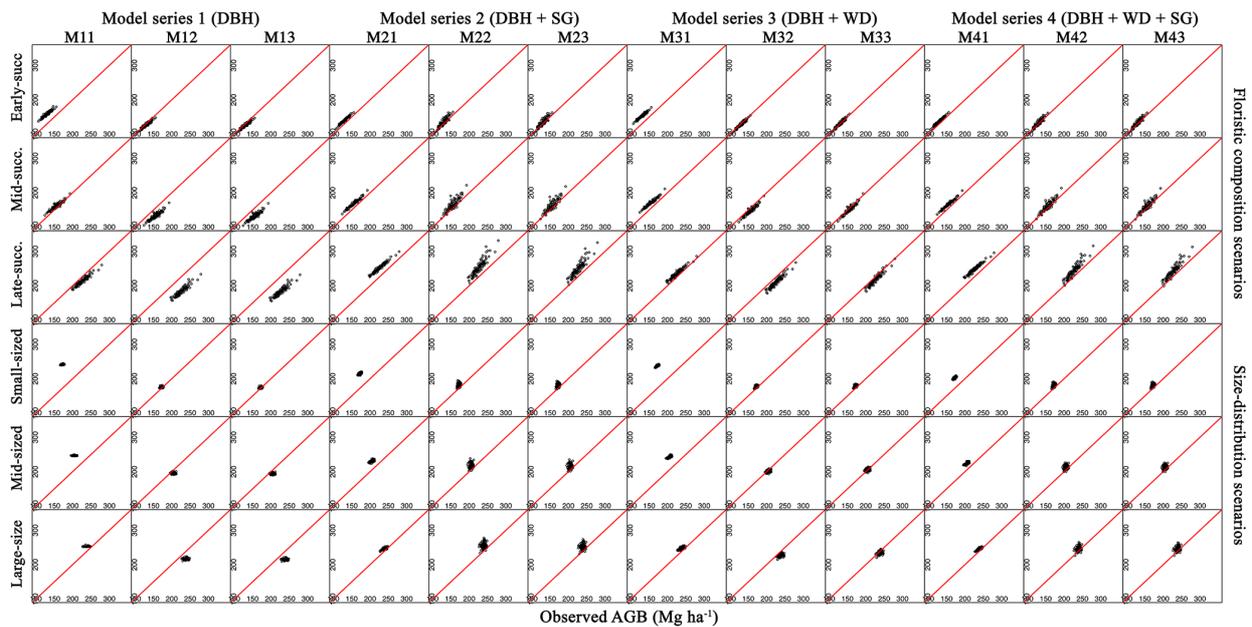


Figure 3. Predicted vs. observed aboveground biomass (AGB) along six forest scenarios composed of 100 1 ha plots. The line of equality (1 : 1 line) is shown as a red/straight line. Forest scenarios were designed to reflect landscape-level variations in floristic composition and size distribution of trees, typical of central Amazon *terra firme* forests. Floristic composition and size-distribution scenarios followed the sampling scheme described in Sect. 2.4.2 of the paper. Models' predictors: diameter at breast height (DBH) (cm), species' successional group (SG) (pioneers, mid- and late successional) and wood density (WD) (g cm^{-3}). See Table 2 for the variance modeling approach of different equations. Note that models containing total tree height (H) as predictor were excluded here.

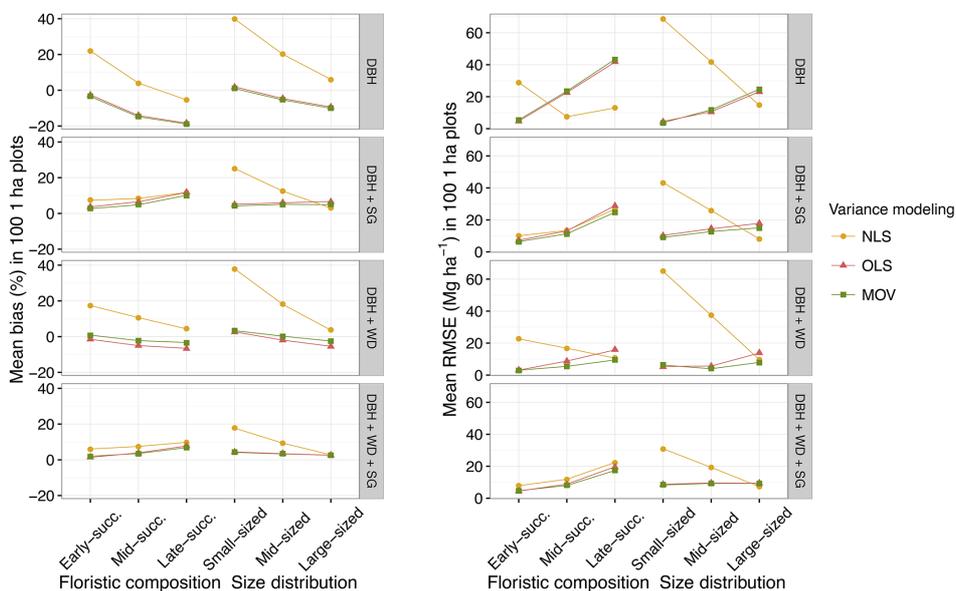


Figure 4. Profiles relating the bias and the root-mean-square error (RMSE) of 12-tree aboveground biomass estimation models tested across six forest scenarios composed of 100 1 ha plots. Forest scenarios (for details see Sect. 2.4.2 of the paper) were designed to reflect landscape-level variations in floristic composition and size distribution of trees, typical of central Amazon *terra firme* forests. Models' predictors: diameter at breast height (DBH) (cm), species' successional group (SG) (pioneers, mid- and late-successional species) and wood density (WD) (g cm^{-3}). Variance modeling approaches: non-linear least square (NLS), ordinary least square with log-linear regression (OLS) and non-linear with modeled variance (MOV). Note that models containing total tree height (H) as predictor were excluded here.

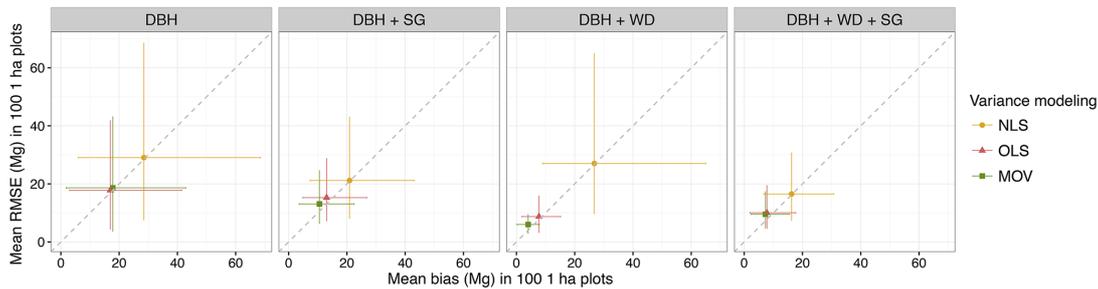


Figure 5. (Correction to Fig. 6 of the paper). Overall performance of 12-tree aboveground estimation models across six forest scenarios composed of 100 1 ha plots. Forest scenarios were designed to reflect landscape-level variations in floristic composition and size distribution of trees, typical of central Amazon *terra firme* forests. Models are rated by the absolute mean bias and root-mean-square error (RMSE), both in Mg. Solid points and bars represent mean and range values, respectively. Models' predictors: diameter at breast height (DBH) (cm), species' successional group (SG) (pioneers, mid- and late-successional species) and wood density (WD) (g cm^{-3}). Variance modeling approaches: non-linear least square (NLS), ordinary least square with log-linear regression (OLS) and non-linear with modeled variance (MOV). Note that models containing total tree height (H) as predictor were excluded here.

Table 1. Contribution of tree compartments to the total aboveground biomass (AGB) (mean), water content of different tree compartments and weighted tree water content of the successional groups included in the paper and this corrigendum (mean \pm 1 standard deviation, both).

Compartments	Contribution to the total AGB (%)	H ₂ O content (%)	Weighted H ₂ O content (%)
Pioneer species ($N = 39$)			
Trunk/bole	65.6	48.1 ± 6.1	49.2 ± 0.9
Thick/coarse branches	11.7	43.7 ± 4.1	
Thin/fine branches	17.8	52.5 ± 7.1	
Leaves	4.7	64.8 ± 7.4	
Flowers/fruits	0.2	61.2 ± 4.8	
Mid-successional species ($N = 22$)			
Trunk/bole	77.4	43.0 ± 4.5	45.0 ± 1.0
Thick/coarse branches	0.0	0.0	
Thin/fine branches	17.0	48.6 ± 3.9	
Leaves	5.6	61.7 ± 9.6	
Flowers/fruits	0.0	0.0	
Late-successional species ($N = 5$)			
Trunk/bole	60.9	41.6 ± 3.3	43.8 ± 1.1
Thick/coarse branches	0.0	0.0	
Thin/fine branches	26.2	42.9 ± 7.7	
Leaves	12.9	56.3 ± 11.8	
Flowers/fruits	0.0	0.0	

The pantropical model also systematically overestimated the AGB of our scenarios (Fig. 2). We observed biases ranging from +29.2% (mid-succession) to +30.8% (early succession) (mean of +29.8%) and RMSE ranging from 40.5 Mg ha^{-1} up to 71.0 Mg ha^{-1} (mean of 56.4 Mg ha^{-1}) (Table 4). Overestimation was also reported in previous studies that tested pantropical models in *terra firme* Amazon forests (Alvarez et al., 2012; Lima et al., 2012; Ngomanda et al., 2014).

In our study area, trees larger than 60 cm diameter at breast height (DBH) occur in densities $< 1 \text{ ha}^{-1}$ (Vieira et al., 2004). Moreover, trees ≤ 40 cm DBH account for more than 90% of the total tree density (Higuchi et al., 2012). We attribute the overestimation of the pantropical model to the great importance that this model gives to large trees (Sect. 4.1 and 4.2, and Fig. S3 of the paper; Figs. 1 and 2 of this corrigendum). As we have shown, the pantropical model does not represent the size distribution of trees from our study region. The results from this corrigendum highlight that site differ-

Table 2. (Correction to Table 1 of the paper). Trees were harvested in the Estação Experimental de Silvicultura Tropical, a contiguous *terra firme* forest reserve near Manaus, Amazonas, Brazil. The corrected AGB values have been calculated using the correction from wet to dry weight.

Variables	Old-growth forest	Secondary forest (23-year old)	Secondary forest (14-year old)
NT	131	346	250
SR	81	63	50
DBH	5.0–85.0	5.0–37.2	5.0–33.1
<i>H</i>	5.9–34.5	3.9–27.0	4.2–27.0
WD	0.348–0.940	0.389–1.000	0.395–1.000
AGB	4.5–4216.5	2.7–861.6	3.9–859.3

Variables: number of trees (NT); species richness (SR); diameter at breast height (DBH) (cm); total tree height (*H*) (m); wood density (WD) (g cm^{-3}); and aboveground biomass (AGB) (dry mass in kg).

ences in size distribution of trees need to be considered both when parameterizing and applying biomass estimation models.

4 Fitting models with the dry mass data

We fit models for estimating dry biomass using the same equations and predictors as in the paper. Before fitting the models, we again tested our predictors for collinearity. Overall, the variance inflation factor (VIF) of the models did not change.

As observed in our models fit with fresh mass data, the non-linear least-square (NLS) approach yielded models with higher coefficient of determination (R^2) and adjusted coefficient of determination (R^2_{adj}) than the models fit with the ordinary least square with the log-linear regression (OLS) and our non-linear with modeled variance (MOV) approach (Table 5). Consequently, the models fit with the NLS approach invariably had lower $S_{yx\%}$ values than those fit with the OLS and MOV approaches. Nonetheless, when considering Deviance Information Criterion (DIC) values as the most important criterion for model selection, our results are consistent with those we reported in the paper. Models fit with the OLS and our MOV approach still yielded the best-fitting models (lower DIC values). The models M33, M43 and M42 had the first, second and third lowest biases for individual tree predictions (underestimation of 0.8 % and overestimation of 3.0 and 3.1 % of dry AGB, respectively).

5 Biomass predictions across the scenarios

The corrected mean AGB (dry) in our 1 ha plots ranged from 107.2 to 170.9 Mg ha^{-1} (floristic composition scenarios) and from 54.1 to 230.2 Mg ha^{-1} (size-distribution scenarios) (Fig. 3). This variation was proportional to that observed for the fresh mass data reported in the paper and values are coherent with those reported for other Amazon regions including secondary (Lima et al., 2007; Saldarriaga et

al., 1998) and old-growth forests (Higuchi et al., 2004; Lima et al., 2012; Vieira et al., 2004).

The goodness of fit of the models for predicting individual tree biomass (Table 5) was also reflected for the reliability of models when predicting AGB across our forest scenarios (Fig. 3). Overall, the patterns reported in the paper did not change. While some models predicted AGB accurately across all different scenarios, others systematically under- or overestimated the “true” AGB values (Fig. 4). As previously reported, despite having the highest R^2 and R^2_{adj} values, the models fit with the NLS approach produced the least reliable landscape-level predictions with biases ranging from -5.4% (underestimation) to $+39.8\%$ (overestimation) (both values from the model M11) leading to RMSE of up to 68.6 Mg ha^{-1} . The models fit with the NLS approach performed better (lower RMSE and bias) at the late-successional and large-sized scenarios. The models fit with the OLS and MOV approaches performed satisfactorily and similarly across most of the scenarios. For model series 2 and 3, the models fit with our MOV approach performed slightly better than those fit with the OLS approach. The models fit with the OLS approach had biases ranging from -18.4 to $+11.9\%$, with maximum RMSE of 41.8 Mg ha^{-1} ; models fit with our MOV approach had biases ranging from -19 to 9.9% , and maximum RMSE of 43.2 Mg ha^{-1} .

As observed from the DIC values of individual tree predictions (Table 5), our MOV and the OLS approaches produced the more reliable (smaller biases and RMSE) predictions when challenged across all scenarios (Fig. 5). As for the models fit with fresh data, independent of applied predictors, the NLS approach invariably had the highest mean and range of values for bias and RMSE. As previously reported, the best-performing model structures for predicting tree AGB at the landscape-level included species-specific predictors and either the OLS or MOV fitting approaches (Table 5 and Figs. 3–5). The best-performing models across all scenarios were M33 (bias of 2.1 % or 4.0 Mg ha^{-1}), M43 (3.7 % or 7.3 Mg ha^{-1}) and M32 (3.9 % or 7.7 Mg ha^{-1}).

Table 3. Parameters (low [2.5 %] and high [97.5 %] confidence interval) of the 24-tree aboveground biomass estimation models fit in this corrigendum. See the Table 2 of the paper for checking the equations and variance modeling approaches, and the Table 5 of this corrigendum for checking models' statistics. Models were fit with dry mass data summarized in the Table 2 of this corrigendum.

Series	Model	SG	b1	b2	b3	b4	c1	c2	
1	M11		0.504 (0.426,0.594)	2.078 (2.035,2.120)			108.8 (103.4,114.6)		
	M12		-1.762 (-1.883,-1.642)	2.329 (2.280,2.380)			0.368 (0.350,0.387)		
	M13		0.183 (0.162,0.207)	2.328 (2.274,2.380)			0.051 (0.041,0.064)	2.424 (2.334,2.517)	
2	M21	pio	0.249 (0.130,0.416)	2.195 (2.025,2.379)			75.17 (71.41,79.16)		
		mid	0.153 (0.102,0.216)	2.436 (2.344,2.532)					
		lat	2.607 (2.226,3.010)	1.683 (1.646,1.723)					
	M22	pio	-1.547 (-1.723,-1.376)	2.203 (2.133,2.274)			0.345 (0.327,0.363)		
		mid	-1.940 (-2.175,-1.705)	2.418 (2.313,2.524)					
		lat	-1.893 (-2.090,-1.694)	2.476 (2.395,2.556)					
M23	pio	0.227 (0.191,0.268)	2.201 (2.131,2.270)			0.076 (0.054,0.105)	2.201 (2.067,2.334)		
	mid	0.156 (0.126,0.193)	2.408 (2.315,2.494)			0.106 (0.062,0.167)	2.105 (1.889,2.333)		
	lat	0.159 (0.134,0.187)	2.472 (2.403,2.538)			0.050 (0.032,0.073)	2.449 (2.289,2.619)		
3	M31		0.885 (0.776,1.008)	2.061 (2.029,2.094)	1.113 (1.022,1.205)		80.35 (76.34,84.55)		
	M32		-1.438 (-1.557,-1.323)	2.370 (2.324,2.416)	0.863 (0.740,0.989)		0.330 (0.313,0.347)		
	M33		0.230 (0.207,0.257)	2.406 (2.366,2.446)	0.880 (0.752,1.012)		0.076 (0.061,0.094)	2.213 (2.125,2.304)	
4	M41	pio	0.165 (0.086,0.280)	2.587 (2.395,2.788)	1.236 (0.977,1.500)		67.81 (64.38,71.51)		
		mid	0.138 (0.075,0.226)	2.457 (2.346,2.576)	-0.098 (-0.460,0.266)				
		lat	2.152 (1.841,2.486)	1.786 (1.744,1.831)	0.555 (0.435,0.679)				
	M42	pio	-1.229 (-1.401,-1.053)	2.279 (2.211,2.345)	0.872 (0.688,1.049)		0.323 (0.307,0.340)		
		mid	-1.857 (-2.130,-1.581)	2.419 (2.319,2.518)	0.196 (-0.216,0.604)				
		lat	-1.684 (-1.907,-1.461)	2.461 (2.384,2.538)	0.548 (0.234,0.867)				
	M43	pio	0.275 (0.231,0.325)	2.324 (2.251,2.396)	0.878 (0.680,1.078)		0.109 (0.075,0.153)	2.009 (1.869,2.155)	
		mid	0.182 (0.139,0.238)	2.409 (2.318,2.494)	0.353 (0.028,0.793)		0.102 (0.060,0.162)	2.121 (1.900,2.348)	
		lat	0.193 (0.159,0.233)	2.460 (2.392,2.527)	0.539 (0.254,0.835)		0.048 (0.031,0.071)	2.442 (2.277,2.619)	
	5	M51		0.033 (0.021,0.049)	1.561 (1.491,1.632)	1.423 (1.241,1.607)		93.60 (88.91,98.52)	
		M52		-2.687 (-2.886,-2.490)	1.930 (1.844,2.015)	0.715 (0.590,0.845)		0.341 (0.324,0.359)	
		M53		0.084 (0.066,0.104)	1.970 (1.872,2.062)	0.621 (0.488,0.765)		0.045 (0.036,0.056)	2.457 (2.363,2.551)
6	M61	pio	0.014 (0.004,0.035)	1.915 (1.715,2.111)	1.276 (0.906,1.664)		67.65 (64.27,71.25)		
		mid	0.068 (0.027,0.133)	2.269 (2.131,2.420)	0.448 (0.109,0.798)				
		lat	0.524 (0.356,0.739)	1.408 (1.349,1.470)	0.803 (0.647,0.955)				
	M62	pio	-2.626 (-2.921,-2.337)	1.817 (1.713,1.927)	0.756 (0.581,0.925)		0.314 (0.298,0.331)		
		mid	-2.743 (-3.046,-2.438)	1.942 (1.784,2.099)	0.742 (0.539,0.942)				
		lat	-2.791 (-3.215,-2.353)	2.088 (1.904,2.270)	0.697 (0.393,0.994)				
	M63	pio	0.086 (0.059,0.118)	1.864 (1.745,1.979)	0.670 (0.482,0.879)		0.072 (0.051,0.100)	2.198 (2.059,2.335)	
		mid	0.078 (0.054,0.108)	2.004 (1.830,2.173)	0.634 (0.411,0.861)		0.081 (0.046,0.132)	2.193 (1.963,2.432)	
		lat	0.068 (0.044,0.099)	2.118 (1.953,2.273)	0.648 (0.386,0.936)		0.048 (0.031,0.071)	2.426 (2.263,2.599)	
	7	M71		0.063 (0.046,0.083)	1.581 (1.530,1.632)	1.342 (1.217,1.478)	1.024 (0.949,1.100)	64.91 (61.66,68.39)	
		M72		-2.253 (-2.441,-2.059)	2.027 (1.952,2.104)	0.605 (0.490,0.717)	0.773 (0.655,0.895)	0.308 (0.293,0.324)	
		M73		0.109 (0.088,0.134)	2.121 (2.047,2.194)	0.839 (0.711,0.966)	0.535 (0.416,0.657)	0.073 (0.057,0.092)	2.206 (2.110,2.305)
8	M81	pio	0.029 (0.010,0.061)	2.306 (2.118,2.513)	0.830 (0.523,1.167)	0.999 (0.764,1.231)	57.16 (54.30,60.21)		
		mid	0.058 (0.028,0.111)	2.072 (1.867,2.308)	0.761 (0.295,1.145)	0.420 (0.007,0.823)			
		lat	0.195 (0.134,0.281)	1.456 (1.401,1.514)	1.124 (0.967,1.276)	0.732 (0.636,0.831)			
	M82	pio	-2.086 (-2.396,-1.784)	1.978 (1.865,2.089)	0.560 (0.392,0.735)	0.710 (0.538,0.885)	0.300 (0.285,0.316)		
		mid	-2.671 (-3.016,-2.327)	1.946 (1.787,2.104)	0.737 (0.540,0.934)	0.162 (-0.221,0.548)			
		lat	-2.545 (-3.010,-2.070)	2.120 (1.938,2.301)	0.621 (0.316,0.915)	0.388 (0.084,0.691)			
M83	pio	0.131 (0.091,0.182)	2.087 (1.976,2.202)	0.761 (0.571,0.957)	0.471 (0.290,0.650)	0.106 (0.074,0.150)	2.005 (1.861,2.147)		
	mid	0.089 (0.059,0.127)	2.006 (1.835,2.170)	0.350 (0.037,0.733)	0.639 (0.427,0.872)	0.080 (0.045,0.132)	2.195 (1.962,2.432)		
	lat	0.087 (0.055,0.129)	2.154 (1.995,2.309)	0.435 (0.153,0.725)	0.575 (0.310,0.852)	0.050 (0.032,0.074)	2.401 (2.234,2.578)		

Model series predictors: 1 (diameter at breast height [DBH]); 2 (DBH and species' successional group [SG]); 3 (DBH and wood density [WD]); 4 (DBH, WD and SG); 5 (DBH and total tree height [H]); 6 (DBH, H and SG); 7 (DBH, H and WD); and 8 (DBH, H, SG and WD). Species' successional groups: pioneer (pio), mid-species (mid) and late-successional species (lat).

Our new results support that predicting biomass correctly at the landscape level in hyperdiverse and structurally complex tropical forests, such as the Amazon, still depends on the collection of plot-based allometric data and forest inventories including information on species composition, tree height and wood density. In forests subjected to more intense disturbance regimes (i.e., strong gradients of floristic composition and size distribution), reliable landscape-level biomass estimates may require models that include predictors approximating species-specific architecture and anatomy, and possible variations in the size distribution of trees.

We would like to emphasize the importance of the aspects related to model parameterization, selection and applicability, as discussed in Sect. 4 of our paper. Furthermore, we confirm the efficacy of our best-performance models for estimating dry aboveground biomass of central Amazon *terra firme* forests, and the adequacy of the methods that we employed. When data on species composition and wood density are available or can be accurately compiled from the literature, we suggest the use of models M33, M43 or M42, respectively. In case wood density data are not available or are available but in insufficient resolution, we suggest the use of model M23.

Table 4. (Correction to Table S4 of the Supplement). Root-mean-square error (RMSE) and bias (absolute and relative values) from tree aboveground biomass predictions across our forest scenarios by using the Chave et al. (2014)'s pantropical estimation model. Chave et al. (2014)'s pantropical estimation model has diameter at breast height (DBH), tree total height (H) (estimated from a DBH: H relationship), wood density (WD) and environmental stress as predictors.

Scenarios	RMSE (Mg ha ⁻¹)	Bias (Mg ha ⁻¹)	Bias (%)
Early-succession	40.5	40.1	30.8
Mid-succession	46.1	45.5	29.2
Late-succession	67.1	66.4	29.3
Small-sized	51.9	51.7	30.1
Mid-sized	61.8	61.6	30.0
Large-sized	71.0	70.8	29.6
Mean	56.4	56.0	29.8

Table 5. Statistics of aboveground biomass estimation models fit in this corrigendum. See Table 2 of the paper for the definition of models, predictors and variance modeling approaches.

Series	Model	Dev	pD	DIC	R^2	R^2_{adj}	$S_{yx\%}$	CF
1	M11	8880.2	2.926	8883.1	0.889	0.888	3.315	1.070
	M12	5924.7	2.963	5927.6	0.867	0.867	3.615	
	M13	5948.1	3.847	5952.0	0.867	0.867	3.619	
2	M21	8342.3	3.647	8345.9	0.947	0.946	2.296	1.061
	M22	5827.3	7.001	5834.3	0.552	0.548	6.593	
	M23	5827.5	10.534	5838.0	0.595	0.592	6.285	
3	M31	8439.3	3.972	8443.2	0.939	0.939	2.449	1.056
	M32	5762.9	4.014	5766.9	0.901	0.901	3.119	
	M33	5792.5	4.805	5797.3	0.882	0.881	3.412	
4	M41	8193.2	1.271	8194.5	0.957	0.956	2.077	1.053
	M42	5732.8	10.007	5742.8	0.719	0.715	5.223	
	M43	5737.6	13.126	5750.7	0.738	0.735	5.056	
5	M51	8661.5	-0.071	8661.4	0.918	0.917	2.853	1.060
	M52	5810.7	4.052	5814.8	0.887	0.886	3.340	
	M53	5858.2	4.652	5862.9	0.882	0.881	3.415	
6	M61	8189.8	-55.307	8134.5	0.957	0.956	2.071	1.050
	M62	5690.5	10.118	5700.7	0.753	0.750	4.895	
	M63	5720.5	11.602	5732.1	0.755	0.752	4.891	
7	M71	8129.0	2.234	8131.2	0.960	0.960	1.980	1.048
	M72	5663.5	5.025	5668.5	0.935	0.934	2.539	
	M73	5715.7	5.512	5721.2	0.927	0.927	2.681	
8	M81	7944.2	-38.934	7905.3	0.969	0.969	1.753	1.046
	M82	5624.8	13.226	5638.0	0.818	0.815	4.205	
	M83	5655.9	13.489	5669.4	0.821	0.818	4.187	

Legend: models' deviance (Dev), effective number of parameters (pD), Deviance Information Criterion (DIC), coefficient of determination (R^2), adjusted coefficient of determination (R^2_{adj}), relative standard error ($S_{yx\%}$) and correction factor (CF) for models fit from ordinary least square with log-linear regressions.

References

- Alvarez, E., Duque, A., Saldarriaga, J., Cabrera, K., de las Salas, G., del Valle, I., Lema, A., Moreno, F., Orrego, S., and Rodríguez, L.: Tree above-ground biomass allometries for carbon stocks estimation in the natural forests of Colombia, *For. Ecol. Manage.*, 267, 297–308, 2012.
- Araújo, T. M., Higuchi, N., and Andrade de Carvalho Júnior, J.: Comparison of formulae for biomass content determination in a tropical rain forest site in the state of Pará, Brazil, *For. Ecol. Manage.*, 117, 43–52, doi:10.1016/S0378-1127(98)00470-8, 1999.
- Brown, I. F., Martinelli, L. A., Thomas, W. W., Moreira, M. Z., Cid Ferreira, C. A., and Victoria, R. A.: Uncertainty in the biomass of Amazonian forests: An example from Rondônia, Brazil, *For. Ecol. Manage.*, 75, 175–189, doi:10.1016/0378-1127(94)03512-U, 1995.
- Chambers, J. Q., Santos, J. dos, Ribeiro, R. J., and Higuchi, N.: Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest, *For. Ecol. Manage.*, 152, 73–84, 2001.
- Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C., Duque, A., Eid, T., Fearnside, P. M., Goodman, R. C., Henry, M., Martínez-Yrizar, A., Mugasha, W., Muller-Landau, H. C., Mencuccini, M., Nelson, B. W., Ngomanda, A., Nogueira, E. M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C. M., Saldarriaga, J. G., and Vieilledent, G.: Improved allometric models to estimate the aboveground biomass of tropical trees, *Glob. Chang. Biol.*, 20, 3177–3190, 2014.
- Higuchi, F. G., Siqueira, J. D. P., Lima, A. J. N., Filho, A. F., and Higuchi, N.: Influence of plot size in Weibull's diameter distribution function precision in a primary forest in Central Amazon, *Floresta*, 42, 599–606, 2012.
- Higuchi, N., Santos, J. dos, Ribeiro, R. J., Minette, L., and Biot, Y.: Biomassa da parte aérea da vegetação da floresta tropical úmida de terra-firme da Amazônia brasileira, *Acta Amaz.*, 28, 153–166, 1998.
- Higuchi, N., Chambers, J. Q., Santos, J. dos, Ribeiro, R. J., Pinto, A. C. M., Silva, R. P. da, Rocha, R. de M., and Tribuzy, E. S.: Carbon balance and dynamics of primary vegetation in the Central Amazon, *Floresta*, 34, 295–304, 2004.
- Lima, A. J. N., Teixeira, L. M., Carneiro, V. M. C., Santos, J. dos, and Higuchi, N.: Biomass stock and structural analysis of a secondary forest in Manaus (AM) region, ten years after clear cutting followed by fire, *Acta Amaz.*, 37, 49–54, 2007.
- Lima, A. J. N., Suwa, R., Ribeiro, G. H. P. M., Kajimoto, T., Santos, J. dos, Silva, R. P. da, Souza, C. A. S. de, Barros, P. C. de, Noguchi, H., Ishizuka, M., and Higuchi, N.: Allometric models for estimating above- and below-ground biomass in Amazonian forests at São Gabriel da Cachoeira in the upper Rio Negro, Brazil, *For. Ecol. Manage.*, 277, 163–172, 2012.
- Muller-Landau, H. C.: Interspecific and inter-site variation in wood specific gravity of tropical trees, *Biotropica*, 36, 20–32, 2004.
- Ngomanda, A., Obiang, N. L. E., Lebamba, J., Mavouroulou, Q. M., Gomat, H., Mankou, G. S., Loumeto, J., Iponga, D. M., Ditsouga, F. K., Koumba, R. Z., Bobé, K. H. B., Okouyi, C. M., Nyangadouma, R., Lépengué, N., Mbatchi, B., and Picard, N.: Site-specific versus pantropical allometric equations: Which option to estimate the biomass of a moist central African forest?, *For. Ecol. Manage.*, 312, 1–9, 2014.
- Plourde, B. T., Boukili, V. K., and Chazdon, R. L.: Radial changes in wood specific gravity of tropical trees: Inter- and intraspecific variation during secondary succession, *Funct. Ecol.*, 29, 111–120, doi:10.1111/1365-2435.12305, 2015.
- Saldarriaga, J. G., West, D. C., Tharp, M. L., and Uhl, C.: Long-Term Chronosequence of Forest Succession in the Upper Rio Negro of Colombia and Venezuela, *J. Ecol.*, 76, 938–958, 1998.
- Suzuki, E.: Diversity in specific gravity and water content of wood among Bornean tropical rainforest trees, *Ecol. Res.*, 14, 211–224, doi:10.1046/j.1440-1703.1999.143301.x, 1999.
- Vieira, S., de Camargo, P. B., Selhorst, D., da Silva, R., Hutyrá, L., Chambers, J. Q., Brown, I. F., Higuchi, N., Santos, J. dos, Wofsy, S. C., Trumbore, S. E., and Martinelli, L. A.: Forest structure and carbon dynamics in Amazonian tropical rain forests, *Oecologia*, 140, 468–479, 2004.
- Williamson, B. G. and Wiemann, M. C.: Measuring wood specific gravity...correctly, *Am. J. Bot.*, 97, 519–524, 2010.

3. ORIGINAL CONTRIBUTIONS

3.4. Paper 4

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Keywords: Biomass accumulation, carbon balance, catastrophic tree mortality, forest dynamics and succession, natural disturbances, tree species demography, regrowth mechanisms, *terra firme* forests

Abstract

Abstract

Forest resilience is the capacity of a forest to recover to its pre-disturbance state. Yet, the rates and mechanisms defining the recovery trajectory from natural disturbances such as recurrent windthrows have not been previously presented for central Amazon forests. We used Landsat imagery to identify a chronosequence of sites that ranged from 4 to 27 yrs after windthrows that created large-size gaps ($> 2000 \text{ m}^2$) in the region surrounding Manaus, Brazil. Detailed forest inventories were conducted to follow forest dynamics in three wind-disturbed and an old-growth forest used as a control. Biomass was estimated with locally parameterized allometric models. We carried full botanical surveys and recorded mechanisms of biomass gain and loss. Blowdowns reduced biomass stocks for at least three decades in areas sustaining high tree mortality/damage, with loss of biomass from late successional species continuing for years after the windthrows. Biomass resilience was enhanced by recruitment and growth of various pioneer and mid-successional species. Biomass accumulation rates in these species were nearly double that observed in the same functional groups in old-growth forest. Over the entire disturbance gradient, biomass gain was dominated by 20 genera from different functional groups and with performance influenced by variations in blowdown tree-mortality intensity. While reduction of biomass resilience in late-successional trees was triggered by species loss, increase of biomass resilience in pioneer trees was triggered by species enrichment. Although the richness of mid-successional species decreased under high disturbance intensities, biomass resilience in this group increased systematically due to key genera and species. Our findings support that blowdowns have relevant implications for biomass/carbon balance and taxonomical attributes of tree communities in Central Amazon forests.

Significance Statement

Significance Statement

In Amazon forests, blowdowns are a major natural disturbance. Understanding biomass dynamics and recovery trajectories from blowdowns is relevant for management and conservation of the Amazon. We identified and monitored biomass and species composition in forest sites identified using remote sensing as having experienced wind-disturbance between 4 and 27 yrs previously. These single-event blowdowns produced changes in biomass stocks and dynamics that persisted for decades. Variations in blowdown tree-mortality drove the partitioning of biomass gain and losses mechanisms among species and successional groups, with various pioneers and mid-successional species making up a greater proportion of biomass stocks and gain in more damaged stands. Although these forests seem to be resilient, blowdowns produce non-negligible effects on community composition and biomass balance that last for decades, and are likely to contribute to broad scale patterns of species diversity and biomass.

Introduction

Following disturbance, the capacity of a forest to recover to its pre-disturbance state is defined as resilience (Holling 1973; Harrison 1979). This process depends on forest resistance to damage and endogenous responses to different levels of disturbance (Peterson et al. 1998; Johnson and Miyanishi 2010; Hodgson et al. 2015). Although small-scale disturbances such as background tree mortality are more frequent, episodic large-scale natural disturbances (e.g. drought, fire, floods, landslides and wind storms) are a worldwide phenomenon that can promote extensive vegetation damage and cause long-term changes in forest structure and dynamics (Dale et al. 1998; Turner et al. 1998; Lugo 2008; Johnson and Miyanishi 2010). By turning significant amounts of biomass into necromass, large-scale disturbances can also change ecosystem functions such as carbon storage (Lindroth et al. 2009; Zeng et al. 2009). The time required to return to pre-disturbance conditions is influenced by rates of relative biomass loss (i.e. vegetation resistance) and gain (i.e. vegetation responses). In tropical forests, decomposition rates are so rapid (i.e. mostly < 20 years for tree stems) (Chambers et al. 2000; Clark et al. 2002; Hérault et al. 2010), that regrowth is in fact the main driver of biomass/carbon recovery (Everham and Brokaw 1996; Chazdon et al. 2007; Rozendaal and Chazdon 2015).

To date, most of the research on biomass resilience in tropical forests has been on the extremes of the available disturbance gradient, i.e. either gap-phase regeneration (Denslow 1980; Brokaw 1985; Hubbell et al. 1999) or severe human disturbances (e.g. shifting agriculture, fire and logging) (Finegan 1996; Guariguata and Ostertag 2001; Chazdon et al. 2007). Depending on size, treefall gaps can have higher light availability and air temperature as well as possible changes in soil and air moisture compared to old-growth forests (Brokaw 1985; Dalling et al. 2004). These environmental differences promote changes in floristic and functional composition through the partition of microsites and resource gradients among species with varied requirements and life histories (i.e. pioneer, mid- and late-successional species) (Grubb 1977; Denslow 1980; Swaine and Whitmore 1988). Even small niche-variations in small canopy-gaps ‘along an old-growth matrix’ can promote tree species diversity (Molino and Sabatier 2001; Bongers et al. 2009; Burslem and Whitmore 2009), which in turn has been stated to have a positive effect on biomass stocks of tropical forests (Poorter et al. 2015).

Introduction

In contrast to small-scale canopy disturbance associated with background tree mortality, human disturbances often implicate soil alterations, strong reductions in biomass and nutrient removal (e.g. logging and fire), which together produce longer-lasting effects on forest structure and floristic composition and may lower biomass resilience (Finegan 1996; Guariguata and Ostertag 2001; Chazdon 2003; Jakovac et al. 2015). Palaeoecological records suggest that tropical forests are in a continuous recovery-process from large-scale natural (mostly by wind) and human disturbances, with a median time of 210 yrs to recover 95.5% of pre-disturbance levels (Cole et al. 2014). Overall, resilience is influenced by site-specific characteristics such as land-use history, abiotic (e.g. soil fertility and climate) and biotic aspects (e.g. community stability, functional and genetic diversity, effectiveness of dispersion and physiological responses) (Peterson et al. 1998; Chazdon 2003; Thompson et al. 2009; Cole et al. 2014; Poorter et al. 2016).

In the Amazon, a prevalent hypothesis is that old-growth forests are dominated by small-scale canopy disturbances ($< 2,000 \text{ m}^2$), which can be seen as an integral feature of a self-replacing system in equilibrium and having little relevance for biomass/carbon dynamics (Gloor et al. 2009; Espírito-Santo et al. 2014), or structural and taxonomic attributes (Uhl et al. 1988; Baker et al. 2015). More recently, however, blowdowns produced by downbursts associated with severe convective systems such as squall lines (Nelson et al. 1994; Garstang et al. 1998) have been identified as a potentially major disturbance regime in Central and Western Amazon (Nelson et al. 1994; Espírito-Santo et al. 2010; Chambers et al. 2013; Negrón-Juárez et al. 2016). Blowdowns vary in size from 900 m^2 (the pixel size in Landsat imagery) (Negrón-Juárez et al. 2011) to thousands of hectares (Nelson et al. 1994) and can cause catastrophic tree mortality, reported as up to 80% at pixel-/plot-level (Marra et al. 2014; Negrón-Juárez et al. 2016; Rifai et al. 2016). The spatial distribution of tree damage and mortality in these events are likely to be controlled by the interaction of abiotic variables such as wind characteristics and topography, with biotic variables, including tree-size distribution, wood density and tree anchoring-capacity (Negrón-Juárez et al. 2016; Ribeiro et al. 2016; Rifai et al. 2016). At the landscape-level, wind disturbance creates a complex mosaic of different-sized patches comprising a range of disturbance intensities, from single treefall gaps to square-kilometer wide blowdowns with strongly altered floristic composition, structure (Chambers et al. 2009; Marra et al. 2014) and soil attributes (Santos et al. 2016). To date, there is no study assessing the rates and mechanisms of tropical forest succession and

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biomass recovery across this vast gradient of conditions created by wind disturbance in Amazon forests.

Although vegetation damage and responses to catastrophic tree mortality events have been extensively studied in tropical and subtropical forests typically affected by large-scale wind disturbances (e.g. cyclones, hurricanes, typhoons and tornadoes) (Everham and Brokaw 1996; Lugo 2008), assessments of biomass resilience and detailed mechanisms of biomass gain and loss as components of resilience have rarely been carried out. In Puerto Rico and Nicaragua forests that lost 50% and 80% of their original biomass after hurricanes, biomass accumulation averaged $16.3 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (5-yr succession) (Scatena et al. 1996) and $5.36 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (11-yr succession, varying from 8 to $22 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) (Mascaro et al. 2005), respectively. Apart from being related to land-use history and abiotic aspects, this strong difference in biomass resilience reported for Puerto Rico and Nicaragua forests also reflected differences in the dominant biomass gain mechanism observed in each of these forests. While in the Puerto Rico forest biomass gain was mostly due to the growth of newly recruited trees from different successional groups (Scatena et al. 1996), resprouting of late-successional species with low growth rates was the dominant biomass gain mechanism in the Nicaragua forest (Yih et al. 1991; Mascaro et al. 2005). General knowledge of tropical forest ecology suggests that biomass resilience to complex wind-disturbances can be enhanced by the contribution of different mechanisms: resprouting of damaged trees or *direct regeneration* (Yih et al. 1991; Bellingham et al. 1995; Mascaro et al. 2005), survival and increased growth of resistant/adapted species released from competition (Everham and Brokaw 1996; Weaver 2002), recruitment of old-growth species by activation of the understory sapling bank (You and Petty 1991; Zimmerman et al. 1994; Burslem et al. 2000), recruitment of seed-dispersed species (Ferguson et al. 1995; Imbert et al. 1998; Vandermeer et al. 2000; Hjerpe et al. 2001) or any combination of these mechanisms (Lawton and Putz 1988; Brokaw and Grear 1991; Walker 1991; Vandermeer et al. 1995). The activation and importance of different biomass gain mechanisms is likely to depend on the size and intensity of the disturbance, pre-disturbance conditions (structure and floristic composition) and abiotic variables (e.g. soil and climate) (Everham and Brokaw 1996; Lugo 2008).

Most of what we know about tropical biomass resilience after catastrophic tree-mortality events comes almost exclusively from human disturbances. Following stand-removing disturbances (e.g. clear-cut and burning in 'shifting agriculture'), regrowth is often

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rapid and biomass recovery is dominated by trees (i.e. lower contribution of lianas, shrubs and herbs) (Saldarriaga et al. 1998; Guariguata and Ostertag 2001; Chazdon et al. 2007). In the initial years post-disturbance, tree recruitment is influenced by dispersal limitations (e.g. distance to an old-growth forest), life history constraints associated with regenerating species and nutrient availability. Unlike in small canopy-gaps, biotic and abiotic conditions in large clearings tend to favor a regenerating cohort dominated by light-demanding and fast-growing pioneer species (Saldarriaga et al. 1998; Mesquita et al. 2001; Chazdon 2003). The fast recruitment and growth of pioneer adapted species often lead to high tree densities and fast canopy closure. Systematic increases in tree density, saturation of resources and increase in competition promote high mortality of smaller trees (i.e. self-thinning process), which can favor the recruitment of long-living species from other more shade-tolerant successional groups (i.e. mid- and late-successional).

Although species enrichment during succession and nutrient availability contribute to a progressive biomass accumulation, recovery trajectories can vary strongly (Mesquita et al. 2001; Norden et al. 2015), with structure and floristic composition remaining different from old-growth forests for decades or centuries (Finegan 1996; Saldarriaga et al. 1998). The higher the disturbance intensity (e.g. soil impacts and burning), the lower is the potential of secondary forests to regenerate from seed- and seedling-bank (Guariguata and Ostertag 2001), and also to remain resilient (Jakovac et al. 2015). Biomass recovery rates in Amazon logged forests were negatively correlated with the amount of logged biomass (average of 75 yrs to recover from 50% logging intensity) (Rutishauser et al. 2015), corroborating that disturbance intensity plays an important role on determining biomass dynamics and recovery. In Neotropical secondary forests regenerating from shifting agriculture and pastures, 90% of the original biomass stocks recovered in a median time of 66 yrs (Poorter et al. 2016). In heavily disturbed forests, apart from tree recruitment and growth, resprouting can also be a key biomass gain mechanism, with greater importance in dry tropical forests (Vieira and Scariot 2006).

Biomass resilience to complex and catastrophic natural disturbances such as Amazon blowdowns is likely to be different from both resilience to background tree mortality creating small canopy-gaps and stand-removing disturbances. We expect this difference because of the complex environment/resources gradient created by blowdowns and differential species' vulnerability and response to wind damage (Marra et al. 2014; Ribeiro et al. 2016; Rifai et al.

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2016). In addition, organic matter is not removed from the disturbed areas and fast decomposition may increase nutrient availability. Previous studies indicated short-term changes in functional composition driven by fast recruitment of pioneer tree species favored in large blowdown gaps (Chambers et al. 2009; Marra et al. 2014). Nonetheless, the employment of diversity along the resources gradient for biomass recovery is not entirely studied and this may be a significant difference between forest resilience to less intense human disturbances (e.g. logging) and windthrows. Unlike in contiguous geometric clear-cuts, in blowdowns different successional groups and biomass gain and loss mechanisms may be relevant for the biomass recovery process. Likely in old-growth forests, in which niche complementarity can increase species diversity and enhance biomass stocks (Poorter et al. 2016), in wind-disturbed Amazon forests, biomass resilience may also be enhanced by a wide spectrum of species adapted to different conditions. Furthermore, we do not know whether the diverse local species pool typical of Central Amazon forests (e.g. 280 tree species ha⁻¹ in Central Amazon) (de Oliveira and Mori 1999) is relevant for biomass recovery from catastrophic natural disturbances or whether resilience is exerted by a limited set of gap specialists.

Apart from overall high species diversity (Zappi et al. 2015), recent investigations have demonstrated hyperdominance of some species in the Amazon (ter Steege et al. 2013; Fauset et al. 2015). Interestingly, species-curve areas are not linear in Amazon forests. For instance, while 1 ha of forest can harbor more than 280 tree species, Carneiro (2004) reported 737 species in 7 ha and Ribeiro et al. (1999) reported *ca.* 1,500 species for a 10,000 ha reserve. In this context, apart from the probably high importance of gap specialists, hyperdominant species may also be important for the biomass recovery process following windthrows, both due to their relative higher survivorship and resprouting ability/capacity.

We expected biomass recovery to be a highly heterogeneous process driven by many species and regeneration modes depending on the intensity and time after disturbance. To study this complex process, we combined remote sensing data on tree mortality (i.e. gap fraction) with forest inventory data (trees \geq 10 cm diameter at breast height [DBH]) on remote sites. We monitored forest dynamics (i.e. growth, resprouting, recruitment and mortality) between 2002 and 2015 in 596 subplots (total area of 19.6 ha) established in three Central Amazon *terra firme* forests disturbed by single blowdown events and a nearby old-growth forest, which was used as a control (Fig. 1). Aboveground biomass (hereafter referred

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as 'biomass') was estimated with locally parameterized biomass estimation models (Chambers et al. 2001; Magnabosco Marra et al. 2016) and full botanical surveys were carried to reveal the contribution of different functional/successional groups, genera and species to the biomass recovery process. Therefore, we employed a chronosequence-approach accounting from four up to 27 yrs of forest recovery. Our chronosequence covers a gradient of disturbance intensity from the background tree mortality captured in available permanent plots (< 4%) (Phillips et al. 2004) up to 70% of blowdown tree-mortality. This unique data set allowed us to show, for the first time, the contribution of species and different mechanisms enhancing biomass resilience to large-scale natural disturbances, including tree growth in diameter, recruitment, resprouting and mortality. Here, we tested the following hypothesis:

- 1) The mortality gradient typical of large-scale wind disturbances produces long-term (27 yrs) effects on forest structure, biomass dynamics and functional composition;
- 2) High tree mortality intensities shift dominant biomass gain mechanisms from growth and recruitment of established late-successional species to recruitment and growth of pioneer and mid-successional species; Moreover, due to the large numbers of damaged/resprouting trees (Marra et al. 2014) and based on evidence from other tropical forests, resprouting of late-successional species is an important biomass recovery mechanism in these forests;
- 3) Under high tree mortality intensities, the importance of biomass gain mechanisms due to pioneer and mid-successional species is enhanced by increase in the number of species (i.e. richness), whereas the importance of biomass gain mechanisms due to late-successional species is weakened by reductions in the number of species.

Methods

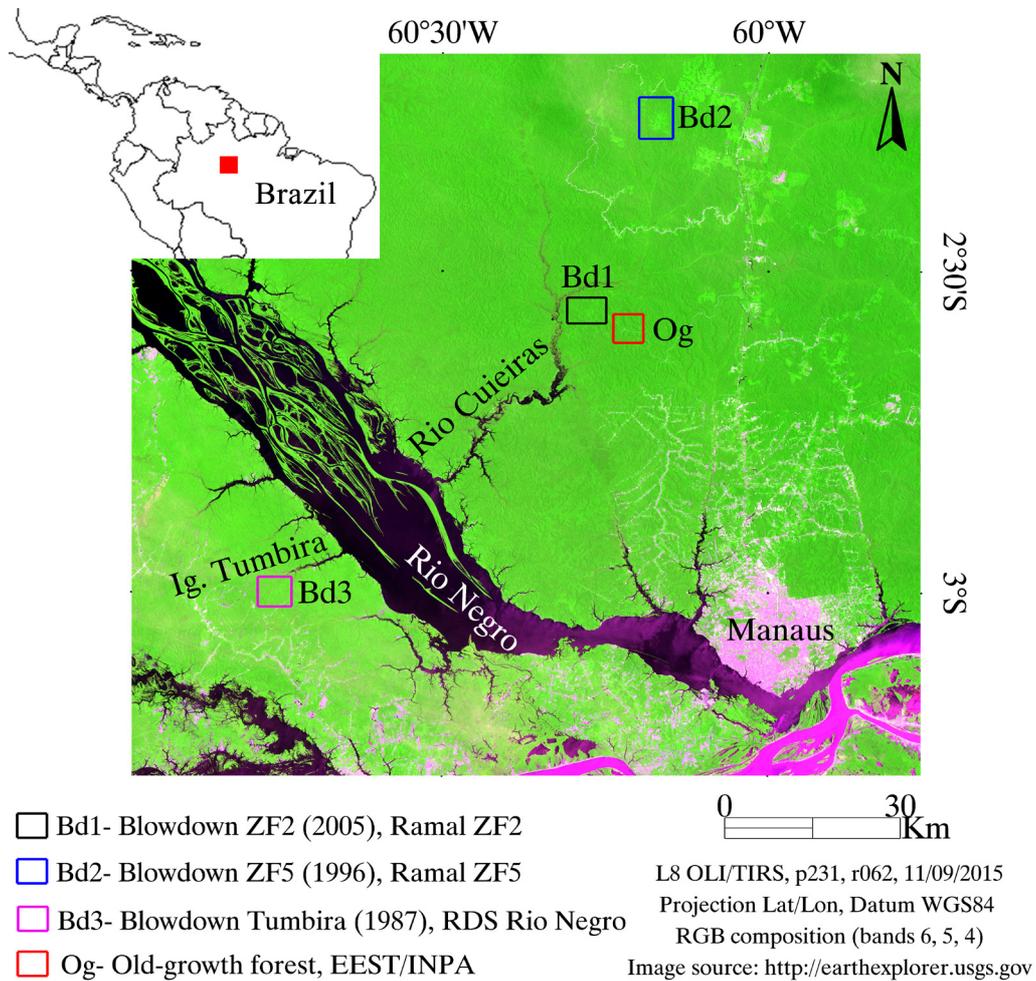


Fig. 1. Study sites (year of blowdown) in Central Amazon, Brazil.

Methods

Methods

Study sites

To study the decadal recovery from past windthrows we used a chronosequence, or a series of sites distributed in space but having different times after disturbance. Our chronosequence is composed of four sites located in the Central Amazon (Fig. 1), including three wind-disturbed forests (Bd1, Bd2 and Bd3) and an old-growth forest (Og) used as control. The four sites included in our chronosequence are covered with typical *terra firme* forest. The *terra firme* forest is the most common forest type in the Amazon basin, originally covering *ca.* 90% of the Brazilian Amazon (Radam 1978; Braga 1979).

The terrain at the study sites is undulating, with altitude in the measured subplots varying from 45 to 121 m a.s.l. (Table S1). Soils in the study region vary in type and texture with local topography. These soils are usually well drained, have high clay content, low pH and low effective cation exchange. Plateaus and the upper portions of slopes have high clay content (Oxisols), whereas soils on slope bottoms and valleys have high sand content (Spodosols) (Chauvel et al. 1987; Telles et al. 2003). Annual precipitation and temperature in Manaus, a city less than 90 km distant from all our study sites, was $2,240 \pm 121 \text{ mm yr}^{-1}$ (mean \pm 95% confidence interval) and $27 \pm 0.16^\circ\text{C}$, respectively (period of 1970-2015, data available in: <http://www.inmet.gov.br/>). This region has a distinct dry season between July and September with monthly precipitation $< 100 \text{ mm}$ (Fig. S1). Site-specific details are provided in the *SI Method* of this article.

Blowdown detection and estimation of tree mortality intensity

We identified blowdowns caused by single storm events analyzing a 21 yrs period (from 1985 to 2005) of Landsat imagery (30 m x 30 m resolution) (<http://www.earthexplorer.usgs.gov>) (Chambers et al. 2013). After excluding imagery data with technical restrictions, blowdowns occurring in other forest types (i.e. white-sandy and floodplain forests) or close to other land uses (e.g. roads, settlements and secondary forests), we selected sites spanning the maximum amplitude in time after disturbance and blowdown tree-mortality intensity. For logistical reasons, accessibility was also considered as a site selection criterion. We selected blowdowns from 2005 (Bb1), 1996 (Bb2) and 1987 (Bb3) (Fig. 1).

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For each disturbed site, we estimated tree mortality caused by the blowdown events by employing Spectral Mixture Analysis (SMA) (Adams et al. 1995) on Landsat imagery. This technique allows for the quantification of the per pixel fraction of the following three selected endmembers (Somers et al. 2011): green vegetation/photosynthetic active (GV), dead plant material/non-photosynthetic vegetation (NPV) and shade. We used the shade endmember to account for differences in angle, topography, shading, and shadows (Adams et al. 1995). Here, we followed an established routine prescribed in previous studies (Negrón-Juárez et al. 2010; Negrón-Juárez et al. 2011; Chambers et al. 2013) (more details in *SI Methods*). The fractions of GV and NPV were then normalized without shade as $GV/(GV+NPV)$ and $NPV/(GV+NPV)$. We calculated the ΔNPV by subtracting the NPV image for the year previous to the blowdown (2 yrs for the Bd2 site, see Fig. 1) from the NPV image after the blowdown. Changes in ΔNPV provide a quantitative measure of tree mortality (Chambers et al. 2007; Negrón-Juárez et al. 2010; Negrón-Juárez et al. 2011). We estimated tree mortality (tree ≥ 10 cm DBH) caused by the blowdowns at plot-level by using a locally parameterized model, which has Landsat-derived ΔNPV as predictor (Negrón-Juárez et al. 2010):

$$\text{Tree mortality (\%)} = (103.22 \times \Delta NPV) - 3.32 [1].$$

Vegetation sampling and biomass estimation

We monitored forest structure in 594 subplots with an area ranging from 250 m² to 400 m² and distributed along transects ranging in size from 200 m to 3,000 m (Tab. S1). Our selected blowdown sites comprise disturbed forest patches spanning a 0–70% tree mortality gradient, including from small- to large-sized gaps. Although several undisturbed forest-patches were encountered along the disturbed forest-matrices included in our blowdown sites, we deliberately sampled undisturbed forest-patches. These were used to test for possible structural differences among sites considering pre-blowdown conditions. In all sites, transects include the typical local topographic variation (i.e. plateaus, slopes and valleys). In each plot, we tagged and measured the DBH of all trees ≥ 10 cm DBH. The blowdown sites were surveyed by the same team, between 2009 and 2015, always in the dry season. Re-measurement of the subplots after several years allowed us to test patterns of biomass recovery and partition with and without the need to substitute space for time. The old-growth forest used as a control is monitored since 1996, at least every two or three years. In this

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study we use data collected in the years 2002 and 2004, for which we had species identification at high resolution (Carneiro 2004; Teixeira et al. 2007) and imagery data confirming that within this time period this forest was not affected by any large blowdown. In the blowdown sites, we collected botanical samples (including flowers and fruits when available) of all recorded tree species. When possible, identification was carried out to the species-level. We assigned the recorded species into three groups relating successional strategies and life histories: pioneers, mid- and late-successional. Our successional group assignment was based on classic studies (Denslow 1980; Brokaw 1985; Swaine and Whitmore 1988; Clark and Clark 1992), studies developed in Amazon *terra firme* forests (Ribeiro et al. 1999; Kammesheidt 2000; Amaral et al. 2009) and those conducted in our study region (Silva et al. 2002; Chambers et al. 2009; Marra et al. 2014; Magnabosco Marra et al. 2016).

We estimated tree biomass (aboveground component) with three locally parameterized allometric models adequate to capture the large variations in tree-size and species composition observed in different successional growth stages (Magnabosco Marra et al. 2016). We used another locally parameterized allometric model (Chambers et al. 2001) to account for biomass losses from damaged trees, i.e. those having total (snapped) or partial loss of crown and/or branches. For these trees, we subtracted the ‘lost biomass’ from the total estimated biomass. We estimated biomass at subplot-level by summing up the biomass of individual trees from each subplot. We classified biomass gain (i.e. regrowth) and loss (i.e. mortality) according to the following mechanisms: growth from recruits (Gr recr), growth from non-damaged trees (Growth), mortality of non-damaged trees (Mort), mortality of resprouters/damaged trees (Mort resp), recruitment (Recr) and growth from resprouters (Resp) with mechanical injuries likely to have been caused by the respective blowdowns (i.e. snapping, uprooting and partial crown loss) (Marra et al. 2014; Ribeiro et al. 2016). Growth from recruits was only measured for the Bd1 (7-10 yrs after disturbance), for which we had three consecutive measures (Tab. S1). Growth from non-damaged trees included growth from survivors and those recruited after the blowdown but before we conducted our surveys.

Statistical analysis

To test our hypotheses, we first pooled subplots from each successional stage into the following disturbance intensity categories: category 1 (undisturbed) tree mortality < 5%

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(Lugo and Scatena 1996; Phillips et al. 2004), category 2 (low disturbance) $5\% \leq$ tree mortality $< 25\%$, category 3 (mid-disturbed) $25\% \leq$ tree mortality $< 45\%$, category 4 (highly-disturbed) tree mortality $\geq 45\%$ (Tab. S1). At second, we used factorial ANOVA to test for structural differences between our old-growth control forest and the undisturbed patches from our different blowdown sites. The disturbance category 1 from our blowdown sites reflected the state of forest that did not suffer the most recent disturbance. In addition, we related subplots' tree mortality intensity (%) to elevation (m) using linear models, and tested for differences in tree mortality among topographic classes with analysis of variance (ANOVA). Terrain elevation was extracted from a digital elevation model with spatial resolution of 30 m x 30 m (Shuttle Radar Topographic Mission -SRTM) (<http://glovis.usgs.gov>).

We tested our first hypothesis, related to the persistent effects of the tree mortality gradient typical of blowdowns on forest structure, by assessing differences in tree density, mean DBH, basal area, WD and AGB among the blowdown sites (i.e. successional stages) included in our chronosequence. We used factorial ANOVA to test for differences among sites and disturbance categories. To assess possible shifts in forest dynamics following wind-disturbance and the influence of disturbance intensity (measured as tree mortality) on these shifts, we compared the growth and mortality rates of different sites and disturbance categories with factorial ANOVA. For that we used data from two consecutive measures taken in each site (Tab. S1). As for structural variables, here we also addressed biomass partition among our three successional groups. For all successional stages, we calculated the relative biomass accumulation/recovery (AGBAcc) as follows:

$$AGBAcc = ((AGB\ gain_{ii} - AGB\ loss_{ii}) \div AGB\ stock_i) \times 100 \quad [2],$$

where AGB is aboveground biomass.

We test our second hypothesis about the relative importance of different gain and loss mechanisms for the overall biomass balance using factorial ANOVA to assess possible differences among blowdown sites and disturbance categories. Here, we also assessed the differential contribution of successional groups through our recorded mechanisms of biomass gain and loss, and their overall importance to the biomass resilience.

As plots vary in total area sampled (Tab. S1), to test our last hypothesis related to the role of taxonomic variation on biomass resilience, we randomly sampled subplots from our different blowdown sites to yield a statistically assembled community with a total area of 3.6-

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ha (hereafter referred as ‘mixed community’) that equally represent our different sites (4-27 yrs after disturbance) and disturbance intensities (categories 1-4). Therefore, our mixed community had 25% of its total area sampled from each of our blowdowns/successional stages (i.e. 4-7 yrs, 7-10 yrs, 14-17 yrs and 24-27 yrs after disturbance). Within each successional stage, we sampled 25% of subplots from each disturbance category. For each of our successional groups, we further assessed variations in species richness along the available disturbance gradient and possible interactions with the recorded biomass gain mechanisms. We also ranked the 20 most important genera within our mixed community by their absolute contribution to the overall biomass gain. Other genera were pooled together. For each of the top-20 genera and the other genera, we assessed species richness attributed to our different biomass gain mechanisms. For the top-20 and other genera, we additionally described variations in biomass gain along our mortality gradient (here as a continuous variable) considering different gain mechanisms. To do so, we related genera weighted biomass gain to tree mortality intensity by using polynomial regressions with 3 degrees of freedom. For fitting these functions, we only consider the mechanisms for which we had five or more observations per genus. Here, we also reported confidence intervals (95%).

We performed all analyses in the R 3.2.1 software platform (R Core Team 2014). Figure 1 was produced using the Environment for Visualizing Images software (ENVI, ITT Industries, Inc, Boulder CO, USA). Other figures were produced using functions from the R package ‘ggplot2’ (Wickham 2009) or self-written functions. All codes used in this study were written by ourselves.

Results

Results***Forest structure, dynamics and functional composition along the disturbance gradient***

While we observed topographic influence on blowdown mortality in Bd1 (Marra et al. 2014), we did not observe significant effects in other sites (more details in *SI Results* and Figs. S2 and S3). Although we found differences in tree density and mean DBH of trees between our old-growth forest and the undisturbed subplots (i.e. disturbance category 1) from our blowdown sites, we did not find significant differences in basal area and biomass (more details in *SI Results* and Table S2). More important, biomass partitioning among functional groups was also similar (see more details in the next subsection and *SI*)

Disturbance categories differed in forest structural attributes (i.e. tree density, mean DBH, basal area and biomass) and wood density for all sites in our chronosequence (Table S3). Within successional stages, the observed variations in these attributes was related to the variation in disturbance intensity, with reductions on tree density, wood density and biomass in areas with greatest tree mortality (category 3 and 4) persisting for at least 27 yrs. Tree density varied among the sites (e.g. from 573 to 703 trees ha⁻¹) in undisturbed plots (Table S3). However, common patterns were observed in subplots from categories 2-4 (most damaged), with initially (4 yrs after disturbance) strong reductions in tree density, but rapid recovery by 7 yrs. Furthermore, we observed increases in tree density between 14-17 yrs after disturbance, but back to considerable reductions marking a self-thinning in the subsequent decade (Table S3 and Fig. S4).

Although basal area (Table S3) and biomass (Fig. 2) recovered 24-27 yrs after disturbance (i.e. no significant differences among disturbance categories), spatial variability was large as evidenced by the large confidence intervals associated with the mean value of these variables. Biomass values ranged from 102.7 ± 46.4 Mg ha⁻¹ (mean \pm 95% confidence interval) (category 4, 4 yrs after disturbance) to 254.8 ± 65.4 Mg ha⁻¹ (category 2, 10 yrs after disturbance) (Table S3). Twenty-seven years after disturbance, we found subplot basal area and biomass values as low as 5.8 m² ha⁻¹ and 70 Mg ha⁻¹, respectively. Apart from reflecting differences in initial damage, this high variation in AGB stocks among subplots suggests strong small-scale variation in biomass resilience.

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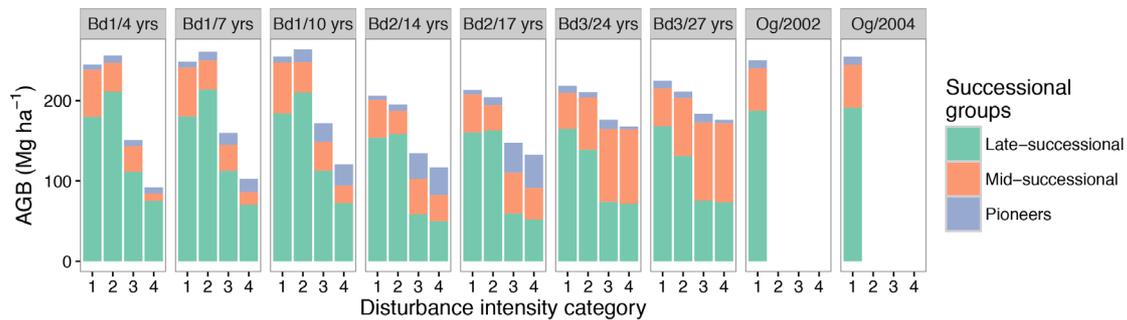


Fig. 2. Aboveground biomass (AGB) stock along a forest chronosequence including blowdowns at different successional stages (4-27 yrs after disturbance) and an old-growth forest in Central Amazon, Brazil. Disturbance categories: 1- tree mortality < 5%; 2- $5\% \leq$ tree mortality < 25%; 3- $25\% \leq$ tree mortality < 45%; 4- tree mortality \geq 45%.

Along with variations in forest structure controlled by initial damage and time after disturbance, we observed a strong variation in the relative importance of our assigned successional groups. Community functional composition was more mixed already 7 yrs after disturbance, with greater contributions of pioneer and mid-successional species (Fig. 2 and Fig. S4). Late-successional species dropped in abundance and in biomass across all the successional stages and disturbed categories and did not recover over 27 yrs. In the blowdown sites, biomass stocks were mostly in pioneer and mid-successional species, though the stocks differed among successional stages, with pioneers accounting for a large fraction in early succession. Biomass stocks in pioneer species largely results from growth of new recruits (i.e. after disturbance), whereas increases in mid-successional species biomass increase represents both recruitment and enhanced growth of trees that were not toppled by wind. Interestingly, the rapid increase of pioneer species in tree density between 7-17 yrs after disturbance did not result in a proportional contribution to biomass recovery. Pioneer species accounted for 36% of tree numbers but only 27% of the total biomass stock between 14-17 yrs after disturbance (averaged between disturbance categories 3 and 4). Still, the contribution of pioneer species in our undisturbed and old-growth control plots was inexpressive. Between 24-27 yrs after disturbance, pioneer species contributed only 4% to the total biomass stocks (categories 3 and 4), while mid-successional species accounted for 53.8%. Late-successional species, which in the old-growth control forest accounted for

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76.7% of the biomass stock (averaged between 2002 and 2004), accounted for only 41.4% of the stock in the disturbance categories 3 and 4, between 14-17 yrs after disturbance (Fig. 2).

The observed increase in importance of gap-specialized and fast-growing species along our disturbance gradient and chronosequence was also evidenced by reductions in the community mean WD (Table S3). Heavily damaged areas comprising large canopy gaps showed a systematic reduction in WD already four years after disturbance. We attribute this pattern to the higher abundance of pioneer and later of mid-successional species, which have lower WD values when compared to late-successional species. Nonetheless, the data from the Bd2 site indicate that WD values become stable 14-17 yrs after disturbance. As presented and discussed in the following sections, this pattern was driven by reductions in the recruitment of mid-successional and especially pioneer species after 17 yrs of disturbance.

Blowdown-driven mortality also strongly affected forest dynamics, including changes in rates of biomass gain (regrowth) and loss (mortality) (Fig 3). Biomass gain increased systematically with disturbance intensity (Fig. 3 and Table S3). Although biomass gain started to decline 14 yrs after disturbance possible due to high tree densities and competition, these areas still had exhibited higher biomass gain than undisturbed areas all over our chronosequence. Biomass gain in category 4 in our Bd1 site (between 4-7 yrs and 7-10 yrs after disturbance) was $8.1 \pm 2.3 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ and $8.1 \pm 2.1 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, respectively. These values were twice as high as those observed in the category 1 of these respective sites and *ca.* 60% higher than those from our old-growth forest. Overall, biomass gain in disturbed areas was significantly higher than that observed in the respective undisturbed forests (Table S3 and Fig. 3). In comparison to the 7-10 yrs stage, biomass gain rates and confidence intervals decreased by *ca.* 25% at the 14-17 yrs stage (gain of $6.1 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ at the categories 3 and 4, respectively). Differences in biomass gain between undisturbed and disturbed forests decreased only in the Bd3 (24-27 yrs after disturbance), with values ranging between $3.9 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (category 1) and $5.6 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (category 2), with the second still significantly higher than the first category.

Results

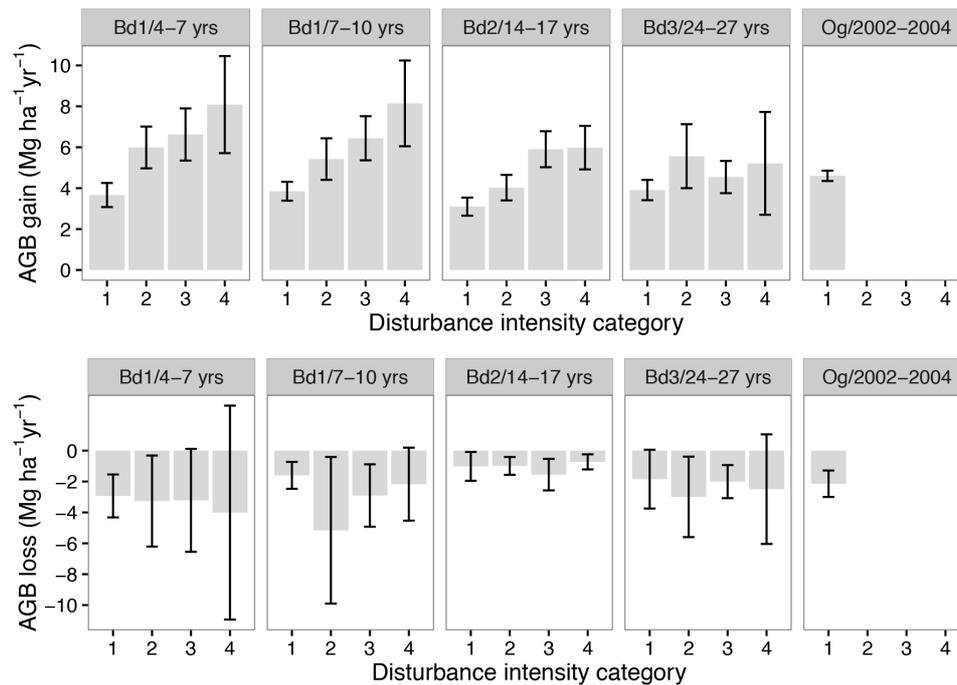


Fig. 3. Aboveground biomass (AGB) balance (gain/regrowth and losses/mortality) (mean \pm 95% confidence interval) along a forest chronosequence including blowdowns at different successional stages (4-27 yrs after disturbance) and an old-growth forest in Central Amazon, Brazil. Disturbance categories: 1- tree mortality < 5%; 2- $5\% \leq$ tree mortality < 25%; 3- $25\% \leq$ tree mortality < 45%; 4- tree mortality \geq 45%.

In highly damaged plots, biomass loss rates along the chronosequence continued to exceed control or low disturbance levels up to 10 yrs following initial disturbance (Fig. 3 and Table S3), with the highest value between 7-10 yrs after disturbance ($-5.3 \pm 4.7 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, category 2). This value exceeded the loss rates in old-growth ($-2.1 \pm 0.9 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) and undisturbed (category 1) forest patches ($1.9 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ averaged over sites) by factor two. This result indicates that post-disturbance mortality events are an important prolonged/delayed effect of blowdowns. Biomass loss decreased between 14-17 yrs after disturbance, especially in heavily damaged areas, where biomass loss dropped down to $-0.9 \pm 0.5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (category 4) (Fig. 3). This lower biomass loss but still high biomass gain reflected the higher tree density that we observed in this stage (Fig. S3 and Table S2). Between 24-27 yrs after disturbance, biomass loss rates increased to $-2.0 \pm 1.1 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ and $-2.5 \pm 3.5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ for category 3 and 4, respectively. This pattern agrees with the reductions in tree density we observed 14-17 yrs after disturbance (Bd2), probably marking a

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self-thinning during this successional stage. Biomass gain exceeded loss in all successional stages, leading to relative biomass accumulation (AGBAcc) ranging from 1% (old-growth control) to nearly 4% in disturbed areas with 10-17 yrs after disturbance (Table S3).

Although 27 yrs after disturbance the biomass stocks and gain rates were again similar to those from the old-growth and undisturbed forests, there were still strong differences in the importance and partitioning of biomass gain and loss mechanisms among successional groups. Overall, changes in dynamics along succession were driven not only by increased biomass gain/accumulation from pioneer and mid-successional but also by considerable biomass loss from late-successional species (more details in *SI Results* and Fig. S5). In Bd1 and Bd2 (4-17 yrs after disturbance), most of the gain was attributable to pioneers species, whereas at Bd3 (24-27 yrs after disturbance), most of the gain was in mid-successional species. This result emphasizes the great importance of pioneer and mid-successional species during the first 27-yr recovery from windthrows. Moreover, the observed increase in biomass loss due to the mortality of pioneer and mid-successional species at Bd3 (24-27 yrs after disturbance) corroborates the occurrence of a self-thinning process between the second and third decade after disturbance. Apart from variations in biomass dynamics and its partitioning among successional groups, blowdowns also enhanced biomass accumulation in small-sized trees (more details in *SI Results* and Fig. S6). This result indicates that gap opening and consequent changes in environmental conditions following blowdowns can also change the typical pattern of old-growth Amazon forests, in which large-sized trees tend to dominate both biomass stocks and dynamics (Slik et al. 2013).

Interactions between taxonomical attributes and mechanisms of biomass resilience

The importance of different biomass gain and loss mechanisms was strongly influenced by variations in disturbance intensity and time after disturbance (Fig. S7). Moreover, changes in the importance of different mechanisms along our chronosequence were driven by changes in functional composition (Fig. 4). Growth from non-damaged trees was the most important biomass gain mechanism in the old-growth ($4.3 \pm 0.2 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) and undisturbed forest patches from our blowdown sites ($2.8 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, averaged among sites) (Fig. S7). In these areas, growth was dominated by late-successional species, with small contribution from mid-successional and negligible contribution from pioneer species (Fig. 4). Overall, the importance of all biomass gain mechanisms performed by late-successional

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species was reduced beyond background mortality-level (category 1), with the exception of a slight increase in growth and recruitment in the Bd1 (7 yrs after disturbance).

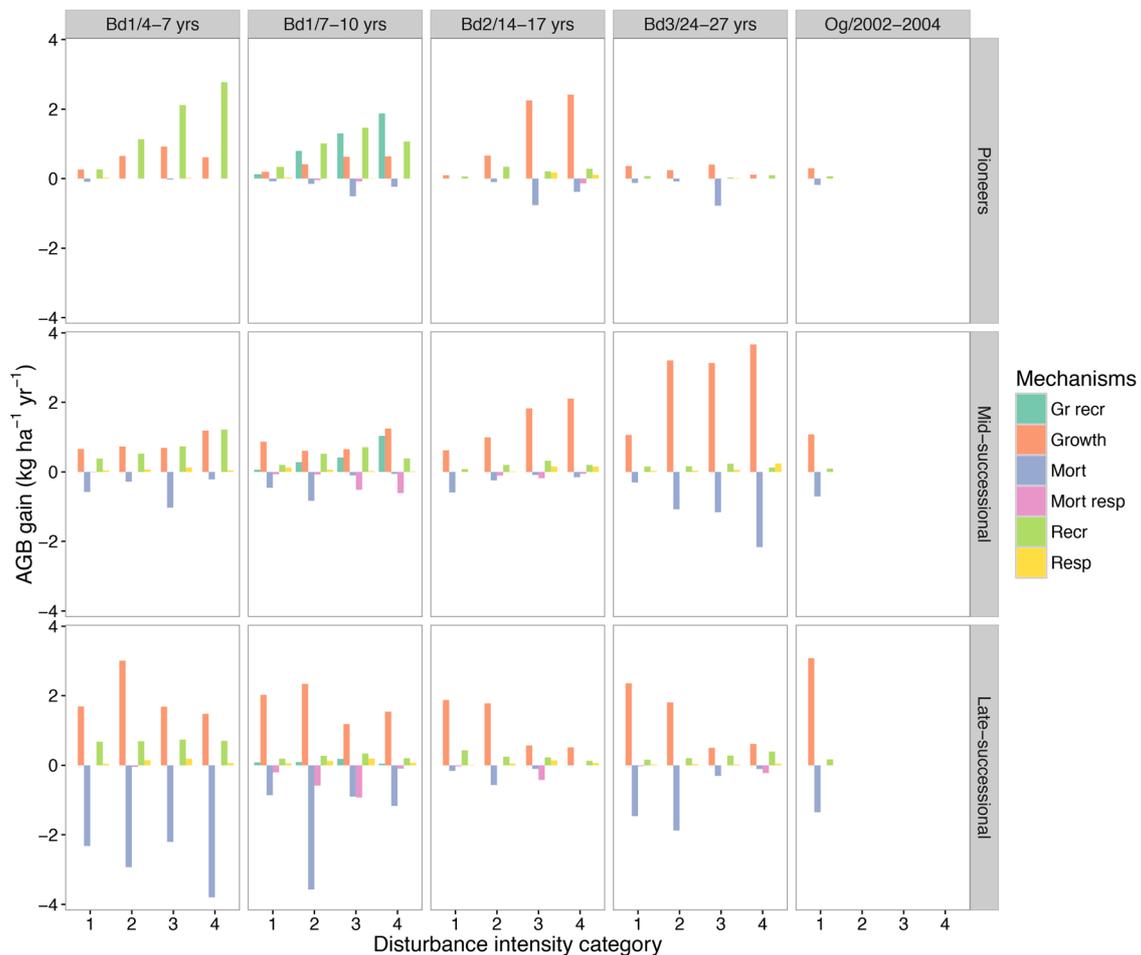


Fig. 4. Mechanisms of aboveground biomass (AGB) gain and loss, and their interactions with variations on the importance of three successional groups along a forest chronosequence including blowdowns at different successional stage (4-27 yrs after disturbance) and an old-growth forest in Central Amazon, Brazil. Disturbance categories: 1- tree mortality < 5%; 2- $5\% \leq$ tree mortality < 25%; 3- $25\% \leq$ tree mortality < 45%; 4- tree mortality \geq 45%. Mechanisms: Gr recr- growth from recruits; Growth- growth from non-damaged trees recorded in the first survey; Mort- mortality; Mort resp- mortality of resprouting trees; Recr- recruitment; Resp- resprouting.

In disturbed areas, although growth from non-damaged trees still represented an important mechanism of biomass gain (maximum of $5.1 \pm 1.5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$), recruitment (maximum of $4.7 \pm 2.3 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) and subsequently growth from recruits (maximum of $3.0 \pm 1.7 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) accounted for an important fraction of the biomass recovery within the

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first 10 yrs after disturbance (Fig. S7 and Table S3). In disturbed areas, the biomass gain of pioneer species through recruitment and growth from recruits overcame the gain through growth of survivors. However, biomass gain from pioneer species decreased drastically in our Bd3 site (24-27 yrs after disturbance), in which biomass gain was dominated by growth of mid-successional species (Fig. 4). Contrary to our expectations, resprouting was not an important biomass gain mechanism in these forests (maximum of $0.47 \pm 0.35 \text{ Mg ha}^{-1} \text{ yr}^{-1}$). Although a broad range of species are in fact able to resprout (Marra et al. 2014), our results suggest that some may die, enter in 'steady-state' or invest resources to recover branches and leaves.

Snapping, uprooting and standing dead comprised the most observed modes of tree death and thus biomass loss in all successional stages (maximum of $-5.3 \pm 4.7 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ in Bd1). The great biomass losses that we observed in Bd1 (7-10 yrs after disturbance) were mainly due to the mortality of late-successional species (Fig. 4). We also observed considerable (maximum of $-1.5 \pm 1.8 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) biomass losses via mortality of resprouters, which in the Bd1 (7-10 yrs after disturbance) outweighed the biomass gain due to resprouters (Fig. S7 and Table S3). Together with the low biomass gain rates, this considerable biomass loss attributable to dying shoots from resprouters provides extra evidence that blowdowns in fact have a delayed mortality effect that may extend for *ca.* 10 yrs.

In our entire sampled area (19.6 ha and 596 subplots) we recorded *ca.* 13,000 trees distributed in 68 botanic families, 275 genera and at least 1,017 species (APGIII classification system) (Stevens 2012). When randomly sampling a mixed community equally representing the different sites and disturbance categories of our chronosequence, we found evidence that biomass resilience, apart from being linked to variations in mechanisms of biomass gain and loss due to changes in functional composition, was also folded/followed by changes in species richness (Fig. 5) and differential performance of genera along our disturbance gradient (Fig. 6). While the amount of pioneer species performing all the different biomass gain mechanisms tended to increase with increasing disturbance intensity (i.e. gap fraction), reductions in the biomass gain due to late-successional species was marked by a decrease in species richness (Fig. 5). Although with minor importance to the recovery process, resprouting was apparently the unique mechanism performed by late-successional trees that was enhanced by increase in species richness. Surprisingly, although higher

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disturbance intensities promoted different mechanisms of biomass gain due to mid-successional species, heavily disturbed areas with the highest biomass gain rates (category 4) had in fact 40% less species than undisturbed areas. In contrast to small-scale canopy disturbance, this result indicates that blowdowns may have a negative effect on recruitment and growth of late-successional species. Whether this reflects a successional shift or a difference between sites will require longer-term observations.

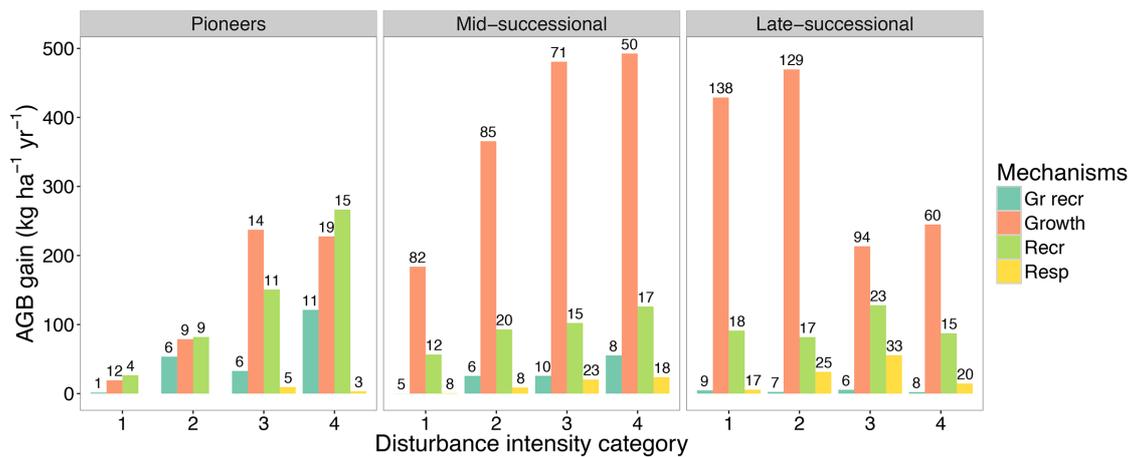


Fig 5. Species richness accounting for different mechanisms of aboveground biomass (AGB) gain performed by different successional groups (i.e. pioneer, mid- and late-successional) in an mixed tree community that represents the typical tree mortality gradient encompassed by Central Amazon forests periodically disturbed by blowdowns. This mixed community includes different blowdown sites (4-27 yrs after disturbance) and an extensive tree mortality gradient (0-70%). AGB gain mechanisms: Gr recr- growth from recruits; Growth- growth from non-damaged trees recorded in the first survey; Recr- recruitment; Resp- resprouting. Species richness within genera for our 3.6-ha sample is given on the top of bars.

Twenty genera (belonging to 16 botanical families and different successional groups) were responsible for 73% of the total biomass gain in our 3.6-ha mixed community, also indicating strong changes in floristic and functional composition due to increased disturbance intensity. The other 27% of the gained biomass was yielded by the remaining 153 genera, which accounted for 60% of the total species richness (Fig 6). Although the biomass gain was dominated by only *ca.* 12% of the total genera richness, these accounted for 40% of the total species richness of our community. While some genera contributed via all of the mechanisms (e.g. *Inga*, *Pourouma* and *Eschweilera*), others were more specialists (e.g. *Tapirira*, *Ocotea*, *Licania* and *Brosimum*) and contributed more via one mechanism. Typical pioneer (e.g.

Results

Cecropia and *Pourouma*) and mid-successional genera (e.g. *Inga* and *Guatteria*) had the greatest biomass gain and species richness in disturbed patches. As observed at individual blowdown sites (Table S4), growth from non-damaged trees and recruitment were the most important biomass gain mechanisms also amongst the top-20 genera in our mixed community. The strong variation in species richness between different mechanisms performed by each of the top-20 genera, indicate strong differences in requirements and performance even for species belonging to the same genus.

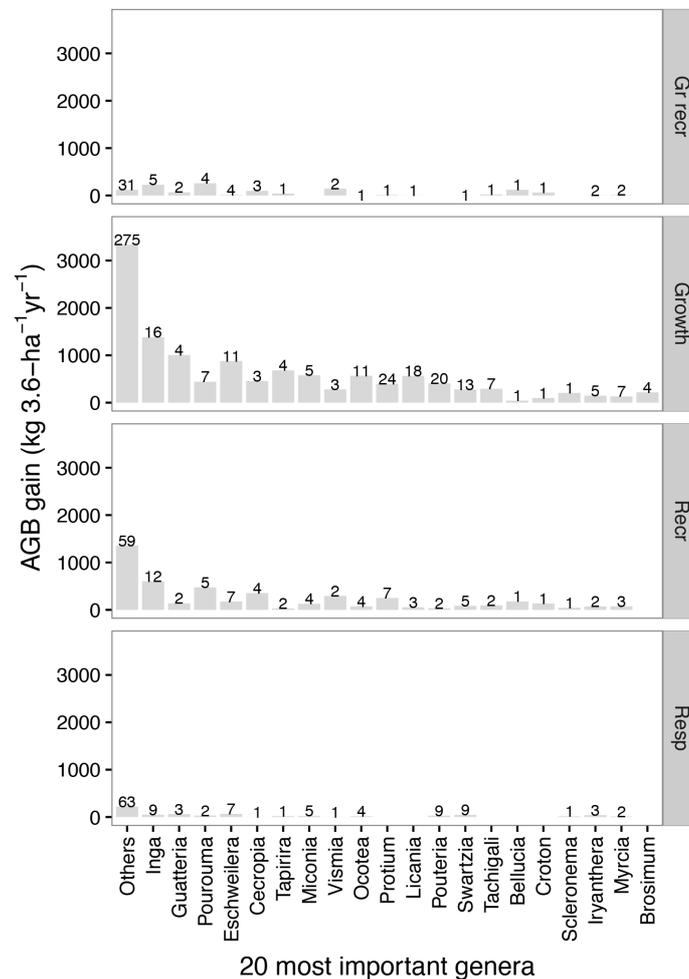


Fig. 6. Partitioning of the absolute aboveground biomass (AGB) gain mechanisms among the top-20 genera (and other genera pooled together) from a 3.6-ha mixed community sampled from our forest chronosequence including blowdowns at different successional stage (4-27 yrs after disturbance) in Central Amazon, Brazil. The blowdown sites encompass an extensive tree-mortality gradient (0-70%). Mechanisms: Gr recr- growth from recruits; Growth- growth from non-damaged trees recorded in the first survey; Recr- recruitment; Resp- resprouting. Species richness within genera for our 3.6-ha sample is given on the top of bars.

Results

Although initial mortality stimulated recruitment and resprouting of the overall community (i.e. other genera pooled together), when considering tree growth solely, biomass gain was negatively influenced by initial mortality (Fig. 7 and Fig. S8 for 95% confidence interval). Therefore, biomass resilience along the extent disturbance gradient created by blowdowns required a ‘joint operation’ of genera with different requirements and abilities, and performing different mechanisms along the initial mortality gradient. Overall, all the 20 genera had ‘unimodal’ curves of biomass gain along our disturbance gradient. *Inga* (Fabaceae), *Pourouma* and *Cecropia* (Urticaceae), *Bellucia* (Melastomataceae) and *Croton* (Euphorbiaceae) had curves of growth and/or recruitment positively related to disturbance intensity. These genera were mostly represented by typical pioneer or mid-successional species, which enhanced biomass resilience (e.g. peaks of biomass gain) above 40% of initial mortality (Fig. 7).

Dominant late-successional genera in Amazon old-growth forests such as *Protium* (Burseraceae), *Licania* (Chrysobalanaceae) and *Brosimum* (Moraceae) (ter Steege et al. 2013) had higher biomass gain in areas with low tree mortality values (category 1, tree mortality < 5%) (Fig. 7). *Protium* had increased biomass gain via recruitment at intermediate disturbance-intensity. Surprisingly, biomass gain in the old-growth dominant genus *Pouteria* was also correlated with tree mortality intensity, suggesting that non-toppled trees from this genus may have increased growth rates in large gaps. Nine of the 20-top genera (belonging to all recorded successional groups) had biomass-gain curves peaking at intermediate disturbance-levels (20-50%) and with reduced values at the extreme of the disturbance gradient. *Eschweilera* and *Swartzia*, also dominant genera in old-growth Amazon forests (ter Steege et al. 2013), had contrasting patterns, with higher biomass at extremes of the disturbance gradient. Apart from *Pouteria*, the 20-top genera in our mixed community had reduced biomass gain via resprouting at intermediate and high disturbance-intensity (category 3 and 4), supporting the low importance of this biomass resilience mechanism. Biomass gain in our mixed community was also dominated by only 20 species, which accounted for 49% of the total biomass gain (more details in *SI Results* and Table S4).

Results

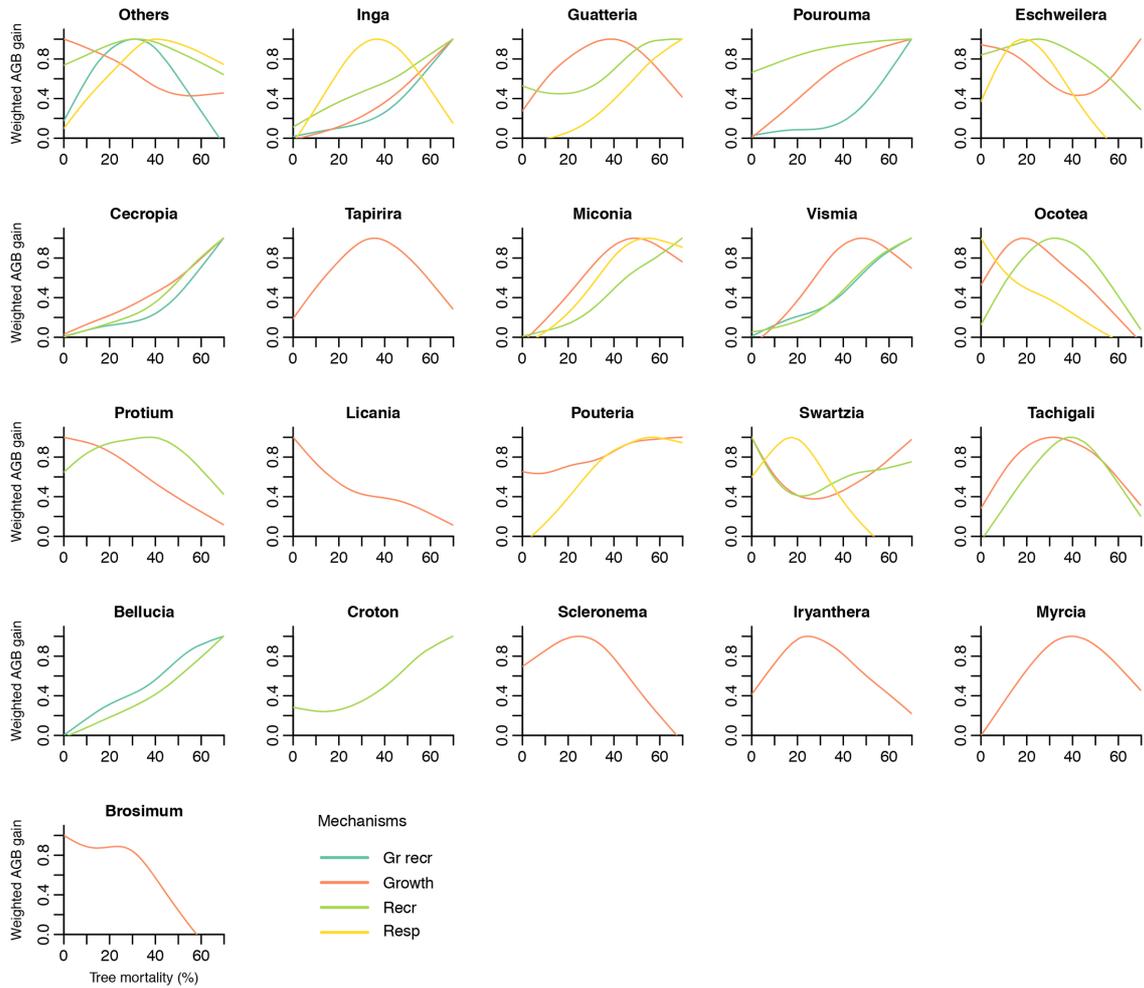


Fig. 7. Curves relating the importance of different aboveground biomass (AGB) gain mechanisms within a 3yr-interval for the top-14 genera (and other genera pooled together) from a tree community sampled from a forest chronosequence including blowdowns at different successional stage (4-27 yrs after disturbance) in Central Amazon, Brazil. Tree mortality intensity (0-70%) was estimated at plot-level from satellite imagery. Mechanisms: Gr recr- growth from recruits; Growth- growth from non-damaged trees recorded in the first survey; Recr- recruitment; Resp- resprouting.

Discussion

Our study offers novel insights into the research of tropical biomass dynamics and resilience to disturbances. We provided the first assessment of forest dynamics following large blowdowns in the Amazon, including interactions between mechanisms of biomass resilience and functional and taxonomic compositional attributes of tree communities. Although our chronosequence is composed of different sites, comparisons between the control site and undisturbed areas indicate no strong site-to-site differences in biomass or community structure. Also, resurveys of the earliest stages following disturbance allow us to compare patterns of initial response, with and without the need to substitute space for time. Even though this is a regional assessment, its results test a hypothesis that has larger implications and can be reasonably extrapolated beyond the region of study (Chambers et al. 2013; Negrón-Juárez et al. 2016). Here, we focus on important implications for understanding landscape patterns of biomass/carbon dynamics and diversity patterns in Amazon forests.

We found strong evidence that blowdowns change structural attributes, functional composition and biomass dynamics of Central Amazon *terra firme* forests for at least three decades following disturbance (Figs. 2 and 3, and *SI Results*). Indeed, recovery from the complex and wide disturbance gradient created by blowdowns involves a diverse cohort of species with different life histories, requirements and mechanisms of resilience varying along temporal and spatial-scales, and depending on individual- and community-level responses. Our findings indicate that this process is markedly different than that from ‘prevalent’ small-scale canopy disturbances associated with background tree mortality. The admixture of genera and species belonging to different successional groups and related changes in mechanisms of biomass resilience that we observed along our disturbance gradient (Figs. 4-7), also support that recovery from blowdowns is different from stand-removing disturbances, where pioneer species tend to dominate biomass gain within the first decades (Finegan 1996; Mesquita et al. 2001; Chazdon 2003).

Although with biomass losses of at least up to 62% (compared with category 1 levels, Table S3), biomass recovery in our blowdown sites was fast (*ca.* 30 yrs) and comparable to that from Amazon logged forests that had lower biomass losses (from 10 to 25%) and predicted recovery time ranging from 10 to 43 yrs (Rutishauser et al. 2015). Biomass recovery in our study sites was also faster than that measured for a nearby secondary forest

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regenerating from clear-cutting and burning (51 yrs) (Lima et al. 2007). In natural fires, clear-cutting and burning or logging, there is combustion and/or removal (timber) of a great part of the nutrients and organic material available from the dead vegetation. In windthrows, part of these nutrients can be incorporated into the soil (Vitousek and Denslow 1986; Santos et al. 2016) and probably re-used by the natural regeneration and surviving trees. Still, in contrast to fragments (Mesquita et al. 1999; Nascimento et al. 2006) or logged areas (Mazzei et al. 2010; Rutishauser et al. 2015), windthrows have a special geometry/shape that leads to a more intense and effective contact between disturbed and undisturbed areas containing the original structure and species pool. Another important aspect is that in blowdowns, as opposed to human disturbances, there is less (or no) soil compaction. In our sites, however, the large variation (confidence intervals) in biomass stocks (Fig. 2 and Table S3) and in rates of biomass gain and loss within subplots of a given disturbance category (Figs. 3 and S5), indicates a large variation in community responses at the landscape-level, with some areas being recovered faster than others.

Biomass loss and gain in our old-growth control and undisturbed forests (Table S2) was within the range of values reported for nearby old-growth forests (accumulation values ranging from $1.65 \text{ Mg ha}^{-1}\text{yr}^{-1}$ to $2.5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) (Higuchi et al. 2004; Vieira et al. 2004; Castilho et al. 2010). Nonetheless, tree mortality following the blowdowns was higher than in our controls (Figs. 3 and S5) and nearby old-growth forests (Higuchi et al. 2004; Vieira et al. 2004; Castilho et al. 2010). Delayed mortality of damaged trees, high competition between recruiting trees, physiological stress due to e.g. desiccation (lower humidity/water availability), increase of temperature, changes in light quality and quantity, and exposure to new smaller-scale wind disturbances are probably associated with this high tree mortality we observed during the first 10 yrs following blowdowns. Delayed mortality is also common in logged forests where logging operations can cause tree damage. In Eastern Amazon, post-mortality events 1 yr after logging represented a biomass loss of $31.1 \pm 16.7 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (Mazzei et al. 2010), six times higher than the maximum loss we observed in our Bd1 site (10 yrs after disturbance, $5.3 \pm 4.7 \text{ Mg ha}^{-1} \text{ yr}^{-1}$).

High tree mortality intensities and subsequent increase in tree density and basal area similar to those we observed along our chronosequence (Table S3) have also been reported for tropical forests disturbed by hurricanes and cyclones (Brokaw and Grear 1991; Scatena et al. 1996; Burslem et al. 2000). Chambers et al. (2009) reported biomass stock in three small

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blowdown patches in Central Amazon *ca.* 6 yrs after disturbance ranging from 89.4 Mg ha⁻¹ to 159.4 Mg ha⁻¹. These values are similar to those we found in intermediate and heavily damaged areas of the Bd1 site, also with four and seven years after disturbance. In the forests disturbed by the hurricane Hugo in Puerto Rico, biomass recovered to 195.0 Mg ha⁻¹ (*ca.* 86% of the pre-disturbance value) five years after disturbance, resulting in a biomass accumulation rate of 16.3 Mg ha⁻¹ yr⁻¹ (Scatena et al. 1996). In our sites (Fig. 1), we detected tree mortality intensities due to the blowdowns as great as 70% (Fig. S2). However, biomass accumulation was not as high (maximum of 5.9 Mg ha⁻¹ yr⁻¹) (Table S3) as the one reported for the disturbed Puerto Rico forests. In contrast to our study, the Puerto Rico forests have higher precipitation (up to 4000 mm yr⁻¹) and volcanic soils (ultisols and inceptisols) with higher nutrient content. These estimates also include other strata and functional types (e.g. saplings and palms). The peak in tree density between 14-17 yrs after disturbance followed by a self-thinning (Fig S4) was also reported for a hurricane damaged forest in Nicaragua (Vandermeer and Cerda 2004). In our sites, this self-thinning process did not lead to strong reductions in basal area or biomass, indicating that possible biomass losses via tree mortality were compensated by gain via growth of established trees and recruitment.

Growth from surviving trees and those recruited after the blowdown - but before our first surveys - were the most important mechanisms allowing the fast biomass recovery that we observed. In addition, the analysis of our mixed community indicated that mechanisms of biomass resilience were influenced by changes in the richness (Fig. 5) and importance of species belonging to different genera and successional groups (Fig. 7). In disturbed patches, biomass recovery was mainly due to species and mechanisms that had lower importance under background tree mortality regimes. In an Eastern Amazon forest, biomass gain four years following logging (mean of 2.6 Mg ha⁻¹ yr⁻¹) was dominated by tree growth (Mazzei et al. 2010), similar to the pattern we observed in our old-growth control forest (Table S2). In our blowdown sites, tree recruitment was the second most important mechanism contributing to biomass resilience. It is worth mentioning that recruitment was mostly exclusive to pioneer and mid-successional genera, including various species. The high number of species able to contribute via this mechanism under the varied conditions created by blowdowns (Fig. 5) suggests that biomass resilience to complex disturbances is enhanced by the diverse species pool typical of these forests (de Oliveira and Mori 1999; Marra et al. 2014).

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The relatively high number of species from pioneer and mid-successional genera that contributed to rapid biomass gain via different mechanisms (growth, resprouting and recruitment), highlight their special ability to rapidly colonize large gaps (Chambers et al. 2009; Marra et al. 2014). In Costa Rica secondary forests with 10-41 yrs after clearing for pasture, second-growth specialist species (i.e. ‘compatible’ to mid-successional species in our approach) dominated biomass stocks and gain (Rozendaal and Chazdon 2015). Just as we observed in our chronosequence, the importance of biomass gain and loss mechanisms also changed during succession in these Costa Rica forests, but tree growth and recruitment were the most important biomass gain mechanisms, respectively. Interestingly, although many species were able to resprout (Figs. 4 and 5) and this was an important mechanism of biomass resilience in other tropical forests disturbed by wind (Yih et al. 1991; Bellingham et al. 1995; Mascaro et al. 2005), it contributed little to the overall biomass accumulation in our study sites (Fig. S7). In fact, resprouting might be a more important mechanism of biomass resilience in small canopy gaps (Putz and Brokaw 1989) and especially in dry tropical forests (Vieira and Scariot 2006).

Interactions between biomass gain mechanisms and taxonomical attributes along our gradient of disturbance suggest a fine partition of the environment, in which the species belonging to the 20-top genera in our mixed community had an optimal performance (i.e. biomass gain) at a specific disturbance level (Fig. 7 and S8). This pattern has also been reported for genera abundance in our Bd1 site (4 yrs after disturbance) (Marra et al. 2014). Interestingly, when pooling all the other genera, we found a clear pattern of reduced biomass gain with increasing disturbance intensity, contrary to that from typical pioneer (*Cecropia* and *Pourouma*), mid- (*Inga*, *Tapirira* and *Gutteria*) or even some late-successional genus (*Eschweilera* and *Swartzia*) (Fig. 7). Although individual-based analysis can provide species-specific information, here growth changes due to different levels of disturbance were evaluated at the subplot level to allow a community-level assessment. We proposed that this lower biomass gain due to late-successional species in our blowdowns sites (Figs. 5 and 7), apart from being influenced by the lower tree density of this group, was also influenced by variation in species responses (Poorter 1999).

Although many species and different biomass gain mechanisms were observed along our disturbance gradient, the fact that 20 genera (from a total of 173) accounted for more than half of the biomass gain in our mixed community (Fig. 6), supports dominance of particular

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genera during forest recovery. Dominance in species abundance (ter Steege et al. 2013) and biomass cycling (*ca.* 1% of the tree species account for 50% of the biomass stock and gain) (Fauset et al. 2015) were reported for old-growth Amazon forests and for forests regenerating from both natural (Kwit et al. 2000; Hjerpe et al. 2001; Weaver 2002) and secondary disturbances (Saldarriaga et al. 1998; Mesquita et al. 2001; Rozendaal and Chazdon 2015). Although we also observed dominance in the biomass recovery in our sites, the dominant cohort typical of old-growth forests changed after the blowdowns. As previously noted, not all genera and species do all the different ‘jobs’. In total, the 20-top genera were represented by 193 species, from which 92 (*ca.* 48%) were recorded contributing to the overall biomass gain through a single mechanism.

Recent studies have demonstrated that even small variations in tree mortality can influence forest structure attributes and dynamics (i.e. tree density, basal area and biomass) at the local- (Toledo et al. 2013), regional- (Schietti et al. 2016) and basin wide-scale (Johnson et al. 2016). Our findings corroborate these studies and provide novel evidence supporting that differences in tree mortality driven by large-scale natural disturbances such as blowdowns have an important influence not only on the structure but also on the species composition and dynamics of Central Amazon *terra firme* forests. Moreover, observed taxonomical variation during succession, suggests that catastrophic natural disturbances may have an important influence on the maintenance and distribution patterns of gap-specialized species in these forests. These findings contradict those from studies that focused on small-scale canopy gaps (< 2000 m²) and reported only minor effects of canopy disturbance on structural attributes, dynamics and diversity of tropical forests (Hubbell et al. 1999), including the Amazon (Uhl et al. 1988; Baker et al. 2015).

AGB stock in our old-growth control forest was 246.8 Mg ha⁻¹. When 70% of the live trees within a 1-ha patch of this forest are killed in a blowdown event (as the maximum tree mortality we observed in our study), 172.8 Mg of necromass or 83.8 Mg C (48.5% of the dry weight) (Silva 2007) is released and deposited on ground. In disturbed subplots of our Bd1 site, 13.7 Mg C (*ca.* 16% of the assumed released value) were incorporated into the soils within the first five years of succession (Santos et al. 2016). Subtracting the 13.7 Mg C incorporated into the soil (not all of which may stay there) from the available 83.8 Mg C released from the dead trees, we can assume that at least *ca.* 70 Mg C will be emitted to the atmosphere. The mean DBH in our old-growth and undisturbed forests was 20.7 ± 0.2 cm;

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the compiled mean WD was $0.702 \pm 0.002 \text{ g cm}^{-3}$. Solving the biomass estimation model used for estimating the biomass of our subplots with these values, which has DBH and WD as predictors (Magnabosco Marra et al. 2016), the mass of a mean-sized tree in our study region is 247 kg. Applying a decomposition rate (k_d) model also fit in our study region (Chambers et al. 2000), this mean-sized tree decomposes at 0.176 yr^{-1} and 95% of its mass is decomposed after 16 yrs. If 95% of the available 70 Mg C is emitted within the first 16 yrs after disturbance (as predicted by the estimated k_d), it gives an emission rate of *ca.* $4.4 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$. This carbon emission rate is higher than the carbon accumulation that we observed in the disturbed subplots from our blowdown sites (which ranged from 0.4 to $2.9 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$). Therefore, we would estimate that the most heavily damaged areas would be net C sources for the decades following disturbance, even though they are accumulating biomass/C at higher rates than old-growth forests (as shown by our results). As damage declines, areas would more quickly return to operate as sink in C balance. This ‘illustration’ emphasizes the importance of blowdowns on the long-term biomass balance and carbon cycle in these forests (Chambers et al. 2013; Negrón-Juárez et al. 2016; Santos et al. 2016). Although disturbance increases tree growth and thus carbon accumulation allowing the interaction of species and biomass gain mechanisms in a complex mortality and recovery gradient, once disturbed by large blowdowns, these forests can remain as a carbon source with different species composition for over three decades. Note that biomass stock was not yet totally recovered in heavily damaged subplots from our Bd3 site (27 yrs after disturbance) (Table S3 and Fig. 2). Moreover, the decomposition rate for trees with DBH larger than mean value of 20.7 cm used in this ‘illustration’ is expected to be lower (Chambers et al. 2000) and thus the decomposition/emission time would be even larger.

Increases on the frequency of natural disturbances due to climate change (Pall et al. 2011; Duffy et al. 2015) or the ongoing intensification of land use resulting in the expansion of fragmented and degraded forests (FAO 2012), can be expected to increase the area of forests with a particular structure and floristic composition (Mesquita et al. 2001; Marra et al. 2014; Norden et al. 2015; Negrón-Juárez et al. 2016). As we have seen, possible shifts towards communities dominated by pioneer species can produce strong reductions in both size of trees (i.e. mean DBH, DBH:total height ratio) and WD, with potential augment on the decomposition rates, reductions in the carbon residence time and consequent quality depletion of timber stocks. Although resilient in terms of biomass stocks, a more intense

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disturbance regime can also be expected to change species and functional composition of these forests. Similar patterns were also reported in a modeling-based study covering Central and Western Amazon (Negrón-Juárez et al. 2016). A possible higher proportion of pioneer or mid-successional species, which are usually smaller, have lower WD, store less biomass in average and have shorter life span when compared to late-successional species (Swaine and Whitmore 1988; Laurance et al. 2004), can in turn increase forest turnover.

Our findings confirm that blowdowns produce a mosaic of forest patches at different successional stages (Chambers et al. 2013) and with particular functional composition and growth rates. A model-based analysis suggested that from 9.1 to 16.9% of tree mortality in Central Amazon is not captured by plot-based approaches (Chambers et al. 2013). In this vast region, blowdowns opening single gaps from 0.6 to 1.4-ha and felling 82 to 205 trees can have an average recurrence rate of *ca.* 840 to 4400 yrs. As trees in this region generally grow slowly and on average can live for centuries (Vieira et al. 2005), even these low recurrence rates can potentially influence long-term dynamics, especially since we have shown that there are processes operating at the larger scales that imply differences between blowdowns and single treefall gaps. Furthermore, if the probability of blowdown events is not constant from year to year but changes with decadal varying climate phenomena (e.g. ENSO), or changes faster than the time-resolution of available imagery data (mostly Landsat), then perhaps the existing remote sensing approaches (that are all to some degree substituting space for time) cannot reliably predict frequency of large-scale natural disturbance events.

We showed that blowdowns amplify environmental gradients, with consequent changes in species and functional composition. More surprising than finding that pioneer and mid-successional species are actually key for early biomass-recovery following blowdowns, which contrasts previous studies that looked at the effects of small canopy-gaps (Uhl et al. 1988; Hubbell et al. 1999; Baker et al. 2015), was the different effect that this wide disturbance gradient can exert in species and genera with presumably opposing growth strategies (Figs. 6 and 7). Actually, we provide novel evidence that species responses (i.e. growth performance) along this wide gradient of disturbance typical of Central Amazon forests do not fundamentally match trivial assumptions such as light demanding species with greater dispersal ability and lower wood density being invariably favored by higher disturbance intensities.

Discussion

The success of species belonging to late-successional genera (i.e. presumably not adapted to large gaps) in our blowdown sites suggests that actually not only classical pioneer species can work as pioneers. This was the case for *Pouteria*, *Swartzia* and *Eschweilera*, all abundant and important genera for the carbon balance in old-growth Amazon forests (ter Steege et al. 2013; Fauset et al. 2015). However, it is important to note that species from these genera contributed relatively less to the biomass recovery process, especially in heavily damaged areas (Fig. 7). The unexpected positive responses of these genera to higher disturbance intensities also suggest that some late-successional species may have a wider plasticity that allow coping with the abrupt environmental/resource changes promoted by blowdowns. Although the elucidation of this aspect requires further investigation, it partially explains why recovery in small canopy-gaps (Uhl et al. 1988; Hubbell et al. 1999) and even following natural disturbances can be dominated by late-successional species (Yih et al. 1991; You and Petty 1991; Zimmerman et al. 1994).

As we have seen, shifts in community composition along the disturbance gradient included changes in the absolute number of species, especially in heavily damaged areas. This pattern was true for the three successional groups assigned in our study. In heavily damaged areas, the observed reductions in richness among mid- and late-successional species and increase (i.e. recruitment) of pioneer species suggest that more intense disturbance regimes can be expected to change both functional and species composition. Moreover, the higher growth of small-sized trees in our disturbed forests (Fig. S6) supports that blowdowns can favor species that usually are suppressed in close-canopy conditions. Significant effects of disturbance on species diversity has been previous reported for Western Amazon forests (Phillips et al. 1994). Based on our findings and previous studies (Chambers et al. 2009; Marra et al. 2014), we propose that apart from associated with edaphic and climate gradients (Quesada et al. 2012; Johnson et al. 2016), this positive effect of disturbance on species diversity is likely to reflect the also higher frequency of blowdowns observed in Central and Western Amazon (Nelson et al. 1994; Espírito-Santo et al. 2010; Negrón-Juárez et al. 2016). Our results also support that the higher abundance of lineages with shorter life spans (Baker et al. 2014) and lower wood density (Quesada et al. 2012) is probably associated with the higher frequency of storms and blowdowns in these regions. In this context, blowdowns seem to play an important role on defining species diversity and distribution by enhancing the

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importance of niche-based process and weakening random processes such as those mediated by seed dispersal.

Conclusive assumptions regarding successional patterns and legacies of blowdowns in Amazon forests still require long-term monitoring. However, we revealed that blowdowns are an important driver of forest structure, functional composition and biomass dynamics. Importantly, we empirically demonstrated that although higher biomass loss due to more intense natural disturbance regimes can be compensated by increase in accumulation rates (i.e. more productive forests), blowdowns could be expected to promote strong changes in functional and species composition. Assumptions from studies that looked at small-scale disturbance events cannot be extrapolate to these larger-scale events.

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References

References

- Adams JB, Sabol DE, Kapos V, et al (1995) Classification of multispectral images based on fractions of endmembers: Application to land-cover change in the Brazilian Amazon. *Remote Sens Environ* 52:137–154.
- Amaral D, Vieira I, Almeida S, et al (2009) Checklist of remnant forest fragments of the metropolitan area of Belém and historical value of the fragments, State of Pará, Brazil. *Bol Mus Para Emílio Goeldi* 4:231–289.
- Baker TR, Diaz DMV, Moscoso VC, et al (2015) Consistent, small effects of tree-fall disturbances on the composition and diversity of four Amazonian forests. *J Ecol* 104:497–506. doi: 10.1111/1365-2745.12529
- Baker TR, Pennington RT, Magallon S, et al (2014) Fast demographic traits promote high diversification rates of Amazonian trees. *Ecol Lett* 17:527–536. doi: 10.1111/ele.12252
- Bellingham P, Tanner E, Healey J (1995) Damage and responsiveness of Jamaican montane tree species after disturbance by a hurricane. *Ecology* 76:2562–2580.
- Bongers F, Poorter L, Hawthorne WD, Sheil D (2009) The intermediate disturbance hypothesis applies to tropical forests, but disturbance contributes little to tree diversity. *Ecol Lett* 12:798–805. doi: 10.1111/j.1461-0248.2009.01329.x
- Braga PIS (1979) Subdivisão fitogeográfica, tipos de vegetação, conservação e inventário florístico da floresta amazônica. *Acta Amaz* 9:53–80.
- Brokaw N (1985) Gap-phase regeneration in a tropical forest. *Ecology* 66:682–687.
- Brokaw N, Grear J (1991) Forest structure before and after the hurricane Hugo at three elevations in the Luquillo Mountains, Porto Rico. *Biotropica* 23:386–392.
- Burslem D, Whitmore T, Brown G (2000) Short-term effects of cyclone impact and long-term recovery of tropical rain forest on Kolombangara, Solomon Islands. *J Ecol* 88:1063–1078.
- Burslem DFRP, Whitmore TC (2009) Species diversity, susceptibility to disturbance and tree population dynamics in tropical rain forest. *J Veg Sci* 10:767–776. doi: 10.2307/3237301
- Carneiro VMC (2004) Composição florística e análise estrutural da floresta primária de terra firme na bacia do Rio Cuieiras, Manaus-AM. M.Sc. Dissertation, Ciências de Florestas Tropicais (CFT), Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil
- Castilho C de, Magnusson W, Araújo R de, Luizão F (2010) Short-term temporal changes in tree live biomass in a Central Amazonian forest, Brazil. *Biotropica* 42:95–103.
- Chambers JQ, Asner GP, Morton DC, et al (2007) Regional ecosystem structure and function: ecological insights from remote sensing of tropical forests. *Trends Ecol Evol* 22:414–23. doi: 10.1016/j.tree.2007.05.001

References

- Chambers JQ, Higuchi N, Schimel JP, et al (2000) Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. *Oecologia* 122:380–388.
- Chambers JQ, Negrón-Juárez RI, Marra DM, et al (2013) The steady-state mosaic of disturbance and succession across an old-growth Central Amazon forest landscape. *Proc Natl Acad Sci* 110:3949–54. doi: 10.1073/pnas.1202894110
- Chambers JQ, Robertson AL, Carneiro VMC, et al (2009) Hyperspectral remote detection of niche partitioning among canopy trees driven by blowdown gap disturbances in the Central Amazon. *Oecologia* 160:107–117.
- Chambers JQ, Santos J dos, Ribeiro RJ, Higuchi N (2001) Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest. *For Ecol Manage* 152:73–84.
- Chauvel A, Lucas Y, Boulet R (1987) On the genesis of the soil mantle of the region of Manaus, Central Amazonia, Brazil. *Experientia* 43:234–241.
- Chazdon RL (2003) Tropical forest recovery: legacies of human impact and natural disturbances. *Perspect Plant Ecol Evol Syst* 6:51–71. doi: 10.1078/1433-8319-00042
- Chazdon RL, Letcher SG, van Breugel M, et al (2007) Rates of change in tree communities of secondary Neotropical forests following major disturbances. *Philos Trans R Soc Lond B Biol Sci* 362:273–289. doi: 10.1098/rstb.2006.1990
- Clark DA, Clark DB (1992) Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecol Monogr* 62:315–344.
- Clark DB, Clark DA, Brown S, et al (2002) Stocks and flows of coarse woody debris across a tropical rain forest nutrient and topography gradient. *For Ecol Manage* 164:237–248. doi: 10.1016/S0378-1127(01)00597-7
- Cole LES, Bhagwat SA, Willis KJ (2014) Recovery and resilience of tropical forests after disturbance. *Nat Commun* 5:3906. doi: 10.1038/ncomms4906
- Dale VH, Lugo AE, MacMahon JA, Pickett STA. (1998) Ecosystem Management in the Context of Large, Infrequent Disturbances. *Ecosystems* 1:546–557. doi: 10.1007/s100219900050
- Dalling JW, Winter K, Hubbell SP (2004) Variation in growth responses of neotropical pioneers to simulated forest gaps. *Funct Ecol* 18:725–736.
- de Oliveira AA, Mori SA (1999) A central Amazonian terra firme forest. I. High tree species richness on poor soils. *Biodivers Conserv* 8:1219–1244.
- Denslow J (1980) Gap partitioning among tropical rainforest trees. *Biotropica* 12:47–55.
- Duffy PB, Brando P, Asner GP, Field CB (2015) Projections of future meteorological drought and wet periods in the Amazon. *Proc Natl Acad Sci* 112:13172–13177. doi: 10.1073/pnas.1421010112

References

- Espírito-Santo F, Gloor M, Keller M, et al (2014) Size and frequency of natural forest disturbances and the Amazon forest carbon balance. *Nat Commun* 5:1–6.
- Espírito-Santo F, Keller M, Braswell B, et al (2010) Storm intensity and old-growth forest disturbances in the Amazon region. *Geophys Res Lett* 37:1–6.
- Everham EM, Brokaw NVL (1996) Forest damage and recovery from catastrophic wind. *Bot Rev* 62:113–185. doi: 10.1007/BF02857920
- Fauset S, Johnson MO, Gloor M, et al (2015) Hyperdominance in Amazonian forest carbon cycling. *Nat Commun* 6:6857. doi: 10.1038/ncomms7857
- Ferguson BG, Boucher DH, Pizzi M, Rivera C (1995) Recruitment and decay of a pulse of *Cecropia* in Nicaraguan rain forest damaged by hurricane Joan: Relation to mutualism with *Azteca* ants. *Biotropica* 27:455–460.
- Finegan B (1996) Pattern and process in neotropical secondary rain forests: The first 100 years of succession. *Trends Ecol Evol* 11:119–124. doi: 10.1016/0169-5347(96)81090-1
- Food and Agriculture Organization of the United Nations and European Commission Joint Research Centre (2012) Global forest land-use change 1990-2005.
- Garstang M, White S, Shugart HH, Halverson J (1998) Convective cloud downdrafts as the cause of large blowdowns in the Amazon rainforest. *Meteorol Atmos Phys* 67:199–212. doi: 10.1007/BF01277510
- Gloor M, Phillips OL, Lloyd JJ, et al (2009) Does the disturbance hypothesis explain the biomass increase in basin-wide Amazon forest plot data? *Glob Chang Biol* 15:2418–2430.
- Grubb P (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol Rev* 52:107–145.
- Guariguata M, Ostertag R (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. *For Ecol Manag* 148:185–206.
- Harrison G (1979) Stability under environmental stress : resistance , resilience , persistence, and variability. *Am Nat* 113:659–669.
- Hérault B, Beauchêne J, Muller F, et al (2010) Modeling decay rates of dead wood in a neotropical forest. *Oecologia* 164:243–251. doi: 10.1007/s00442-010-1602-8
- Higuchi N, Chambers JQ, Santos J dos, et al (2004) Carbon balance and dynamics of primary vegetation in the Central Amazon. *Floresta* 34:295–304.
- Hjerpe J, Hedenås H, Elmqvist T (2001) Tropical rain forest recovery from cyclone damage and fire in Samoa. *Biotropica* 33:249–259. doi: 10.1111/j.1744-7429.2001.tb00176.x
- Hodgson D, McDonald JL, Hosken DJ (2015) What do you mean, “resilient”? *Trends Ecol Evol* 30:503–506. doi: 10.1016/j.tree.2015.06.010

References

- Holling C (1973) Resilience and stability of ecological systems. *Annu Rev Ecol Syst* 4:1–23. doi: 10.1146/annurev.es.04.110173.000245
- Hubbell SP, Foster RB, O'Brien ST, et al (1999) Light-Gap Disturbances, Recruitment Limitation, and Tree Diversity in a Neotropical Forest. *Science* 283:554–557.
- Imbert D, Rousteau A, Labbe P (1998) Hurricanes and biological diversity in tropical forest - the example of Guadeloupe. *Acta Oecologica* 19:251–262.
- Jakovac C, Peña-Claros M, Kuyper T, Bongers F (2015) Loss of secondary-forest resilience by land-use intensification in the Amazon. *J Ecol* 103:67–77. doi: 10.1111/1365-2745.12298
- Johnson E, Miyanishi K (eds) (2010) *Plant disturbance ecology: the process and the response*. Elsevier, Academic Press, Burlington, MA
- Johnson M., Galbraith D, Gloor E, et al (2016) Variation in stem mortality rates determines patterns of aboveground biomass in Amazonian forests: implications for dynamic global vegetation models. *Glob Chang Biol*. doi: 10.1111/gcb.13315
- Kammesheidt L (2000) Some autecological characteristics of early to late successional tree species in Venezuela. *Acta Oecologica* 21:37–48.
- Kwit C, Platt WJ, Slater HH (2000) Post-hurricane regeneration of pioneer plant species in south Florida subtropical hardwood hammocks. *Biotropica* 32:244–251. doi: 10.1111/j.1744-7429.2000.tb00467.x
- Laurance W, Nascimento H, Laurance S, et al (2004) Inferred longevity of Amazonian rainforest trees based on a long-term demographic study. *For Ecol Manage* 190:131–143. doi: 10.1016/j.foreco.2003.09.011
- Lawton RO, Putz FE (1988) Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. *Ecology* 69:764–777.
- Lima AJN, Teixeira LM, Carneiro VMC, et al (2007) Biomass stock and structural analysis of a secondary forest in Manaus (AM) region, ten years after clear cutting followed by fire. *Acta Amaz* 37:49–54.
- Lindroth A, Lagergren F, Grelle A, et al (2009) Storms can cause Europe-wide reduction in forest carbon sink. *Glob Chang Biol* 15:346–355. doi: 10.1111/j.1365-2486.2008.01719.x
- Lugo A (2008) Visible and invisible effects of hurricanes on forest ecosystems: an international review. *Austral Ecol* 33:368–398.
- Lugo A, Scatena F (1996) Background and catastrophic tree mortality in tropical moist, wet, and rain forests. *Biotropica* 28:585–599.
- Magnabosco Marra D, Higuchi N, Trumbore S, et al (2016) Predicting biomass of hyperdiverse and structurally complex Central Amazon forests – a virtual forest approach using extensive field data. *Biogeosciences* 13:15537–15581. doi: 10.5194/bgd-12-15537-2015
- Marra DM, Chambers JQ, Higuchi N, et al (2014) Large-scale wind disturbances promote tree diversity in a

References

- central Amazon forest. *PLoS One* 9:e103711. doi: 10.1371/journal.pone.0103711
- Mascaro J, Perfecto I, Barros O, et al (2005) Aboveground biomass accumulation in a tropical wet forest in Nicaragua following a catastrophic hurricane disturbance. *Biotropica* 37:600–608. doi: 10.1111/j.1744-7429.2005.00077.x
- Mazzei L, Sist P, Ruschel A, et al (2010) Above-ground biomass dynamics after reduced-impact logging in the Eastern Amazon. *For Ecol Manage* 259:367–373. doi: 10.1016/j.foreco.2009.10.031
- Mesquita R, Delamônica P, Laurance WF (1999) Effect of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. *Biol Conserv* 91:129–134. doi: 10.1016/S0006-3207(99)00086-5
- Mesquita R, Ickes K, Ganade G, Williamson G (2001) Alternative successional pathways in the Amazon Basin. *J Ecol* 89:528–537.
- Molino J, Sabatier D (2001) Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. *Science* 294:1702–1704. doi: 10.1126/science.1060284
- Nascimento HEM, Andrade a. CS, Camargo JLC, et al (2006) Effects of the surrounding matrix on tree recruitment in Amazonian forest fragments. *Conserv Biol* 20:853–860. doi: 10.1111/j.1523-1739.2006.00344.x
- Negrón-Juárez RI, Chambers JQ, Guimaraes G, et al (2010) Widespread Amazon forest tree mortality from a single cross-basin squall line event. *Geophys Res Lett* 37:1–5.
- Negrón-Juárez RI, Chambers JQ, Marra DM, et al (2011) Detection of subpixel treefall gaps with Landsat imagery in Central Amazon forests. *Remote Sens Environ* 115:3322–3328.
- Negrón-Juárez RI, Holm J, Magnabosco Marra D, et al (2016) Vulnerability of Amazon forests to storm-driven tree mortality. *Sci Adv* in review.
- Nelson B, Kapos V, Adams J, et al (1994) Forest disturbance by large blowdowns in the Brazilian Amazon. *Ecology* 75:853–858.
- Norden N, Angarita HA, Bongers F, et al (2015) Successional dynamics in Neotropical forests are as uncertain as they are predictable. *Proc Natl Acad Sci U S A* 112:8013–8018.
- Pall P, Aina T, Stone D a, et al (2011) Anthropogenic greenhouse gas contribution to flood risk in England and Wales in autumn 2000. *Nature* 470:382–5. doi: 10.1038/nature09762
- Peterson G, Allen C, Holling C (1998) Ecological resilience, biodiversity, and scale. *Ecosystems* 1:6–18.
- Phillips O, Baker T, Arroyo L, et al (2004) Pattern and process in Amazon tree turnover, 1976-2001. *Philos Trans R Soc Lond B Biol Sci* 359:381–407.
- Phillips O, Hall P, Gentry A, et al (1994) Dynamics and species richness of tropical rain forests. *Proc Natl Acad Sci* 91:2805–2809.
- Poorter L (1999) Growth responses of 15 rain forest tree species to a light gradient; the relative importance of

References

- morphological and physiological traits. *Funct Ecol* 13:396–410.
- Poorter L, Bongers F, Aide TM, et al (2016) Biomass resilience of Neotropical secondary forests. *Nature*. doi: 10.1038/nature16512
- Poorter L, van der Sande MT, Thompson J, et al (2015) Diversity enhances carbon storage in tropical forests. *Glob Ecol Biogeogr* 24:1314–1328. doi: 10.1111/geb.12364
- Putz F, Brokaw N (1989) Sprouting of broken trees on Barro Colorado Island, Panama. *Ecology* 70:508–512.
- Quesada CA, Phillips OL, Schwarz M, et al (2012) Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences* 9:2203–2246. doi: 10.5194/bg-9-2203-2012
- R Core Team (2014) R: A language and environment for statistical computing.
- Radam (1978) Programa de Integração Nacional- Levantamentos dos Recursos Naturais. Ministério das Minas e Energia, Brasil, Brasília
- Ribeiro GHM, Chambers JQ, Peterson CJ, et al (2016) Mechanical vulnerability of Central Amazon tree species to windthrow in convective storms. *For Ecol Manage* in review.
- Ribeiro JELS, Hopkins MJG, Vicentini A, et al (1999) Flora da Reserva Ducke: Guia de Identificação das Plantas Vasculares de uma Floresta de Terra-firme na Amazônia Central. INPA, Manaus
- Rifai SW, Urquiza Muñoz JD, Negrón-Juárez RI, et al (2016) Landscape-scale consequences of differential tree mortality from catastrophic wind disturbance in the Amazon. *Ecol Appl*. doi: 10.1002/eap.1368
- Rozendaal D, Chazdon R (2015) Demographic drivers of tree biomass change during secondary succession in northeastern Costa Rica. *Ecol Appl* 25:506–516. doi: 10.1890/14-0054.1
- Rutishauser E, Baraloto C, Blanc L, et al (2015) Rapid tree carbon recovery in Amazonian logged forests. *Curr Biol* 25:R787–R788. doi: 10.1016/j.cub.2015.07.034
- Saldarriaga JG, West DC, Tharp ML, Uhl C (1998) Long-Term Chronosequence of Forest Succession in the Upper Rio Negro of Colombia and Venezuela. *J Ecol* 76:938–958.
- Santos LT dos, Magnabosco Marra D, Trumbore S, et al (2016) Windthrows increase soil carbon stocks in a Central Amazon forest. *Biogeosciences* 13:1299–1308. doi: 10.5194/bg-12-19351-2015
- Scatena F, Moya S, Estrada C, Chinea J (1996) The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico. *Biotropica* 28:424–440.
- Schiatti J, Martins D, Emilio T, et al (2016) Forest structure along a 600 km transect of natural disturbances and seasonality gradients in central-southern Amazonia. *J Ecol*. doi: 10.1111/1365-2745.12596
- Silva R da (2007) Alometria, estoque e dinâmica da biomassa de florestas primárias e secundárias na região de Manaus (AM). Ph.D. Dissertation, Universidade Federal do Amazonas, Brazil

References

- Silva RP da, Santos J dos, Tribuzy ES, et al (2002) Diameter increment and growth patterns for individual tree growing in Central Amazon, Brazil. *For Ecol Manage* 166:295–301.
- Slik JWF, Paoli G, Mcguire K, et al (2013) Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Glob Ecol Biogeogr* 22:1261–1271. doi: 10.1111/geb.12092
- Somers B, Asner G, Tits L, Coppin P (2011) Endmember variability in Spectral Mixture Analysis: a review. *Remote Sens Environ* 115:1603–1616. doi: 10.1016/j.rse.2011.03.003
- Stevens PF (2012) Angiosperm Phylogeny Website. <http://www.mobot.org/MOBOT/research/APweb/>.
- Swaine MD, Whitmore TC (1988) On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75:81–86.
- Teixeira L, Chambers J, Silva A, et al (2007) Projeção da dinâmica da floresta natural de Terra-firme, região de Manaus-AM, com o uso da cadeia de transição probabilística de Markov. *Acta Amaz* 37:377–384.
- Telles EC, Camargo PB, Martinelli LA, et al (2003) Influence of soil texture on carbon dynamics and storage potential in tropical forest soils of Amazonia. *Global Biogeochem Cycles* 17:1–12.
- ter Steege H, Pitman NCA, Sabatier D, et al (2013) Hyperdominance in the Amazonian Tree Flora. *Science* 342:1243092–1243092. doi: 10.1126/science.1243092
- Thompson I, Mackey B, McNulty S, Mosseler A (2009) Forest Resilience, Biodiversity, and Climate Change - a synthesis of the biodiversity/resilience/stability relationship in forest ecosystems. Montreal
- Toledo JJ de, Magnusson W, Castilho C (2013) Competition, exogenous disturbances and senescence shape tree size distribution in tropical forest: evidence from tree mode of death in Central Amazonia. *J Veg Sci* 24:651–663.
- Turner M, Baker W, Peterson C, Peet R (1998) Factors Influencing Succession: Lessons from Large, Infrequent Natural Disturbances. *Ecosystems* 1:511–523.
- Uhl C, Clark K, Dezzio N, Maquirino P (1988) Vegetation dynamics in Amazonian treefall gaps. *Ecology* 69:751–763.
- Vandermeer J, Cerda I (2004) Height dynamics of the thinning canopy of a tropical rain forest: 14 years of succession in a post-hurricane forest in Nicaragua. *For Ecol Manage* 199:125–135. doi: 10.1016/j.foreco.2004.05.033
- Vandermeer J, la Cerda I de, Boucher D, et al (2000) Hurricane Disturbance and Tropical Tree Species Diversity. *Science* 290:788–791.
- Vandermeer J, Mallona J, Boucher D, et al (1995) Three years of ingrowth following catastrophic hurricane damage on the Caribbean coast of Nicaragua: Evidence in support of the direct regeneration hypothesis. *J Trop Ecol* 11:465–471.
- Vieira D, Scariot A (2006) Principles of natural regeneration of tropical dry forests for restoration. *Restor Ecol*

References

- 14:11–20. doi: 10.1111/j.1526-100X.2006.00100.x
- Vieira S, de Camargo PB, Selhorst D, et al (2004) Forest structure and carbon dynamics in Amazonian tropical rain forests. *Oecologia* 140:468–479.
- Vieira S, Trumbore S, de Camargo PB, et al (2005) Slow growth rates of Amazonian trees: consequences for carbon cycling. *Proc Natl Acad Sci* 102:18502–7. doi: 10.1073/pnas.0505966102
- Vitousek P, Denslow J (1986) Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. *J Ecol* 74:1167–1178.
- Walker L (1991) Tree damage and recovery from Hurricane Hugo in Luquillo experimental forest, Puerto Rico. *Biotropica* 23:379–385.
- Weaver PL (2002) Chronology of hurricane induced changes in Puerto Rico's lower montane rain forest. *Interciencia* 27:252–258.
- Wickham H (2009) *ggplot2: elegant graphics for data analysis*. Springer New York
- Yih K, Boucher DH, Vandermeer JH, Zamora N (1991) Recovery of the rain forest of southeastern Nicaragua after destruction by hurricane Joan. *Biotropica* 23:106–113.
- You C, Petty WH (1991) Effects of hurricane Hugo on *Manilkara bidentata*, a primary tree species in the Luquillo Experimental Forest of Puerto Rico. *Biotropica* 23:400–406.
- Zappi DC, Ranzato Filardi FL, Leitman P, et al (2015) Growing knowledge: An overview of Seed Plant diversity in Brazil. *Rodriguesia* 66:1085–1113. doi: 10.1590/2175-7860201566411
- Zeng H, Chambers J, Negrón-Juárez R, et al (2009) Impacts of tropical cyclones on U.S. forest tree mortality and carbon flux from 1851 to 2000. *Proc Natl Acad Sci U S A* 106:7888–92. doi: 10.1073/pnas.0808914106
- Zimmerman JK, Everham EM, Waide RB, et al (1994) Responses of tree species to hurricane winds in subtropical wet forest in Puerto-Rico: Implications for tropical tree life histories. *J Ecol* 82:911–922.

Supporting information

Mechanisms of Amazon biomass resilience to windthrows

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Methods

Study sites

Forests in the region of study have dense understory, closed canopy (Braga 1979) and high tree species diversity (de Oliveira and Mori 1999). Fabaceae, Lecythidaceae, Sapotaceae, Chrysobalanaceae and Burseraceae are amongst the botanic families with the highest tree density per hectare (Silva et al. 2002; Marra et al. 2014). Tree dominant height, defined as the average height of trees in the upper 10% height class, is 30.2 ± 2.9 m (Higuchi 2015), but some emergent species such as *Dinizia excelsa* Ducke (Fabaceae), *Cariniana decandra* Ducke (Lecythidaceae) and *Caryocar pallidum* A.C. Sm. (Caryocaraceae) can grow up to more than 40 m height. Trees larger than 100 cm in DBH occur in densities < 1 tree ha^{-1} (Vieira et al. 2004) and those with $\text{DBH} \leq 50$ cm account for more than 90% of the total tree density (Higuchi et al. 2012). In our Bd1 site, soils from disturbed areas were reported to have higher carbon stocks and organic carbon content than those from undisturbed areas, with carbon stocks being positively related to clay content and tree mortality intensity (Santos et al. 2016).

The old-growth forest used as a control area is located at the *Estação Experimental de Silvicultura Tropical* (EEST), a 21,000 ha reserve of the *Instituto Nacional de Pesquisas da Amazônia* (INPA) (Fig. 1). We used permanent plots (two transects of 20 x 2500 m) installed as part of the *Projeto Jacaranda* (Higuchi et al. 1998) in 1996 and monitored for forest structure and floristic composition at least every two to three years since 1998 by the *Laboratório de Manejo Florestal* (LMF) (Table S1). This forest has had no large natural or human disturbances for at least the last 55 yrs. The Bd1 from 2005 (total area of *ca.* 250 ha) is located at a large forest patch accessible from the *Ramal-ZF2* road, and contiguous to the EEST (Table S1). The Bd1 site, also described in previous related studies (Negrón-Juárez et al. 2010; Marra et al. 2014; Santos et al. 2016), is mainly located in an area owned and administered by the *Superintendência da Zona Franca de Manaus* (SUFRAMA). The Bd2 from 1996 (*ca.* 900 ha) is located *ca.* 35 km north from the Bd1 in a forest accessible from the *Ramal-ZF5* road, also owned and administrated by the SUFRAMA. The Bd3 from 1987 (*ca.* 75 ha) is located at the *Reserva de Desenvolvimento Sustentável* (RDS) do *Rio Negro*, a 102,978.83 ha reserve created in 2008, regulated and protected by the *Centro Estadual de Unidades de Conservação* and the *Secretaria de Estado do Meio Ambiente e*

Methods

Desenvolvimento Sustentável do Amazonas (CEUC/SDS), and the *Instituto de Proteção Ambiental do Amazonas* (IPAAM).

Blowdown detection and estimation of tree mortality intensity

Before performing Spectral Mixture Analysis (SMA) (Adams et al. 1995) to account for the tree-mortality fraction on a per-pixel basis, we first corrected the images for atmospheric ‘interferences’ and converted it to reflectance using the Atmospheric CORrection Now (ACORN) software (ImSpec LLC, Boulder, CO). For the required scenes, we applied the Carlotto technique (Carlotto 1999), which corrects for haze and smoke contamination. We then calibrated scenes previous to the selected windthrows by regressing each band individually against the encoded radiance from the images containing windthrows using temporally invariant targets (Furby and Campbell 2001). In windthrow areas, the large amount of dead vegetation, wood and litter (non-photosynthetic vegetation [NPV]) have high reflectance in Landsat band five (centered at 1.65 μm). This signal lasts for about a year before new leaves obscure high levels of NPV (Negrón-Juárez et al. 2010; Negrón-Juárez et al. 2016). We applied SMA to all available scenes. For a detailed explanation on the applied methods and routine, see references (Negrón-Juárez et al. 2010; Negrón-Juárez et al. 2011; Chambers et al. 2013; Marra et al. 2014).

Vegetation sampling and biomass estimation

Botanical exsiccates from the blowdowns sites were added to the herbarium of the *Instituto Federal de Educação, Ciência e Tecnologia do Amazonas* (IFAM). Most exsiccates from the old-growth forest containing flowers and/or fruits were added to the herbarium of the INPA, while sterile ones were added to the EEST collection (Carneiro 2004; Teixeira et al. 2007).

Aboveground stand biomass (hereafter referred as biomass) in our chronosequence was estimated using biomass estimation models parameterized with 727 trees locally harvested. These models have diameter at breast height (DBH) (cm) + wood density (WD) (g cm^{-3}) (M33), DBH + species’ successional group assignment (M23) and DBH solely (M13) as independent variables (Magnabosco Marra et al. 2016). We another locally parameterized model to account for biomass losses from damaged trees. This model includes DBH, tree total height (H) (estimated from a DBH: H) and height of failure/breaking as independent

Methods

variables (Chambers et al. 2001). We compiled WD data from studies developed in the Amazon (Fearnside 1997; Nogueira et al. 2005; Laurance et al. 2006; Nogueira et al. 2007; Chave et al. 2009; Magnabosco Marra et al. 2016). For species where more than one WD value was found, we used the mean value. For species where no published WD data was available or where the identification was carried out to the genus level (32.5% of the total individual observations), we used the mean value for all species from the same genus occurring in Central Amazon. For trees identified only to the family level (2.7% of the total), we used the mean value of genera belonging to that family and reported for the Central Amazon. For 11 unidentified trees we did not assign any successional group or wood density value.

In our surveys, trees with irregular trunks (e.g. *Protium* spp. and *Eschweilera* spp.), buttresses (e.g. *Sloanea* spp. and *Swartzia* spp.), aerial roots (e.g. *Cecropia* spp. and *Xylopia* spp.), damaged and wound trunks were measured above-mentioned irregularities. To avoid error in repeated measurements, we marked the height at which diameter measures were taken with paint.

Results

Results*Forest structure, dynamics and functional composition along the disturbance gradient*

We only found a significant positive relationship between tree mortality intensity and elevation in the Bd1 (Fig. S2). In this site, subplots at higher elevation had an overall higher blowdown tree-mortality intensity than those at lower elevation. In the sites Bd2 and Bd3, high tree mortality intensity values were observed both in subplots at low (valleys) and high elevation (slopes and plateaus). When comparing blowdown tree-mortality among topographic classes, valleys from the Bd1 had tree mortality significantly lower than slopes and plateau (Fig. S3). Slopes from the Bd2 site had tree mortality significantly higher than plateaus and valleys. In the Bd3 site, we found no differences in tree mortality related to topography. Despite the higher tree mortality observed in plateaus of the Bd1 site (Fig. S2), which was also reported in a previous study (Marra et al. 2014), topography does not seem to be a major factor controlling tree mortality across the larger region. There is no inherent difference in the force required to pull over trees from plateaus and valleys according to mechanical tests conducted in nearby areas (Ribeiro et al. 2016). Instead, landscape variations in tree mortality caused by wind disturbance may reflect biotic (e.g. lianas, root architecture, etc.) and abiotic (e.g. wind formation and dissipation above and below canopy, wind speed and/or force required to blow trees, etc.) factors still not investigated in Amazon forests.

Mean tree density, basal area, wood density and biomass in the old-growth and undisturbed patches from our blowdown sites ranged from 573 tree ha⁻¹ to 703 tree ha⁻¹, 23.8 m² ha⁻¹ to 27.3 m² ha⁻¹, 0.696 g cm³ to 0.715 g cm³ and 203.9 Mg ha⁻¹ to 249.2 Mg ha⁻¹, respectively (Table S2).

In the portions of the blowdown sites with higher initial damage, we observed large effects on the biomass balance partitioning among successional groups (Fig. S5). As suggested for tree density and biomass stocks, the importance of pioneer species increased substantially from 4 to 17 years after disturbance, with an abrupt reduction 24 years after disturbance. Between 4 and 10 years after disturbance, pioneer species accumulated more than half of the total accumulated biomass. Mid-successional species also increased biomass accumulation already 4 years after disturbance and had a peak of biomass accumulation

Results

between 27 and 24 years after disturbance. At this stage, mid-successional species contributed more than half of the total accumulated biomass in the disturbance categories 2-4.

Apart from strong differences in biomass dynamics and functional composition along our chronosequence, we also observed differences in how biomass gain partitioned among different-sized trees, as defined using DBH classes (Fig. S6). Again, this effect was controlled by disturbance intensity. While in the old-growth and undisturbed forest patches from our blowdown sites (category 1) biomass gain was smaller and mostly associated with large-sized trees (DBH \geq 40), in disturbed forest patches (i.e. category 2-4) smaller trees (DBH $<$ 40 cm) increased their contribution to the total biomass gain. Although large-sized trees were more abundant in less damaged areas, large-sized trees from heavily damaged areas also showed an increasing in gain rates. This result suggests that some late-successional and tall canopy trees that survived were also favored in large gaps.

Interactions between taxonomical attributes and mechanisms of biomass resilience

Biomass gain due to the 20-top species in our mixed community varied from 45.4 kg ha⁻¹ yr⁻¹ to 315.5 kg ha⁻¹ yr⁻¹. Each of the 20 species was responsible for between 1 and 6% of the biomass accumulated (Table S4). These species belong to different successional groups and genera, and had mean DBH and WD varying from 12.3 cm to 28.2 cm and from 0.379 g cm⁻³ to 0.878 g cm⁻³, respectively. Mid-successional species made up the majority of species (8 species), followed by pioneers (7) and late-successional species (5). Tree density also varied strongly among species (from 2 to 26 trees ha⁻¹). The majority of these species were recorded in all of our different sites, successional stages and disturbance intensities. Moreover, they contributed to biomass gain via all mechanisms we assessed. The 5-top species, *Guatteria olivacea* R.E. Fr., *Inga pezizifera* Benth., *Pourouma tomentosa* Mart. ex Miq., *Cecropia sciadophylla* Mart. and *Tapirira guianensis* Aubl., accounted for 23.8% of the total AGB gain of our mixed community (see *Methods* sections for details). Interestingly, none of the 5-top species are typical late-successional species or occurred in high abundances in our old-growth control forest.

Tables

Tables

Table S1. Site description and sampling design of a forest chronosequence including three blowdowns at different successional stage (4-27 yrs after disturbance) and an old-growth forest in Central Amazon, Brazil.

Sites	Coord	YrD	SYr	NTr	Alt	DI	TM	NSb	SbD	TSA
Bd1 (Ramal-ZF2, SUPRAMA)	2°33'43" S 60°16'00" W	2005	2009, 2012 and 2015	2 (100), 2 (600) and 2 (1000)	(53,117)	1	< 5%	71	10 x 25	1.775
						2	5% ≤ TM < 25%	40	10 x 25	1
						3	25% ≤ TM < 45%	23	10 x 25	0.575
						4	TM ≥ 45%	10	10 x 25	0.25
Bd2 (Ramal-ZF5, SUPRAMA)	2°15'09" S 60°10'24" W	1996	2010 and 2013	1 (3000)	(87,116)	1		23	10 x 30	0.69
						2		37	10 x 30	1.11
						3		23	10 x 30	0.69
						4		17	10 x 30	0.51
Bd3 (Igarapé Tumbira, RDS Rio Negro)	3°00'00" S 60°45'11" W	1987	2011 and 2014	2 (1500)	(45,75)	1		50	10 x 30	1.5
Og (EEST/INPA)	2°36'40" S 60°12'10" W	-	2002 and 2004	2 (2500)	(63,121)	1		250	20 x 20	10

Coord- latitude and longitude; YrD- year of disturbance; SYr- survey years; NTr- number of transects (length [m]); Altitude (m a.s.l.) range across monitored subplots (minimum and maximum values); DI- disturbance intensity category; TM- tree mortality intensity range of disturbance categories; NSb- number of monitored subplots; SbD- subplots' dimensions (m); and TSA- total sampled area (ha).

Tables

Table S2. Structural attributes (mean \pm 95% confidence interval) of different topographic classes in undisturbed subplots (category 1, tree mortality intensity $<$ 5%) of three blowdown sites (first survey) and an old-growth forest (2004) in Central Amazon, Brazil.

Sites	Topographic classes						
	NSp	TD	mDBH	BA	WD	AGB	
Bd1	all	591 \pm 51 ^a	21.5 \pm 0.6 ^a	26.9 \pm 2.8	0.696 \pm 0.010	239.6 \pm 32.8	
	plateau	12	610 \pm 143	21.3 \pm 1.5	28.5 \pm 7.6	0.731 \pm 0.018	273.2 \pm 99.1
	slope	37	631 \pm 78 ^a	21.1 \pm 0.8	28.1 \pm 4.3	0.703 \pm 0.012	249.9 \pm 48.6
Bd2	valley	22	513 \pm 66	22.2 \pm 1.3	24.1 \pm 4.0	0.666 \pm 0.018	204.0 \pm 49.8
	all	23	703 \pm 75 ^b	18.7 \pm 0.8 ^b	23.8 \pm 3.1	0.715 \pm 0.015	203.9 \pm 32.1
	plateau	7	686 \pm 148	19.1 \pm 1.8	24.1 \pm 7.0	0.716 \pm 0.032	203.7 \pm 75.5
Bd3	slope	7	833 \pm 173 ^a	18.6 \pm 1.1	28.2 \pm 4.7	0.727 \pm 0.037	250.2 \pm 47.1
	valley	9	614 \pm 87	18.4 \pm 1.8 ^a	20.2 \pm 5.4	0.705 \pm 0.027	168.0 \pm 53.5
	all	50	573 \pm 39	20.2 \pm 0.8 ^b	23.8 \pm 2.8	0.699 \pm 0.014	211.6 \pm 31.4
Og	plateau	26	551 \pm 53	20.5 \pm 1.2	23.8 \pm 4.1	0.711 \pm 0.018	215.6 \pm 47.2
	slope	19	570 \pm 64	20.1 \pm 1.3	23.3 \pm 4.5	0.689 \pm 0.025	207.5 \pm 50.2
	valley	5	693 \pm 164	18.7 \pm 4.0 ^b	25.1 \pm 14.9	0.671 \pm 0.068	206.4 \pm 154.7
	all	250	599 \pm 17	21.2 \pm 0.3 ^a	27.3 \pm 1.2	0.702 \pm 0.004	249.2 \pm 13.9
	plateau	65	650 \pm 32	20.9 \pm 0.6	28.8 \pm 2.4	0.710 \pm 0.007	263.7 \pm 29.0
	slope	134	596 \pm 24	21.0 \pm 0.4	26.8 \pm 1.6	0.706 \pm 0.006	245.9 \pm 19.9
	valley	51	542 \pm 31	22.1 \pm 0.7	26.8 \pm 2.2	0.684 \pm 0.009	239.5 \pm 25.1

Variables: NSp- number of subplots; TD- tree density (trees ha⁻¹); mDBH- mean diameter at breast height (DBH) (cm) for trees with DBH \geq 10 cm; BA- basal area (m² ha⁻¹); WD- wood density (g cm⁻³); AGB- aboveground biomass (Mg ha⁻¹). Different letters assign significant difference (p $<$ 0.05) between sites and topographic classes assessed with factorial ANOVA. ^aSlopes from Bd1 are not different in tree density than those from Bd2 and ^bvalleys from Bd1 are not different in mDBH than those from Bd2.

Tables

Sites	TAD	DI	TD	mDBH	BA	AGB	WD	AGB balance Gain/reg rowth	Loss/mor tality	AGB Acc	AGB gain/loss mechanisms				Loss/mortality			
											Growth	Gr recr	Recr	Resp	Mort	Mort resp		
Bd3	27 yrs	2	596 ± 71	20.0 ± 2.0	23.6 ± 5.0	198.8 ± 63.0	0.653 ± 0.027 [†]	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	
		3	568 ± 63	19.3 ± 1.3	22.8 ± 5.4	172.6 ± 65.2	0.606 ± 0.020 [*]	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	
		4	529 ± 84	18.2 ± 2.5	19.6 ± 10.0	166.1 ± 134.2	0.613 ± 0.027 [*]	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM
		1	574 ± 34	20.4 ± 0.8	24.3 ± 2.6	217.8 ± 30.2	0.700 ± 0.014	3.9 ± 0.59	-1.9 ± 1.9	0.92	0.3 ± 0.1	0.06 ± 0.03	0.07 ± 0.07	0.07 ± 0.07	0.06 ± 0.03	-1.8 ± 1.9	-0.02 ± 0.05	
		2	588 ± 75	20.1 ± 1.6	24.4 ± 5.1	206.5 ± 62.0	0.653 ± 0.028 [†]	5.6 ± 1.6 [†]	-3.0 ± 2.6	1.26	0.4 ± 0.3	5.1 ± 1.5 [†]	NM	0.4 ± 0.3	0.07 ± 0.07	-3.0 ± 2.6	0	
		3	551 ± 56	20.0 ± 1.3	23.7 ± 5.5	180.2 ± 65.7	0.609 ± 0.019 [*]	4.6 ± 0.8	-2.0 ± 1.1	1.44	0.5 ± 0.4	3.9 ± 0.6	NM	0.5 ± 0.4	0.09 ± 0.06	-2.0 ± 1.1	0	
		4	524 ± 132	18.9 ± 2.1	20.6 ± 10.7	174.3 ± 141.0	0.613 ± 0.029 [*]	5.2 ± 2.5	-2.5 ± 3.5	1.55	0.6 ± 0.6	4.3 ± 2.3	NM	0.6 ± 0.6	0.29 ± 0.69	-2.3 ± 3.5	-0.22 ± 0.37 [†]	
		1	597 ± 17	21.0 ± 0.3	26.9 ± 1.1	244.3 ± 13.6	0.703 ± 0.004	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM
Og 2002	> 40 yrs	1	599 ± 17	21.2 ± 0.3	27.3 ± 1.2	249.2 ± 13.9	0.702 ± 0.004	4.6 ± 0.2	-2.1 ± 0.9	1.00	4.3 ± 0.2	NM	0.3 ± 0.1	NM	-2.1 ± 0.9	NM		
Og 2004	> 40 yrs	1	599 ± 17	21.2 ± 0.3	27.3 ± 1.2	249.2 ± 13.9	0.702 ± 0.004	4.6 ± 0.2	-2.1 ± 0.9	1.00	4.3 ± 0.2	NM	0.3 ± 0.1	NM	-2.1 ± 0.9	NM		

TAD- time after disturbance; DI- disturbance intensity (1- tree mortality < 5%, 2- 5% ≤ tree mortality < 25%, 3- 25 ≤ tree mortality < 45% and 4- tree mortality ≥ 45%); TD- tree density (trees ha⁻¹); mDBH- mean diameter at breast height (DBH) (cm) for trees with DBH ≥ 10 cm; BA- basal area (m² ha⁻¹); AGB- aboveground biomass stock (Mg ha⁻¹); Wood density (g cm⁻³); Gain/regrowth- AGB gain rate (Mg ha⁻¹ yr⁻¹); Loss/mortality- AGB loss (Mg ha⁻¹ yr⁻¹); AGBAcc- relative AGB accumulation/recovery; Growth- AGB gain from non-damaged trees (survivors and recruits) already recorded in the first survey (Mg ha⁻¹ yr⁻¹); Gr recr- AGB gain from recruits (Mg ha⁻¹ yr⁻¹); Recr- AGB gain via recruitment (Mg ha⁻¹ yr⁻¹); Resp- AGB gain from resprouters (Mg ha⁻¹ yr⁻¹); Mort- AGB loss via mortality (Mg ha⁻¹ yr⁻¹); Mort resp- AGB loss via mortality of resprouting trees (Mg ha⁻¹ yr⁻¹); and NM- non-measured. Significance codes from factorial ANOVA for testing differences between the old-growth (category 1) and the disturbed subplots (category 2, 3 and 4) in each study site: p < 0.001^{*}; p < 0.01[†]; p < 0.05[‡]; p < 0.1[§].

Tables

Table S4. 20-top species (i.e. highest aboveground biomass gain) in our mixed community comprising a 0-70% tree mortality gradient and 4-27 yrs succession following windthrows.

Species	HyperDom	Abs AGB gain	Rel AGB gain	AGB gain	Abs TD	TD	mean DBH	SG	WD	Bd	DI	Mec
1 <i>Guatteria olivacea</i> R.E. Fr.	209	1135.8	6.0	315.5	90	25	18.8	mid	0.510	1-4	1-4	1-5
2 <i>Inga peziifera</i> Benth.	465	1070.5	5.7	297.4	38	11	15.9	mid	0.650	1-4	1-4	1-5
3 <i>Pourouma tomentosa</i> Mart. ex Miq.	291	878.7	4.7	244.1	66	18	15.0	pio	0.379	1-4	1-4	1-4
4 <i>Cecropia sciadophylla</i> Mart.	87	745.0	4.0	206.9	66	18	16.0	pio	0.412	1-3	1-4	1-5
5 <i>Tapirira guianensis</i> Aubl.	44	635.0	3.4	176.4	43	12	25.2	mid	0.481	1-4	1-4	1-5
6 <i>Miconia manauara</i> R. Goldenb., Caddah & Michelang.	NR	589.8	3.1	163.8	53	15	14.4	pio	0.637	3	2-4	1,3-6
7 <i>Eschweilera coriacea</i> (DC.) S.A. Mori	1	474.0	2.5	131.7	95	26	20.4	lat	0.801	1-4	1-4	1-6
8 <i>Ocotea guianensis</i> Aubl.	315	473.0	2.5	131.4	11	3	25.3	mid	0.630	4	2-4	1,3
9 <i>Vismia cayennensis</i> (Jaeq.) Pers.	1172	454.9	2.4	126.4	30	8	15.2	pio	0.490	1-3	1-4	1-4,6
10 <i>Inga leiocalycina</i> Benth.	373	361.8	1.9	100.5	30	8	19.6	mid	0.560	1-4	2-4	1-6
11 <i>Bellucia dichotoma</i> Cogn.	1120	340.7	1.8	94.6	19	5	14.1	pio	0.607	1,2,4	2-4	1-3
12 <i>Croton matourensis</i> Aubl.	638	293.9	1.6	81.6	14	4	18.4	pio	0.620	1-4	1-4	1-3
13 <i>Scleronema micranthum</i> (Ducke) Ducke	93	267.3	1.4	74.2	35	10	23.4	lat	0.595	1-4	1-4	1,3,4,6
14 <i>Vismia guianensis</i> (Aubl.) Pers.	1118	261.0	1.4	72.5	22	6	15.4	pio	0.475	1-4	1,3,4	1-3
15 <i>Protium hebetatum</i> Daly	27	240.0	1.3	66.7	57	16	12.3	lat	0.579	1-4	1-4	1-5
16 <i>Eschweilera micrantha</i> (O. Berg) Miers	111	238.7	1.3	66.3	28	8	19.4	lat	0.860	1-4	1-4	1,3-5
17 <i>Inga paraensis</i> Ducke	886	212.1	1.1	58.9	22	6	21.0	mid	0.820	3,4	1-4	1,4,5
18 <i>Inga</i> spp.		188.4	1.0	52.3	16	4	13.7	mid	0.614	1-4	1-4	1-3,5
19 <i>Goupia glabra</i> Aubl.	38	179.6	1.0	49.9	8	2	28.2	mid	0.730	2-4	1,3,4	1,4
20 <i>Licania oblongifolia</i> Standl	283	163.4	0.9	45.4	16	4	23.9	lat	0.878	1-4	1,2,4	1,4,5
Total		9203.7	48.8	2556.6	759	211						

HyperDom: hyperdominance tree species ranking (ter Steege et al. 2013); Abs AGB gain- absolute aboveground biomass gain in our 3.6-ha mixed community (kg yr⁻¹); Rel AGB gain- relative (%) aboveground biomass gain in our 3.6-ha mixed community; AGB gain- aboveground biomass gain (kg ha⁻¹ yr⁻¹); Abs TD- absolute tree density in our

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3.6-ha mixed community; TD- tree density (tree ha⁻¹); mean DBH- mean diameter at breast height (DBH) of trees ≥ 10 cm DBH (cm); SG- species' successional group assignment; WD- wood density (g cm⁻³); Bd- blowdowns in which the species were recorded (1- 4-7 yrs, 2- 7-10 yrs, 3- 14-17 yrs and 4- 24-27 yrs after disturbance); DI- disturbance intensity in which the species where recorded; Mec- AGB gain and loss mechanisms (1- growth from non-damaged trees recorded in the first survey, 2- growth from recruits, 3- recruitment, 4- resprouting, 5- mortality and 6- mortality from resprouting trees); and NR- not recorded.

Figures

Figures

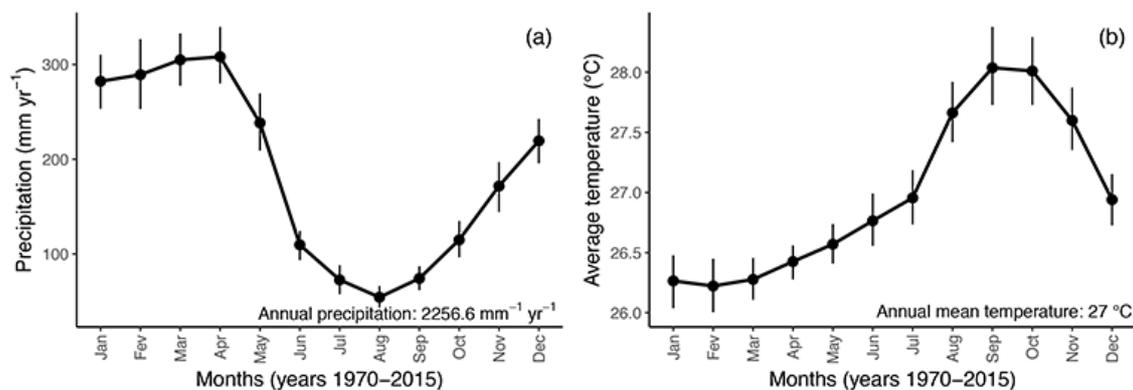


Fig. S1. (a) Annual precipitation (mm yr^{-1}) and (b) mean temperature ($^{\circ}\text{C}$) in Manaus (less than 90 km distant from our study sites) for the period of 1970-2015. Points and bars represent the monthly mean \pm 95% confidence interval, respectively. Data available in: <http://www.inmet.gov.br> (accessed in 03/02/2016).

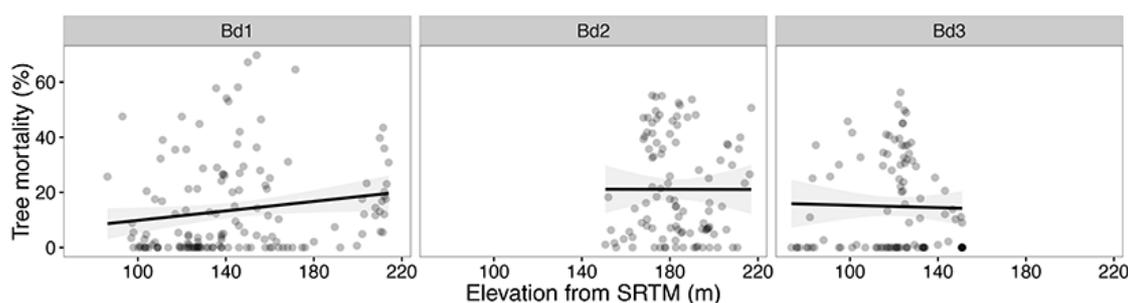


Fig. S2. Relationship between tree mortality intensity (%) and elevation (m) in three blowdown sites located in Central Amazon, Brazil. Elevation data at the plot-level was extracted from SRTM imagery with 30 x 30 m resolution (<http://earthexplorer.usgs.gov/>). Summary of linear regressions: Bd1 ($r^2_{\text{adj}} = 0.02$, $F = 4.13$ and $p = 0.044$); Bd2 ($r^2_{\text{adj}} = -0.01$, $F = 6.29^{-5}$ and $p = 0.993$); and Bd3 ($r^2_{\text{adj}} < -0.009$, $F < 0.063$ and $p = 0.802$).

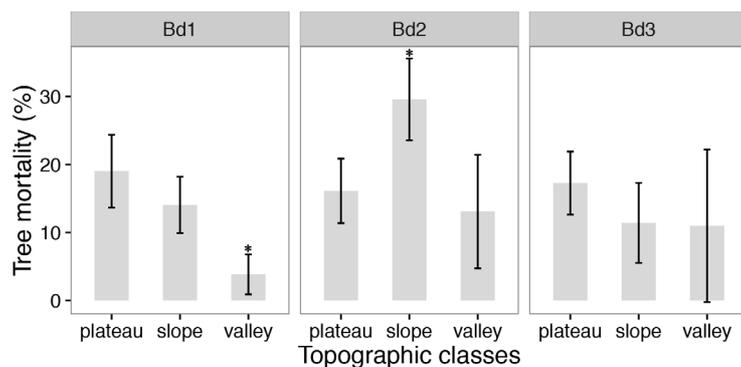


Fig. S3. Tree mortality intensity for different topographic classes in three blowdown sites located in Central Amazon, Brazil. Factorial ANOVA among topographic classes within sites: Bd1 ($F = 7.3$; $p < 0.001$); Bd2 ($F =$

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8.8; $p < 0.001$); Bd3 ($F = 1.5$; $p < 0.239$). Significant difference from post hoc tests (Tukey HSD) ($p < 0.05$) among topographic classes within sites is identified with a '*' on the top of the bars.

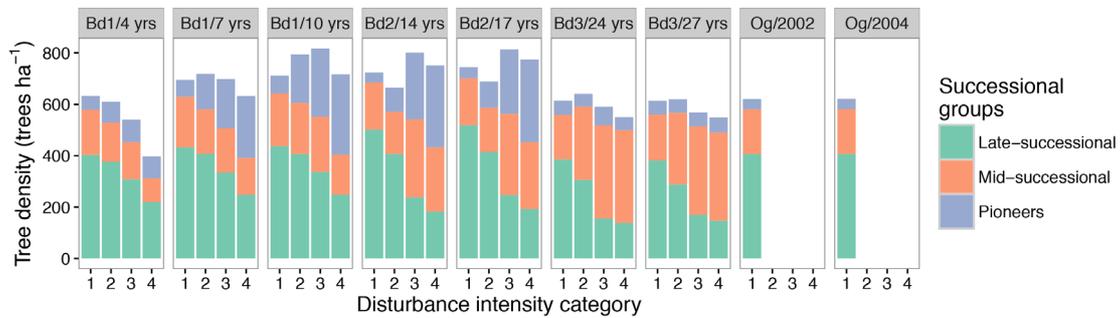


Fig. S4. Partitioning of the tree density among successional groups along a forest chronosequence including blowdowns at different successional stages (4-27 yrs after disturbance) and an old-growth forest in Central Amazon, Brazil. Disturbance categories: 1- tree mortality < 5%; 2- 5% ≤ tree mortality < 25%; 3- 25% ≤ tree mortality < 45%; 4- tree mortality ≥ 45%.

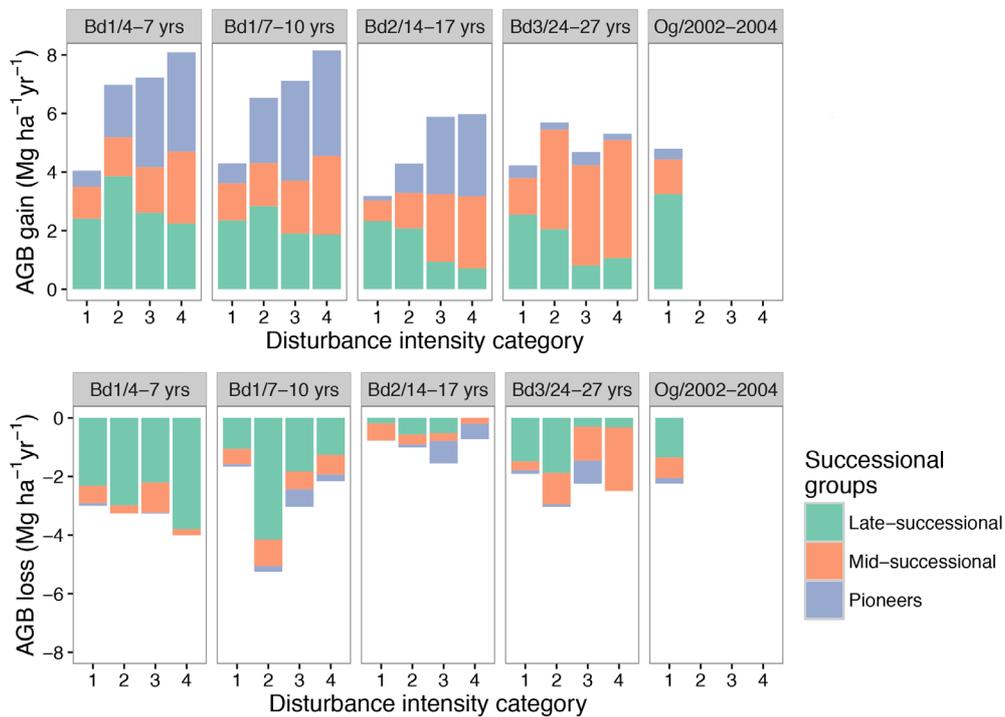


Fig. S5. Partitioning of the aboveground biomass (AGB) balance (gain/regrowth and loss/mortality) among successional groups along a forest chronosequence including blowdowns at different successional stages (4-27 yrs after disturbance) and an old-growth forest in Central Amazon, Brazil. Disturbance categories: 1- tree mortality < 5%; 2- 5% ≤ tree mortality < 25%; 3- 25% ≤ tree mortality < 45%; 4- tree mortality ≥ 45%.

Figures

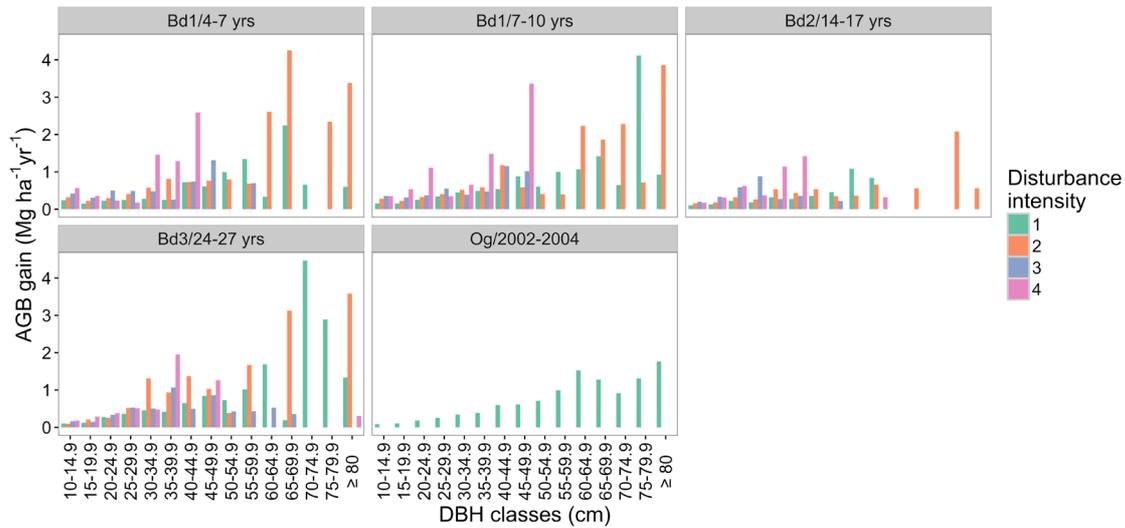


Fig. S6. Aboveground biomass (AGB) gain along different diameter at breast height (DBH) classes (cm) along a forest chronosequence including blowdowns at different successional stages (4-27 yrs after disturbance) and an old-growth forest in Central Amazon, Brazil. Disturbance categories: 1- tree mortality < 5%; 2- $5\% \leq$ tree mortality < 25%; 3- $25\% \leq$ tree mortality < 45%; 4- tree mortality $\geq 45\%$.

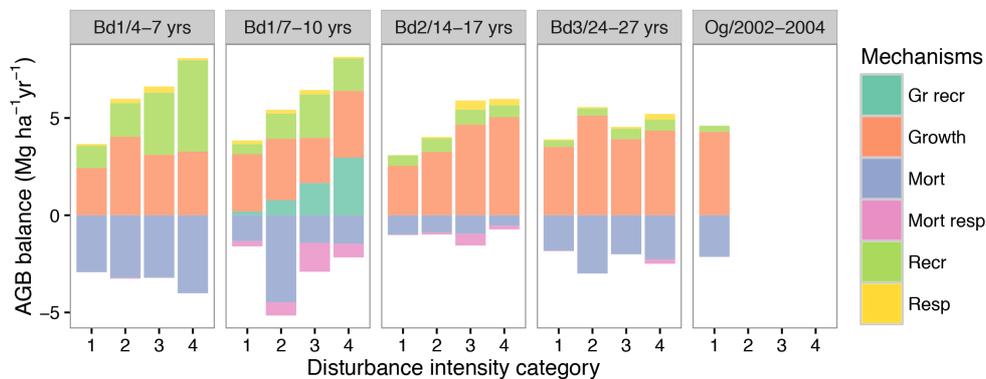


Fig. S7. Partitioning of the aboveground biomass (AGB) gain and loss mechanisms along a forest chronosequence including blowdowns at different successional stage (4-27 yrs after disturbance) and an old-growth forest in Central Amazon, Brazil. Disturbance categories: 1- tree mortality < 5%; 2- $5\% \leq$ tree mortality < 25%; 3- $25\% \leq$ tree mortality < 45%; 4- tree mortality $\geq 45\%$. Mechanisms: Gr recr- growth from recruits; Growth- growth from non-damaged trees recorded in the first survey; Mort- mortality; Mort resp- mortality of resprouting trees; Recr- recruitment; Resp- resprouting.

Figures

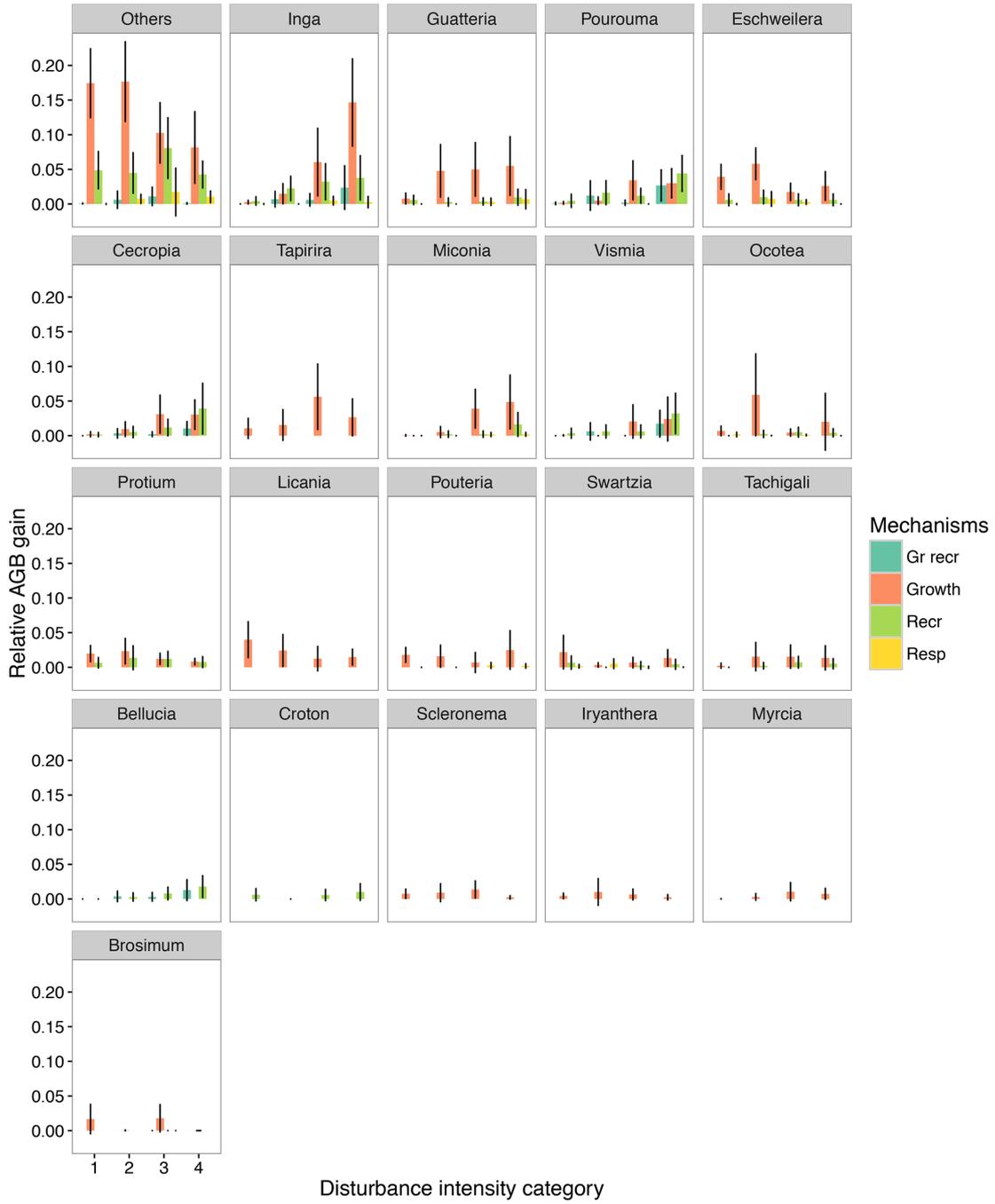


Fig. S8. Relative aboveground biomass (AGB) gain (mean \pm 95% confidence interval) for the top-20 genera (and other genera pooled together), and AGB gain partition among mechanisms within a 3yr-interval. Data is from a mixed tree community sampled from a forest chronosequence including blowdowns at different successional stage (4-27 yrs after disturbance) in Central Amazon, Brazil. Tree mortality intensity (0-70%) was estimated at plot-level from satellite imagery. Mechanisms: Gr recr- growth from recruits; Growth- growth from non-damaged trees recorded in the first survey; Recr- recruitment; Resp- resprouting. Disturbance categories: 1-

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tree mortality < 5%; 2- $5\% \leq$ tree mortality < 25%; 3- $25\% \leq$ tree mortality < 45%; 4- tree mortality \geq 45%. For this analysis we only consider the mechanisms for which we had five or more observations per genus.

References

References

- Adams JB, Sabol DE, Kapos V, et al (1995) Classification of multispectral images based on fractions of endmembers: Application to land-cover change in the Brazilian Amazon. *Remote Sens Environ* 52:137–154.
- Braga PIS (1979) Subdivisão fitogeográfica, tipos de vegetação, conservação e inventário florístico da floresta amazônica. *Acta Amaz* 9:53–80.
- Carlotto M (1999) Reducing the effects of space-varying, wavelength-dependent scattering in multispectral imagery. *Int J Remote Sens* 20:3333–3344.
- Carneiro VMC (2004) Composição florística e análise estrutural da floresta primária de terra firme na bacia do Rio Cuieiras, Manaus-AM. M.Sc. Dissertation, Ciências de Florestas Tropicais (CFT), Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil.
- Chambers JQ, Negron-Juarez RI, Marra DM, et al (2013) The steady-state mosaic of disturbance and succession across an old-growth Central Amazon forest landscape. *Proc Natl Acad Sci U S A* 110:3949–54. doi: 10.1073/pnas.1202894110
- Chambers JQ, Santos J dos, Ribeiro RJ, Higuchi N (2001) Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest. *For Ecol Manage* 152:73–84.
- Chave J, Coomes D, Jansen S, et al (2009) Towards a worldwide wood economics spectrum. *Ecol Lett* 12:351–66.
- de Oliveira AA, Mori SA (1999) A central Amazonian terra firme forest. I. High tree species richness on poor soils. *Biodivers Conserv* 8:1219–1244.
- Fearnside PM (1997) Wood density for estimating forest biomass in Brazilian Amazonia. *For Ecol Manage* 90:59–87.
- Furby S, Campbell N (2001) Calibrating images from different dates to “like-value” digital counts. *Remote Sensing of Environment. Remote Sens Environ* 77:186–196. doi: 10.1016/S0034-4257(01)00205-X
- Higuchi F (2015) Dinâmica de volume e biomassa da floresta de terra firme do Amazonas. Ph.D. Dissertation, Engenharia Florestal, Universidade Federal do Paraná (UFPR), Brazil.
- Higuchi FG, Siqueira JDP, Lima AJN, et al (2012) Influence of plot size in Weibull’s diameter distribution function precision in a primary forest in Central Amazon. *Floresta* 42:599–606.
- Higuchi N, Santos J dos, Vieira G, et al (1998) Análise estrutural da floresta primária da bacia do rio Cuieiras, ZF-2, Manaus-AM, Brasil. In: Higuchi N, Campos M, Sampaio P, Santos J dos (eds) *Pesquisas Florestais para Conservação da Floresta e Reabilitação de Áreas Degradadas da Amazônia*. Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, pp 51–81.
- Laurance WF, Nascimento HEM, Laurance SG, et al (2006) Rain forest fragmentation and the proliferation of successional trees. *Ecology* 87:469–482.
- Magnabosco Marra D, Higuchi N, Trumbore S, et al (2016) Predicting biomass of hyperdiverse and structurally complex Central Amazon forests – a virtual forest approach using extensive field data. *Biogeosciences* 13:15537–15581. doi: 10.5194/bgd-12-15537-2015
- Marra DM, Chambers JQ, Higuchi N, et al (2014) Large-scale wind disturbances promote tree diversity in a

References

- central Amazon forest. *PLoS One* 9:e103711. doi: 10.1371/journal.pone.0103711
- Negrón-Juárez RI, Chambers JQ, Guimarães G, et al (2010) Widespread Amazon forest tree mortality from a single cross-basin squall line event. *Geophys Res Lett* 37:1–5.
- Negrón-Juárez RI, Chambers JQ, Marra DM, et al (2011) Detection of subpixel treefall gaps with Landsat imagery in Central Amazon forests. *Remote Sens Environ* 115:3322–3328.
- Negrón-Juárez RI, Holm J, Magnabosco Marra D, et al (2016) Vulnerability of Amazon forests to storm-driven tree mortality. *Sci Adv* (in review).
- Nogueira EM, Fearnside PM, Nelson BW, França MB (2007) Wood density in forests of Brazil’s “arc of deforestation”: Implications for biomass and flux of carbon from land-use change in Amazonia. *For Ecol Manage* 248:119–135.
- Nogueira EM, Nelson BW, Fearnside PM (2005) Wood density in a dense forest in central Amazonia, Brazil. *For Ecol Manage* 208:261–286.
- Ribeiro GHM, Chambers JQ, Peterson CJ, et al (2016) Mechanical vulnerability of Central Amazon tree species to windthrow in convective storms. *For Ecol Manage* (in review).
- Santos LT dos, Magnabosco Marra D, Trumbore S, et al (2016) Windthrows increase soil carbon stocks in a Central Amazon forest. *Biogeosciences* 13:1299–1308. doi: 10.5194/bgd-12-19351-2015
- Silva RP da, Santos J dos, Tribuzy ES, et al (2002) Diameter increment and growth patterns for individual tree growing in Central Amazon, Brazil. *For Ecol Manage* 166:295–301.
- Teixeira L, Chambers J, Silva A, et al (2007) Projeção da dinâmica da floresta natural de Terra-firme, região de Manaus-AM, com o uso da cadeia de transição probabilística de Markov. *Acta Amaz* 37:377–384.
- Vieira S, de Camargo PB, Selhorst D, et al (2004) Forest structure and carbon dynamics in Amazonian tropical rain forests. *Oecologia* 140:468–479.

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This dissertation addresses whether large-scale natural disturbances contribute to patterns of different forest attributes in the Amazon. Specifically, I assessed the effects of windthrows on the interaction between tree species composition, forest dynamics and important components of the carbon balance in Central Amazon forests. The four papers presented here provide new evidence indicating that the wide disturbance gradient, uniquely associated with windthrows, affects important forest attributes for decades. This was supported by observed variations in forest structure, species composition and diversity, all controlled by blowdown tree-mortality (Marra et al. 2014a; Magnabosco Marra et al. 2016b). In disturbed areas, tree-mortality intensity and clay content had positive and independent effects on soil carbon stocks and soil organic carbon, indicating that disturbance-driven vegetation dynamics can influence soil attributes (Santos et al. 2016), at least in the decade following disturbance. In the study on tree allometry, I was able to show that variations in floristic composition and tree size-distribution, typical of these wind disturbed forests, can lead to significant landscape differences in tree architecture and consequently in allometry, compromising reliable biomass estimates (Magnabosco Marra et al. 2016a). The unique forest chronosequence of sites recovering from single blowdown events allowed me to reveal unknown landscape-interactions between disturbance intensity, biomass dynamics and partitioning among species, genera and functional groups (Magnabosco Marra et al. 2016b). Although these forests seem to be resilient and are able to recover biomass in *ca.* 30 yrs, shifts in species and functional composition persist much longer. I showed that biomass resilience to windthrows is a process supported by a high number of species, each performing the task of restoring biomass in different niches by different biomass gain mechanisms along the disturbance intensity gradient. This is in contrast to the widely held view that a limited number of pioneer species generally dominates early successional biomass dynamics. These results have important implications for different aspects and processes regulating the functioning of Central Amazon forests and other tropical forests affected by large-scale natural disturbances. Here, I discuss the major implications with high relevance for future research on tropical forestry and ecology. Study-specific aspects are discussed in the respective papers.

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4.1. Variation of windthrow tree-mortality across the landscape

The results that I found regarding tree damage and mortality patterns associated with windthrows add new knowledge to previous studies developed in the same region (Chambers et al. 2009b; Negrón-Juárez et al. 2010b; Negrón-Juárez et al. 2011). In the Central Amazon forests I studied, blowdowns caused higher tree mortality (up to 70% in a given area) (Marra et al. 2014a; Magnabosco Marra et al. 2016b) than that reported for forests known to be more frequently damaged by hurricanes (Zimmerman et al. 1994; Bellingham et al. 1995; Vandermeer et al. 1995; Scatena et al. 1996). Recent studies have also shown that blowdowns are a major disturbance regime in Western Amazon forests, causing similar (up to 80% in given area) tree mortality intensities (Negrón-Juárez et al. 2016; Rifai et al. 2016). As discussed in the next subsections, the magnitude and intensity of damage and tree mortality associated with blowdowns can ‘reset’ these forests by opening space and changing biotic and abiotic conditions.

I detected a significant effect of topography on blowdown tree-mortality intensity only in one of my study sites (Bd1), in which higher tree mortality rates were observed in areas at high elevation (i.e. plateaus and top of slopes). This same pattern has been reported for other wind-damaged tropical and subtropical forests (Brokaw and Gear 1991; Walker 1991; Boose et al. 2004; Negrón-Juárez et al. 2014), and for Western Amazon forests also affected by blowdowns (Rifai et al. 2016). By contrast, I did not observe such pattern in two other study sites (Bd2 and Bd3), in which valley areas also experienced high blowdown tree-mortality values. While at the landscape-scale plateaus may account for a larger affected area due to their larger proportional area in relation to slopes and valleys (Radam 1978; Rizzini 1997), I would not expect the relatively lower elevation range typical of Central Amazon forests (from 45 to 121 m a.s.l.) (Magnabosco Marra et al. 2016b) to strongly influence landscape patterns of tree mortality due to windthrows. Supporting this idea, we recently revealed that tree mechanical resistance to failure (i.e. snapping or uprooting) is similar in plateaus and valleys of a Central Amazon *terra firme* forest (Ribeiro et al. 2016), which are known to have strong differences in clay and sand content (Ranzani 1980; Telles et al. 2003).

Although susceptibility to damage and mortality was not directly addressed here, these contrasting results suggest that apart from elevation (i.e. as a proxy for wind exposure) and topographic aspects, other abiotic and biotic aspects may be relevant for defining tree

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mortality patterns. The importance of different factors is also likely to change between sites/regions and to be event specific, inducing a high degree of idiosyncrasy. As shown by Ribeiro et al. (2016), biotic aspects defining tree resistance to failure/mortality are tree size, shape (i.e. slenderness) and wood density. Possible important variables that remain to be investigated are crown architecture and mechanical stability, wood anatomy, root morphology, liana abundance and diversity - the last three relating to anchoring capacity. Wind characteristics such as speed, duration, dissipation area and canopy-wind interactions are relevant abiotic aspects (Fujita 1990; Garstang et al. 1998) also poorly studied in Amazon forests.

The complex environmental gradient to which tropical forests are exposed poses extra challenges for understanding processes and mechanisms defining patterns of vegetation structure, species composition, diversity and biomass/carbon dynamics. As supported by the studies comprising this dissertation (Marra et al. 2014a; Santos et al. 2016; Magnabosco Marra et al. 2016b), remote sensing allows us to investigate complex environmental gradients and vegetation responses otherwise unavailable to researchers. This in turn, can help to generate new perspectives on relevant processes such as vulnerability and resilience of forests to disturbances (Adams and Gillespie 2006; Chambers et al. 2007; Chambers et al. 2013; Asner 2013; Clark et al. 2015; Negrón-Juárez et al. 2016). Without remote sensing data, identifying and dating blowdown sites would not have been possible. More importantly, the measures of tree mortality intensity applied here (ΔNPV) were also based on remote sensing data.

The vegetation patterns that I observed, and their relationship with measures of tree mortality intensity, confirm the appropriateness of research methodologies proposed in previous studies developed by our research team (Chambers et al. 2009b; Negrón-Juárez et al. 2010b; Negrón-Juárez et al. 2011). In vast and heterogeneous tropical forests such as the Amazon, the combination of remote sensing and detailed forest inventories can improve the knowledge acquired in small permanent plots. As we showed in a recent study, small plots allocated randomly can fail to capture important processes and mechanisms defining forest attributes and functioning such as tree mortality associated with large-scale disturbances (Chambers et al. 2013). Thus, reliable landscape-level assessments of forest dynamics require multidisciplinary approaches such as the one employed in this dissertation.

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4.2. Interactions between windthrows, species composition and diversity

Evaluating floristic composition and forest dynamics following natural disturbances is *per se* a complex task. Doing so in diverse tropical forests such as the Amazon is even more challenging. Critical aspects include the need for species identification at a high taxonomical level (i.e. time-consuming activity), logistic limitations, technical restrictions and even impossibility of naively/unrestrictedly using a generic pantropical allometric model for estimating biomass and studying recovery dynamics (see more details in paper 3) (Magnabosco Marra et al. 2016a). Consequently, large-scale natural disturbances are underrepresented in tropical forestry and ecology research. This aspect is likely to have largely contributed to the diffusion of the ‘paradigm’ that canopy disturbance has only a minor role defining forest attributes.

I showed that blowdowns produce a wide and complex disturbance gradient ranging from single treefall gaps to heavily damaged areas extending over hundreds of hectares (Marra et al. 2014a; Magnabosco Marra et al. 2016b). Hence, blowdowns decrease the fraction of old-growth forest and thereby increase the landscape heterogeneity of Amazon forests, which is not promoted by treefall gaps associated with background tree mortality ‘typical’ of old-growth forests (Hubbell et al. 1999; Baker et al. 2015). In wind-disturbed areas, survivors and new trees coexist along a wide environment gradient, markedly different from that encountered under old-growth/single tree gap conditions (Magnabosco Marra et al. 2016b). These findings have different and important implications for the understanding of processes and mechanisms regulating species composition and forest dynamics in Central Amazon forests.

More heterogeneous forests are likely to enable different species to coexist (Vandermeer et al. 2000; Molino and Sabatier 2001; Wright 2002). I observed this pattern in Bd1 (4 yrs after disturbance), where mid-disturbed areas had a higher number of rare species (i.e. mixture of survivors and new recruits) than areas at the extremes of the tree mortality gradient (Marra et al. 2014a). My analyses of this early-successional stage also indicated a short-term negative effect of disturbance intensity on both species richness and Shannon diversity (Marra et al. 2014a). As I argued in paper 1, in early stages, a decrease in species richness and diversity in heavily damaged areas was caused by strong reductions in tree density due to initial blowdown tree-mortality. Further investigation including the entire

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forest chronosequence of wind-disturbed forests indicated that these observed shifts in species and functional composition persist in the longer-term succession and result in strong changes in forest dynamics (Magnabosco Marra et al. 2016b). Together with the related changes in soil carbon stocks due to the large deposition of organic matter from dead trees (see next subsection) (Santos et al. 2016), these findings support the idea that blowdowns have a unique trajectory of recovery. As previously noted, these results show that high mortality rates (i.e. above 25%) due to windthrows can ‘reset’ tree communities towards early-successional stages and promote ‘secondary’ succession.

Conflicting hypotheses (e.g. niche and neutral) have been tested to describe patterns of species composition, diversity and coexistence in tropical forests (Grubb 1977; Denslow 1980a; Hubbell et al. 1999; Brokaw and Busing 2000). While the niche hypothesis predicts that species establishment and distribution are mainly driven by plant-environmental/habitat interactions (i.e. species having specific requirements) (Vandermeer 1972; Grubb 1977), the neutral hypothesis predicts that stochastic events (e.g. seed dispersion and arrival) drive patterns of species turnover (Hubbell 2005). In gaps associated with background tree mortality, species richness can be more strongly influenced by stochastic events (Hubbell et al. 1999; Baker et al. 2015). This pattern can weaken the competitive strength (i.e. chance survival) of trees adapted to higher light levels (Brokaw and Busing 2000), which can minimize or constrain shifts in species composition and diversity during small gap-phase recovery (i.e. neutral based processes) (Hubbell et al. 1999; Baker et al. 2015). By contrast, species composition and diversity in the forest chronosequence that I studied were strongly affected by the disturbance gradient produced by windthrows (Marra et al. 2014a; Magnabosco Marra et al. 2016b). This result supports the importance of niche-based processes defining composition and diversity of Central Amazon tree communities.

Although stochastic processes such as competition and soil nutrients may have influenced Amazon tree species diversification and evolutionary adaptations, the idea of old-growth communities at equilibrium (i.e. low effects of niche-based processes driven by disturbance) does not fully explain the great diversity of these forests (Wright 2002; Gravel et al. 2006). In addition to being tremendously numerous (Zappi et al. 2015), Amazon tree species also have a great diversity of architectures, morphologies, anatomies, dispersal syndromes, establishment and growth strategies (Hallé et al. 1978; Braga 1979; Ribeiro et al.

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1999; Camargo et al. 2008). Such diversity is likely to require periodic large-scale disturbances (Longman and Jeník 1974; Everham and Brokaw 1996; Foster et al. 1998; Cole et al. 2014) creating wide environmental gradients to be ‘expressed’ and maintained for generations. As I have observed, blowdowns can ‘reset’ these forests by opening space and changing resources. More than creating new space for natural regeneration, blowdowns allow connectivity between disturbed and undisturbed patches. This gives a chance to those species usually suppressed under old-growth conditions to disperse, establish and gain importance (e.g. increase in abundance and biomass). The extant gradient of disturbance associated with blowdowns, and the observed diverse cohort of species during recovery, highlight the importance of windthrows in Amazon forests. In this region, periodic forest blowdowns are likely to be one important disturbance regime allowing the full expression of tropical tree species’ architecture (i.e. the ‘Sylvigenesis’ concept) (Hallé et al. 1978).

I believe that blowdowns provide a unique scenario for assessing relevant and still unknown aspects of tropical tree communities such as species’ responses to different disturbance intensities or their ecological role with respect to different functional groups. Note that even species with contrasting functional characteristics (e.g. pioneers and late-successional) appeared to be adapted to a wider gradient of environmental conditions. This was indicated by the many species that successfully colonized areas that experienced mid-level disturbance intensities (Marra et al. 2014a; Magnabosco Marra et al. 2016b). However, it is important to note the differences between mid-disturbance specialists and mid-successional species. While the first is probably related to plant-features conveying ‘niche-adaptability’, the later is probably more related to random-based processes influencing species substitution along time (i.e. forest succession) (Denslow 1980a; Shugart and West 1980; Swaine and Whitmore 1988). Overall, this pattern suggests that Amazon tree species can have a wider plasticity and adaptability than previously assumed.

4.3. Functional diversity and biomass dynamics following windthrows

Different studies have found that shade-tolerant and long-living (i.e. late-successional) species are dominant (i.e. higher biomass stocks and accumulation rates) in old-growth forests subjected to background tree mortality (Vieira et al. 2004; Fauset et al. 2015; Rozendaal and Chazdon 2015). Low disturbance conditions encountered in old-growth

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forests reduce biomass stocks and accumulation due to mid-successional and pioneer species, which was also clear from my results (Magnabosco Marra et al. 2016b).

I revealed a large and differential effect of tree mortality intensity (i.e. gap size fraction) on floristic composition and structure of Central Amazon forests. I found that blowdowns can change recruitment and consequently species demography and biomass dynamics (Marra et al. 2014a; Magnabosco Marra et al. 2016b). This finding contradicts previous studies that focused on small canopy-gaps and reported only a minor or no effects of disturbances on tree community dynamics (Uhl et al. 1988; Hubbell et al. 1999; Baker et al. 2015). As previously noted (Sousa 1984; Denslow et al. 1998), the effects of canopy disturbance on tree communities is clearly related to the size of the gap (i.e. tree-mortality intensity) (Marra et al. 2014b; Magnabosco Marra et al. 2016b). Interestingly, I showed that biomass recovery following large-scale wind disturbance involves many species and functional types rather than typical pioneer or classical gap-specialists that follow human disturbances (Mesquita et al. 2001; Chazdon et al. 2007).

Biomass dynamics in the wind-disturbed sites that I studied were dominated not only by species from classical pioneer genera (e.g. *Cecropia*, *Pourouma* and *Vismia*) but many species and genera with different requirements and that usually do not reach this same importance both following treefall (i.e. old-growth conditions) and human disturbances involving stand-removing. These include: *Guatteria olivacea* R.E. Fr., *Inga pezizifera* Benth., *I. paraensis* Ducke, *Miconia manauara* R. Goldenb., Caddah & Michelang., *Ocotea guianensis* Aubl. and *Tapirira guianensis* Aubl. (see ‘Supplement information’ in paper 4) (Magnabosco Marra et al. 2016b). Simultaneously, not only light- and ‘disturbance-demanding’ species increased biomass stocks and accumulation following blowdowns. Some late-successional species (mostly survivors), which also have high abundance and biomass stocks in old-growth Amazon forests (ter Steege et al. 2013; Fauset et al. 2015) such as *Eschweilera coriacea* (DC.) S.A. Mori, *Protium hebetatum* Daly and *Licania oblongifolia* Standl, were also important in the blowdown sites that I studied (Magnabosco Marra et al. 2016b).

The greater biomass in light-demanding and short-lived species that I found up to 27 yrs after disturbance, provides evidence that periodic blowdowns have a significant effect on important landscape processes and mechanisms regulating biomass partitioning and

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distribution between species (Magnabosco Marra et al. 2016b). If these forests evolved under the current or even higher frequency and intensity of blowdowns, it is likely that their occurrence within old-growth forest matrices is a major mechanism allowing high species diversity levels and promoting the functionality of light-demanding species (Salo et al. 1986; Everham and Brokaw 1996; Vandermeer et al. 2000).

It is worth mentioning, that at least 15 of the 100 most important tree genera in old-growth Amazon forests have species with pioneer or mid-successional syndromes (e.g. *Cecropia*, *Inga* and *Pourouma*) (ter Steege et al. 2013), as defined in the papers 1 and 2 (Marra et al. 2014a; Magnabosco Marra et al. 2016b). In addition, the cohort of species colonizing the blowdowns that I studied contains many more species than just typical pioneers. Obviously, the wide light gradient typical of blowdowns supports a large number of species exploiting particular light conditions. The great importance of species with some level of light requirement and associated recruitment strategies also corroborates the importance of large-scale disturbance dynamics in Amazon forests. In large and contiguous old-growth forests, blowdowns can work as ‘refuge’ or ‘islands’ for a wide range of species requiring different levels of light conditions above the range realized in the old-growth matrix for establishment, growth and reproduction.

4.4. Windthrows and soil carbon stocks

Together with colleagues, I revealed an interesting interaction between tree biomass dynamics and soil carbon stocks (Santos et al. 2016). I showed that not only tree community attributes (such as structure and dynamics) are influenced by soils in these forests (Castilho et al. 2006; Toledo et al. 2011; Quesada et al. 2012), but that tree community dynamics (i.e. tree mortality) can also affect soil attributes such as soil carbon stocks and soil organic carbon.

The incorporation of a considerable fraction of the organic matter released from dead trees, with consequent increase of soil carbon stocks, suggests a lower potential carbon emission following blowdowns. Although our data supports the hypothesis that clay-rich soils incorporate greater amounts of carbon, clay-poor soils also showed significant increases in carbon stocks. This result indicates that despite typical soil texture differences between plateau and valley forests from this region (Ranzani 1980; Telles et al. 2003) and even a possible lower frequency of damaging winds in valley forests, a possible increase in tree

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mortality due to a higher frequency of blowdowns will produce shifts in soil carbon stocks independently of topography (i.e. at the landscape level).

Interestingly, we do not know how much of the incorporated carbon is actually from the above or the belowground plant material. While tree uprooting may allow the incorporation of organic matter into lower soil horizons, this mode of tree death is also related to the exposure of mineral soil from deeper horizons to the surface (Putz 1983; Ribeiro et al. 2014; Marra et al. 2014a), which could decrease topsoil carbon stocks. I argued that a considerable amount of the incorporated soil carbon in disturbed areas is potentially from belowground plant material (i.e. roots), which is already incorporated into the soil. An interesting question to be addressed in future research is how much of the incorporated soil carbon following wind disturbance it actually stabilized or again released in the mid-term. More precise estimates of soil carbon stocks and balance in Central and Western Amazon forests typically disturbed by blowdowns need to account for landscape variations in tree mortality (Santos et al. 2016).

Great losses of carbon and nutrients due to less frequent natural disturbances can be gradually recovered before the next disturbance event (Bellingham et al. 1996; Everham and Brokaw 1996; Cole et al. 2014). As I have seen, blowdowns can increase soil carbon stocks in Central Amazon forests to similar values as those reported for other forest types developed in different soils and climate (Santos et al. 2016). This result suggests that macro and micronutrients released during plant decomposition can also be incorporated into the soil and re-used by the natural regeneration. In contrast, frequently disturbed forests may not regain any nutrients (e.g. defoliation, leaching and combustion), which can lead to decrease in tree growth and forest resilience (Lin et al. 2003).

In this context, a future climate scenario leading to more intense and frequent storms, is also likely to promote shifts in Central Amazon forests via feedbacks on the carbon/nutrient cycling between vegetation and soil. Moreover, decomposition in these forests is partially controlled by the size and density of the woody material (i.e. trees) (Chambers et al. 2000; Hérault et al. 2010). Interestingly, although heavily damaged areas had higher increases in soil carbon stocks, partially attributable to the higher amount of dead plant material (Santos et al. 2016), they were also colonized by species that have smaller sizes (i.e. mean DBH) and lower wood density (Magnabosco Marra et al. 2016b). Under

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increased frequency of blowdowns, these forests may not reach old-growth stage before the next disturbance event. Consequently, tree communities may be dominated by pioneer and/or mid-successional species (Magnabosco Marra et al. 2016b), which can directly affect tree mortality rates, wood decomposition, nutrient leaching and emission rates. In the long-term, such changes may also contribute to an increase in vulnerability and a decrease in forest resilience to windthrows.

4.5. Monitoring biomass and carbon in Amazon forests

I showed that blowdowns shift important determinants of forest biomass, such as size distribution of trees, wood density and tree architecture (Magnabosco Marra et al. 2016a). More importantly, I showed that estimating biomass of forests subjected to strong variations in floristic composition and size of trees requires allometric models parameterized with local data and including predictors that capture the intrinsic variations in tree architecture (Magnabosco Marra et al. 2016a). When these precautions are not met, landscape biomass estimates can have large associated biases. This is critical when (1) using biomass estimation models in a different forest/successional stage than that where the model was parameterized or (2) when floristic composition and size distribution of trees from the target forests is different from that in the forest where the model was parameterized.

Research on biomass/carbon stocks and dynamics in tropical forests still relies on pantropical or global biomass estimation models (Brown et al. 1989; Chave et al. 2005; Chave et al. 2014). A common assumption is that these models capture site and landscape differences in important aspects defining stand biomass, such as size distribution and architecture of trees (Magnabosco Marra et al. 2016a). Nonetheless, I showed that an available pantropical model (Chave et al. 2014) systematically overestimated stand biomass of Central Amazon forests varying in structure and species composition (Magnabosco Marra et al. 2016a). In addition, I confirmed that old-growth forests in Central Amazon are a mosaic of successional stages recovering from past disturbance (Chambers et al. 2013; Cole et al. 2014; Magnabosco Marra et al. 2016b).

Future research on biomass and carbon dynamics in the Amazon, including integration of field data on remote-sensing-based models for biomass estimation, needs to address the revealed landscape variation in structure and floristic composition typical of wind-disturbed forests (Magnabosco Marra et al. 2016b). Since these forests comprise of a

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mosaic of different successional stages, with trees of various architectures sorted into different forest layers, site-specific models are needed for reliable stand biomass predictions. Alternatively, existing biomass estimation models can be ‘re-adjusted’. For instance, by using measures of tree dominant height (Lima 2010; Lima et al. 2012; Higuchi 2015). The parameterization approach that I used in the paper 3 was adequate to treat the typical heteroscedascity of allometric data sets, which is often neglected (Sileshi 2014), and can be reapplied in future studies dealing with other data sets (Magnabosco Marra et al. 2016a). A similar approach has been previous suggested and also yielded better model fits (Mascaro et al. 2011).

Apart from employing an adequate modeling approach, the availability of a large allometric data set (i.e. 727 trees from 135 species) allowed me to use a ‘virtual forest’ approach to test the yielded models against forest scenarios (see ‘Material and methods’ of paper 3) (Magnabosco Marra et al. 2016a). This was extremely helpful when selecting the most parsimonious biomass estimation model. I could also have used one half of the data set for the model parameterization and tested the yielded models with the second half for which I had the observed weight. Instead of the model ‘evaluation’ procedure that I developed in paper 3 (Magnabosco Marra et al. 2016a), this approach would have allowed for a model ‘validation’ (i.e. testing the model with an ‘independent’ data set).

The wide disturbance gradient promoted by Amazon blowdowns seems to be underrepresented in available permanent plots (Negrón-Juárez et al. 2011; Magnabosco Marra et al. 2016a). Moreover, available allometric data on trees may not represent the entire gradient of disturbance available in tropical forests, e.g. variations in size distribution and species composition following disturbance. The extant gradient could be accounted for by deliberately sampling trees on naturally and human disturbed areas (Nelson et al. 1999; Silva 2007; Ribeiro et al. 2014). As also discussed in the paper 3 (Magnabosco Marra et al. 2016a), our model’s suitability could be improved by the inclusion of useful parameters such as tree height or by employing local measures of wood density. However, using predicted height measures or compiled wood density values is likely to produce uncertainties of unknown magnitude. Promising technologies such as Lidar and multispectral sensors are progressively increasing our capacity of monitoring forest structure and dynamics. These allow the acquisition of important variables such as tree height, canopy density, chemistry composition,

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phenology and species composition (Kellner and Asner 2009; Levick et al. 2012; Goodman et al. 2014; Sawada et al. 2015).

4.6. Amazon forest resilience to different disturbances

To contextualize my results and better understand how variations in disturbance intensity affect aboveground biomass/carbon dynamics during recovery, I compiled data on forest structure and biomass/carbon dynamics from 22 studies conducted in Amazon forests (Table 1). I focused on similar forest types (mainly *terra firme* forests), with relatively similar soil types but varying in land use. Thus, each site included in this analysis is related to a different type and intensity of disturbance and recovery time (i.e. time after disturbance). Further, I compared these data with those from the paper 4 (Magnabosco Marra et al. 2016b) to assess how biomass/carbon dynamics following windthrows differs from that in old-growth and disturbed forests. For all the forest sites, I calculated the relative biomass accumulation (AGBAcc) as following:

$$AGBAcc = ((AGBstock_{ii} - AGBstock_i) \div AGBstock_i) \times 100 [2],$$

where AGB is aboveground biomass (modified from Magnabosco Marra et al. 2016b).

On average, old-growth forests store more biomass (301.7 Mg ha⁻¹, ranging from 221 Mg ha⁻¹ to 399.7 Mg ha⁻¹) than forests recovering from different types of disturbance (157.4 Mg ha⁻¹, ranging from 49 Mg ha⁻¹ to 365.8 Mg ha⁻¹). However, old-growth forests have lower AGBAcc (0.8%, ranging from 0.3% to 1.7%) than that of wind-disturbed and secondary forests recovering from different types or intensities of human disturbances (2.9%, ranging from -9.9% to 14.3%). In comparison with secondary forests, wind-disturbed forests have lower mean values of biomass stocks (123.1 Mg ha⁻¹ and 168.6 Mg ha⁻¹, respectively). Nonetheless, AGBAcc in wind-disturbed forests was higher than that in secondary forests (3.6% and 2.5%, respectively). Again, it is important to note that the oldest wind-disturbed forest included in this analysis only has a 27yr-recovery period (Magnabosco Marra et al. 2016b), whereas recovery periods for forests subjected to other types of disturbance have longer recovery periods (see references in Table 1).

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Rf	Domain	Forest type	Region	Soil type	Precip	Land use	min DBH	TD	BA		C												
									AGB	St	St	NA	Mo	NA	St	To	Gr	Rc	Mo	NA	AGB Acc		
21	Amazon	Lowland evergreen rainforest	BR, Bragantina, Peixe-Boi	NR	NR	10 yrs after shifting agriculture	5			4.4												2.1 [‡]	
13	Amazon	Lowland evergreen rainforest	BR, Bragantina, Peixe-Boi	Oxisols and Ultisols	2000-3000	10 yrs after shifting agriculture	5			49.8 [§]													
21	Amazon	Lowland evergreen rainforest	BR, Bragantina, Peixe-Boi	NR	NR	5 yrs after shifting agriculture	5			2.6												1.2 [‡]	
22	Neotropics	Lowland evergreen rainforest	BR, Bragantina, Peixe-Boi	Vr	750-4000	20 yrs secondary forest	5**			122.0												3.1	5.0
22	Neotropics	Lowland forests	45 sites in 8 countries	Vr	750-4000	(different land uses) 10 yrs secondary forest	5			67.1 ^{††}													
10	Amazon	<i>Terra firme</i> forest	BR, Manacapuru, RDS Rio Negro, SAWI	Oxisol, Ultisols and Spodosols	2300 ^{‡‡}	27 yrs after blowdown	10	524	20.6	174.3	5.2	4.6 ^{§§}	0.6	-2.5	2.7	84.5 [†]	2.5 [†]	2.2 ^{§§§}	0.3 [†]	-1.2 [†]	1.3 [†]		1.5
10	Amazon		BR, Manacapuru, RDS Rio Negro, SAWI	Oxisol, Ultisols and Spodosols	2300 ^{‡‡}	24 yrs after blowdown	10	529	19.6	166.1							80.6 [†]						
10	Amazon		BR, Presidente Figueiredo, ZF-5, SAWI	Oxisol, Ultisols and Spodosols	2500 ^{‡‡}	17 yrs after blowdown	10	774	19.8	132.7	6.1	5.5 ^{§§}	0.6	-0.9	5.2	64.4 [†]	3.0 [†]	2.7 ^{§§§}	0.3 [†]	-0.4 [†]	2.5 [†]		3.9
10	Amazon		BR, Presidente Figueiredo, ZF-5, SAWI	Oxisol, Ultisols and Spodosols	2500 ^{‡‡}	14 yrs after blowdown	10	750	17.6	117.1							56.8 [†]						
10	Amazon		BR, Manaus, ZF-2, SAWI	Oxisol, Ultisols and Spodosols	2400 ^{‡‡}	10 yrs after blowdown	10	716	17.5	120.6	8.1	6.4 ^{§§}	1.7	-2.2	5.9	58.5 [†]	3.9 [†]	3.1 ^{§§§}	0.8 [†]	-1.1 [†]	2.9 [†]		4.9
10	Amazon		BR, Manaus, ZF-2, SAWI	Oxisol, Ultisols and Spodosols	2400 ^{‡‡}	7 yrs after blowdown	10	632	14.6	102.7	8.1	3.4 ^{§§}	4.7	-4.1	4.0	49.8 [†]	3.9 [†]	1.6 ^{§§§}	2.3 [†]	-2.0 [†]	1.9 [†]		3.9
22	Amazon		BR, Manaus, ZF-2, NASA	Oxisol, Ultisols and Spodosols	2100	ca. 6 yrs after blowdown	5	1550	15.2	132.0							64.0 [†]						
10	Amazon		BR, Manaus, ZF-2, SAWI	Oxisol, Ultisols and Spodosols	2400 ^{‡‡}	4 yrs after blowdown	10	380	11.3	90.5							43.9 [†]						

Attributes: Rf- reference study; Precip- precipitation (mm yr⁻¹); minDBH- minimum diameter at breast height (DBH) recorded; TD- tree density (ha⁻¹); BA- basal area (m²); AGB(C)- aboveground biomass (carbon); St- AGB (carbon) stocks (Mg ha⁻¹ yr⁻¹); To- total AGB (carbon) gain (Mg ha⁻¹ yr⁻¹); Gr- AGB (carbon) gain via tree growth in diameter (Mg ha⁻¹ yr⁻¹); Rc- AGB (carbon) loss via tree recruitment (Mg ha⁻¹ yr⁻¹); Mo- AGB (carbon) gain via tree mortality (Mg ha⁻¹ yr⁻¹); NA- AGB

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(carbon) net accumulation ($\text{Mg ha}^{-1} \text{yr}^{-1}$); AGB(carbon)/Acc- relative AGB (carbon) recovery (%); Vr- various (for details consult the respective reference); NR- not reported. *Measured in a 2000 m^2 plot. Studies: 1- Carvalho Jr. et al. 1995; 2- Higuchi et al. 1997 (in the logged forests values were averaged over a 9 yr-period after logging operations); 3- Chambers et al. 2001; 4- Baker et al. 2004; 5- DeWalt & Chave 2004; 6- Higuchi et al. 2004; 7- Vieira et al. 2004; 8- Lima et al. 2007; 9- Teixeira et al. 2007; 10- This study (category 4 with tree mortality $\geq 45\%$); 11- Schiethi et al. 2016; 12- Saldarriaga et al. 1998; 13- Johnson et al. 2001; 14- Salomão et al. 2002; 15- Rice et al. 2004; 16- Mazzei et al. 2010; 17- Phillips et al. 1998; 18- FAO 2010; 19- Laurance et al. 1997; 20- Rutishauser et al. 2015; 21- Salomão et al. 1998; 22- Poorter et al. 2015; 23- Chambers et al. 2009.

† Carbon content of 48.5% (Silva 2007)

‡ Carbon content of 47% (IPCC, 2006)

§ Water content of 47.4% (Magnabosco Marra et al. 2016)

¶ Include palm species

Includes trees ≥ 5 cm DBH

|| Estimated from Table 1 (Mazzei et al. 2010).

** In three sites only trees ≥ 10 cm DBH were measured

†† Estimated from SI S1 Table 1 (Poorter et al. 2016)

‡‡ <http://www.cprm.gov.br/>

§§ Includes AGB growth from resprouters

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When compared with sites subjected to selective logging, which had a mean AGBAcc of -0.2% (ranging between -9.9% and 2.0%) and can be viewed as having an intermediate level of disturbance (i.e. between clear-cut and natural background tree mortality), our blowdown sites had higher AGBAcc (mean of 3.6%, ranging between 1.5% and 4.9) (Table 1). Interestingly, while logging intensity appears to be negatively related with biomass recovery (Rutishauser et al. 2015; Vidal et al. 2016), tree mortality intensity from wind seems to positively affect AGBAcc (Magnabosco Marra et al. 2016b). This apparently higher resilience to wind damage may be related to the lower impacts caused by winds in comparison to logging. It is also important to note that logging has biomass/carbon recovery dynamics more similar to windthrow than with other human disturbances. This result confirms that from the biomass/carbon recovery perspective, logging produces less impact on these forests than other conventional land-uses (Higuchi et al. 1997; Teixeira et al. 2007; Rutishauser et al. 2015; Vidal et al. 2016). Also similar to windthrow disturbance, logging produces a ‘delayed’ mortality effect, which accounts for important losses of biomass/carbon following logging operations (Rutishauser et al. 2015). This highlights the importance of employing reduced-impact logging techniques (Figueiredo et al. 2007).

As discussed in the different papers comprising this dissertation (Marra et al. 2014a; Magnabosco Marra et al. 2016a; Santos et al. 2016; Magnabosco Marra et al. 2016b), blowdowns produce low soil impacts (e.g. compaction), release large amounts of organic matter and probably nutrients via decomposition of dead plant-material, and allow mid- and late-successional species (survivors) to participate in the initial successional cohort. Interestingly, AGBAcc in a secondary forest recovering from clear cutting was more than twice as high (between 10% and 14.3%) as the maximum AGBAcc observed in wind-disturbed forests (4.9%) (Table 1). The typical low growth rates of late-successional trees potentially surviving wind-disturbance (e.g. growth rates ranging from -0.48 to 11.41 mm yr⁻¹ in an old growth forest) (Silva et al. 2002) and the initial high stem density in forests recovering from wind-disturbance (from 380 to 1550 trees ha⁻¹) may partially explain the higher biomass accumulation following clear cutting. In the last, pioneers with low wood density and high growth rates are likely to dominate early succession (Finegan 1996; Mesquita et al. 2001; Chazdon 2003).

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Observed differences in biomass accumulation, and thus in AGBAcc between different old-growth forests (Table 1), are likely to be caused by site-specific characteristics such as forest structure and species composition, soil and precipitation (Vieira et al. 2004; Saatchi et al. 2007; Quesada et al. 2012). However, biomass/carbon differences between sites with similar forest structure, soils and precipitation are probably related to the use of different biomass estimation models, which can yield different results (Clark and Kellner 2012; Sileshi 2014). While some studies relied on site-specific models, others relied on generic global or pantropical models. As I have shown in paper 3 (Magnabosco Marra et al. 2016a), these models can produce estimates with large associated uncertainties, especially when employed to estimate biomass of tropical forests under specific disturbance regimes or successional stages.

The three studies in which mechanisms of biomass/carbon resilience were reported (Table 1), corroborate some of my results from paper 4 (Magnabosco Marra et al. 2016b). Apart from storing higher biomass/carbon stocks, old-growth forest dynamics is mainly dominated by biomass gain and loss from established trees, with a lesser contribution from recruitment. In old-growth forests, biomass losses via tree mortality are compensated for by higher gains from the growth of surviving trees, which often results in positive biomass accumulation. Apart from drastically changing biomass/carbon stocks, disturbances promote strong shifts in mechanisms of biomass gain and loss. Overall, the greater AGBAcc observed in wind- and human-disturbed forests is due to strong changes in biomass gain and loss mechanisms. Although wind and logging promote 'delayed' mortality with important biomass losses, recruitment during early-succession is fast and consist of an efficient mechanism of biomass recovery. As time proceeds, growth of pioneer and mid-successional trees recruited after disturbance dominates biomass gain. At late-succession, recruitment becomes less important and dominated by shade-tolerant species, such as in old-growth forests (Finegan 1996; Chazdon et al. 2007; Magnabosco Marra et al. 2016b).

Accumulation of biomass in old-growth forests over the last decades has been observed in different regions in the Amazon (Lewis et al. 2004; Phillips et al. 2004; Pan et al. 2011). In contrast, more recent studies reported that although these forests may have worked as a carbon sink over the last decades, they actually show a long-term decreasing trend of biomass/carbon accumulation (Brienen et al. 2015) and shifts in species and trait composition

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(van der Sande et al. 2016). In Amazon forests, reductions in biomass/carbon accumulation were related to an increase in mortality associated with recent greater climate variability and reductions in the residence time of the biomass/carbon due to short tree longevity (Brienen et al. 2015).

Although for this vast and complex region drought has been assigned as one of the main causes of the observed increase in mortality rates (Phillips et al. 2009; Lewis et al. 2011), there is no empirical study that shows a direct causal relationship between specific drought events associated with decadal varying climate phenomena (e.g. ENSO) and tree mortality captured in plot-based studies. By contrast, biomass fluctuations in the forest chronosequence that I studied were significantly influenced by disturbance-related tree mortality intensity (Magnabosco Marra et al. 2016b). These findings agree with previous studies, which showed that heavy rainfall and large-scale wind disturbances have also contributed to observed increase in tree mortality in Central Amazon forests (Negrón-Juárez et al. 2010b; Higuchi et al. 2011; Chambers et al. 2013). In addition, my findings suggest that blowdowns have a potentially significant influence on regional gradients and temporal fluctuations of biomass dynamics typically reported for the Amazon basin (Baker et al. 2004b; Lewis et al. 2004; Phillips et al. 2004).

In the Amazon forest, which has previously been assumed to be at equilibrium and dominated by small-scale disturbance dynamics, a current issue is the degree to which the fraction of tree mortality associated with blowdowns is captured by small-scale permanent plots used for inferring long-term changes in biomass/carbon dynamics (Fisher et al. 2008; Lloyd et al. 2009; Chambers et al. 2009a; Chambers et al. 2013). As already noted, tree mortality can influence forest structure (i.e. size distribution of trees, tree density, basal area and biomass) from local- to basin-wide scales (Toledo et al. 2013; Johnson et al. 2016; Schiatti et al. 2016). As with historical and recent human disturbance (Prance 1972; FAO 2012; IPCC 2014; Clement et al. 2015), gradual climate change has been associated with patterns of tree species composition and diversity (Wright 2005; Bonan 2008; Nepstad et al. 2008). Although I did not assess the frequency and spatial distribution of blowdowns across regions and whether vegetation responses are captured in available permanent plots, the results from my various studies confirm that large-scale wind disturbances are likely to exert a strong influence on these observed patterns. Indeed, Central Amazon forests are likely to be

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in a continuous recovery process from different types and levels of disturbance and may carry the legacy of past disturbances for a long time (Chambers et al. 2013; Cole et al. 2014; Clement et al. 2015).

The changes in different forest attributes that I observed following windthrows partly corroborate the results from modeling studies that have suggested significant changes in species composition and biomass stocks once these forests are subjected to higher disturbance regimes (Holm et al. 2014; Negrón-Juárez et al. 2016). As supported by the chronosequence of blowdown sites (4-27 yrs after disturbance) that I studied, windthrows can be expected to initially reduce tree density and biomass stocks due to the high immediate tree mortality. In the subsequent years, recruitment of pioneer and mid-successional species adapted to ‘larger’ gap conditions will produce important effects in the regenerating forests. These may include reduction in the size of trees, shifts in the DBH-height relationship, reduction in community mean wood density, biomass stocks and biomass/carbon resilience due to the overall shorter life span of pioneer and/or mid-successional species (Ribeiro et al. 2014; Marra et al. 2014a; Magnabosco Marra et al. 2016b).

In case climate change and predicted oscillations in the current precipitation regime result in an augmentation of the frequency and intensity of windthrows in the Amazon region (Allan et al. 2010; Min et al. 2011; Davidson et al. 2012; IPCC 2014), significant and long-lasting changes in different forest attributes can be expected. Forests that already experience higher background tree mortality rates are likely to be more adapted to novel disturbance regimes and will probably suffer less severe changes in e.g. floristic composition (Holm et al. 2014; Negrón-Juárez et al. 2016). The results from paper 4 included in this dissertation (Magnabosco Marra et al. 2016b) suggest that more frequent blowdowns can be expected to produce severe changes in floristic composition and biomass dynamics. A shorter interval between windthrows may prevent these forests to return to old-growth stages. As observed in similar forests subjected to intense land use, consecutive disturbances in a shorter time interval are likely to reduce vegetation resilience and carbon storage capacity (Jakovac et al. 2015; Rutishauser et al. 2015; Chazdon et al. 2016). Although there is no study on Amazon secondary-forest responses to windthrows, the results from this dissertation and previous studies conducted in other tropical forests suggest that these forests may be more vulnerable due to their possible lower resistance (i.e. smaller trees with lower wood density)

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(Zimmerman et al. 1995; Canham et al. 2010; Ribeiro et al. 2016; Rifai et al. 2016) and resilience (Everham and Brokaw 1996; Norden et al. 2009; Cole et al. 2014).

Although our knowledge regarding the longer-term legacy of blowdowns in these forests is still limited by the availability of satellite imagery and forest monitoring data, I have shown that forests respond rapidly in the first decades following disturbance in terms of tree growth and biomass recovery. Biomass recovery is mediated by a partitioning of the environment by species from different functional groups. Some of the shifts that I found in mechanisms of biomass resilience following blowdowns were also reported for less severe human disturbances, including logging. By contrast, remaining trees in logged forests can show no growth (i.e. increase in DBH) during the first years following logging operations (Chambers et al. 2001). Nonetheless, similar to logged forests (Higuchi et al. 1997; Mazzei et al. 2010; Vidal et al. 2016), blowdowns can promote a ‘delayed’ tree mortality that represents considerable biomass losses during the first years after disturbance. Importantly, areas experiencing tree mortality rates $\geq 45\%$ can remain with different structure, composition and dynamics for at least 27 yrs. My study sites with similar conditions had lower tree density, basal area and biomass (12%, 25% and 30%, respectively) than that from my old-growth control forest. Apart from that, biomass dynamics in wind-disturbed areas still had a greater contribution of biomass gain mechanisms less important in old-growth forests, such as recruitment and growth of pioneer and mid-successional species (Magnabosco Marra et al. 2016b).

4.7. Final considerations

Studying a new topic in the Amazon has provided me extra challenges and singular experiences. Experiencing and working in remote and old-growth parts of this impressive forest was definitely a remarkable opportunity in my academic and professional training. The results of the different studies comprising this dissertation are my contribution to the understanding of processes and mechanisms regulating diversity and dynamics of tree communities in tropical forests. These results provide novel and complementary information on the vulnerability and resilience of the forests to large-scale disturbances. As primary information on tree species distribution and diversity at the landscape level is essential to conservation strategies, but still scarce in these forests and typically restricted to single multi-hectare forest plots, the data set that I acquired has itself a great value and can be used in a

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wide range of contexts and for multiple research questions unrelated to the topic of my dissertation. This dissertation also provides a baseline with which to study the long-term resilience and recovery of these blowdown-affected sites.

5. OUTLOOK

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Rapid land-use change and degradation of old-growth tropical forests contribute to increasing atmospheric concentration of CO₂ and other greenhouse gases (IPCC 2007; Malhi et al. 2008; IPCC 2014), which have a direct influence on climate regulation (Bonan 2008; Min et al. 2011). Under current climate change predictions, the frequency of extreme weather events, i.e. droughts, flooding and storms are expected to increase in the Amazon region (Davidson et al. 2012; Duffy et al. 2015). Although there is still associated uncertainties in future weather-scenarios, a possible increase in the frequency and intensity of tree mortality associated with blowdowns may cause strong effects on different attributes of Central and Western Amazon forests, as predicted by different studies combining empirical data and modeling-approaches (Chambers et al. 2013; Holm et al. 2014; Negrón-Juárez et al. 2016).

In face of the magnitude and complexity of Amazon forests, this dissertation provides important knowledge on the effects of large-scale natural disturbances on different attributes of tree communities. To the previous literature, I have added novel information on landscape-scale patterns of tree mortality and damage, soil alterations and community responses along the disturbance gradient, including biomass dynamics and resilience along *ca.* 30 yrs of succession. In part, the results from the single studies comprising my dissertation corroborate previous studies, which show that in the Central Amazon increased tree mortality rates due to higher frequency of blowdowns may result in significant changes in composition, structure and dynamics (turnover). Moreover, high disturbance intensities may have different effects on species with different ecology and life histories, which in turn can drive long-term changes in species demography and thus patterns of distribution and diversity. Under rapid land-use change and uncertain future weather scenarios, the sustainability of carbon stocks and biodiversity of tropical forests such as the Amazon requires management and conservationist actions. These rely on advanced knowledge about the vulnerability, resilience and successional trajectories following disturbance events (Cole et al. 2014; Lewis et al. 2015; Trumbore et al. 2015; Poorter et al. 2016).

The environmental and disturbance gradients created by blowdowns provide a unique opportunity to assess mechanisms of vegetation resilience, ecological and evolutionary processes regulating biodiversity patterns in complex and hyperdiverse Amazon forests. A

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current demand in this research field is to maintain and expand comparable forest monitoring projects that allow us to better understand forest dynamics and responses to different types and intensities of disturbances. An urgent and challenging task is to synthesize and apply current and future knowledge in order to develop efficient conservation and management strategies that can minimize human impacts on these unique and vital forests.

6. CONCLUSION

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This dissertation has shown that wide and complex tree mortality gradients associated with windthrows produce decadal landscape-level shifts in different attributes of Central Amazon *terra firme* forests. While long-term research is needed to assess the legacy of these extreme events in Amazon forests, my results indicate that blowdowns have a significant impact on patterns of tree species composition, diversity and distribution, and thus biomass dynamics and carbon cycle. I showed how fundamental processes of ecosystem resilience are supported by the striking diversity of these forests where hundreds of species contribute in numerous ways and under contrasting conditions to restore biomass losses. As blowdowns can ‘reset’ Amazonian old-growth forests to earlier successional stages, I propose that they have also relevant interactions with other organisms and taxa.

7. REFERENCES

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- Adams JB, Gillespie AR (2006) *Remote Sensing of Landscapes with Spectral Images*. Cambridge University Press, Cambridge.
- Adams JB, Sabol DE, Kapos V, et al (1995) Classification of multispectral images based on fractions of endmembers: Application to land-cover change in the Brazilian Amazon. *Remote Sens Environ* 52:137–154.
- Adis J (1990) Thirty million arthropod species - too many or too few? *J Trop Ecol* 6:115–118. doi: 10.1017/S0266467400004107
- Allan R (2011) Human influence on rainfall. *Nature* 470:344–345. doi: 10.1029/2009JD013384
- Allan R, Soden B, John V, et al (2010) Current changes in tropical precipitation. *Environ Res Lett*. doi: 10.1088/1748-9326/5/2/025205
- Araujo RF de, Nelson BW, Chambers JQ, Tavares JV (2013) Extent and distribution of forest blowdowns across Amazonia, caused by a single squall line in January of 2005. In: *Anais XVI Simpósio Brasileiro de Sensoriamento Remoto*. INPE, Foz do Iguaçu, pp 3352–3357.
- Asner GP (2013) Geography of forest disturbance. *Proc Natl Acad Sci U S A* 110:3711–2.
- Baker TR, Diaz DMV, Moscoso VC, et al (2015) Consistent, small effects of tree-fall disturbances on the composition and diversity of four Amazonian forests. *J Ecol* 104:497–506. doi: 10.1111/1365-2745.12529
- Baker TR, Pennington RT, Magallon S, et al (2014) Fast demographic traits promote high diversification rates of Amazonian trees. *Ecol Lett* 17:527–536. doi: 10.1111/ele.12252
- Baker TR, Phillips O, Malhi Y, et al (2004a) Variation in wood density determines spatial patterns in Amazonian forest biomass. *Glob Chang Biol* 10:545–562. doi: 10.1111/j.1529-8817.2003.00751.x
- Baker TR, Phillips OL, Malhi Y, et al (2004b) Increasing biomass in Amazonian forest plots. *Philos Trans R Soc Lond B Biol Sci* 359:353–65. doi: 10.1098/rstb.2003.1422
- Banin L, Feldpausch TR, Phillips OL, et al (2012) What controls tropical forest architecture? Testing environmental, structural and floristic drivers. *Glob Ecol Biogeogr* 21:1179–1190.
- Bellingham P, Tanner E, Healey J (1995) Damage and responsiveness of Jamaican montane tree species after disturbance by a hurricane. *Ecology* 76:2562–2580.
- Bellingham P, Tanner E, Rich P, Goodland T (1996) Changes in light below the canopy of a Jamaican montane rainforest after a hurricane. *J Trop Ecol* 12:699–722.
- Bonan GB (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320:1444–1449. doi: 10.1126/science.1155121
- Bongers F, Poorter L, Hawthorne WD, Sheil D (2009) The intermediate disturbance hypothesis applies to tropical forests, but disturbance contributes little to tree diversity. *Ecol Lett* 12:798–805. doi: 10.1111/j.1461-0248.2009.01329.x
- Boose E, Serrano M, Foster D (2004) Landscape and regional impacts of hurricanes in Puerto Rico. *Ecol Monogr* 74:335–352.
- Bordon NG (2012) Banco de sementes de uma floresta tropical madura e alterada por downburst na Amazônia Central. M.Sc. Dissertation, Ciências de Florestas Tropicais (CFT), Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil.
- Bormann F, Likens G (1979) Catastrophic disturbance and the steady state in northern hardwood forests. *Am Sci* 67:660–669.
- Braga PIS (1979) Subdivisão fitogeográfica, tipos de vegetação, conservação e inventário florístico da floresta amazônica. *Acta Amaz* 9:53–80.
- Brienen R, Phillips O, Feldpausch T, et al (2015) Long-term decline of the Amazon carbon sink. *Nature* 519:344–348.

7. REFERENCES

- Brokaw N, Busing R (2000) Niche versus chance and tree diversity in forest gaps. *Trends Ecol Evol* 15:183–188.
- Brokaw N, Grear J (1991) Forest structure before and after the hurricane Hugo at three elevations in the Luquillo Mountains, Porto Rico. *Biotropica* 23:386–392.
- Brokaw N, Scheiner S (1989) Species composition in gaps and structure of a tropical forest. *Ecology* 70:538–541.
- Brown IF, Martinelli LA, Thomas WW, et al (1995) Uncertainty in the biomass of Amazonian forests: An example from Rondônia, Brazil. *For Ecol Manage* 75:175–189. doi: 10.1016/0378-1127(94)03512-U
- Brown S, Gillespie AJR, Lugo AE (1989) Biomass estimation methods for tropical forests with applications to forest inventory data. *For Sci* 35:881–902.
- Camargo J, Ferraz I, Mesquita M, et al (2008) *Guia de Propágulos & Plântulas da Amazônia vol.1*, 1st edn. INPA, Manaus.
- Canham C, Thompson J, Zimmerman J, Uriarte M (2010) Variation in susceptibility to hurricane damage as a function of storm intensity in Puerto Rican tree species. *Biotropica* 42:87–94.
- Carneiro VCM, Higuchi N, Santos J dos, et al (2005) *Composição Florística e Análise Estrutural da Floresta de Terra Firme na Região de Manaus, Estado do Amazonas, Brasil*. V Congresso Florestal Nacional A Floresta e as Gentes, Viso, Portugal.
- Carneiro VMC (2004) *Composição florística e análise estrutural da floresta primária de terra firme na bacia do Rio Cuieiras, Manaus-AM*. M.Sc. Dissertation, Ciências de Florestas Tropicais (CFT), Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil.
- Carvalho Jr JA, Santos JM, Santos JC, et al (1995) A tropical rainforest clearing experiment by biomass burning in the Manaus region. *Atmos Environ* 29:2301–2309.
- Castilho C, Magnusson W, Araújo R, et al (2006) Variation in aboveground tree live biomass in a central Amazonian Forest: Effects of soil and topography. *For Ecol Manage* 234:85–96.
- CDEA (1992) *Amazonia without myths*. Commission on Development and Environment for Amazônia (Tratado de Cooperação da Amazônia), New York, Hong Kong.
- Chambers JQ, Asner GP, Morton DC, et al (2007) Regional ecosystem structure and function: ecological insights from remote sensing of tropical forests. *Trends Ecol Evol* 22:414–23. doi: 10.1016/j.tree.2007.05.001
- Chambers JQ, Higuchi N, Schimel JP, et al (2000) Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. *Oecologia* 122:380–388.
- Chambers JQ, Higuchi N, Schimel JP (1998) Ancient trees in Amazonia. *Nature* 391:135–136. doi: 10.1038/34325
- Chambers JQ, Negrón-Juárez RI, Hurr G, et al (2009a) Lack of intermediate-scale disturbance data prevents robust extrapolation of plot-level tree mortality rates for old-growth tropical forests. *Ecol Lett* 12:E22–E25.
- Chambers JQ, Negrón-Juárez RI, Marra DM, et al (2013) The steady-state mosaic of disturbance and succession across an old-growth Central Amazon forest landscape. *Proc Natl Acad Sci* 110:3949–54. doi: 10.1073/pnas.1202894110
- Chambers JQ, Robertson AL, Carneiro VMC, et al (2009b) Hyperspectral remote detection of niche partitioning among canopy trees driven by blowdown gap disturbances in the Central Amazon. *Oecologia* 160:107–117.
- Chambers JQ, Santos J dos, Ribeiro RJ, Higuchi N (2001) Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest. *For Ecol Manage* 152:73–84.
- Chauvel A, Lucas Y, Boulet R (1987) On the genesis of the soil mantle of the region of Manaus, Central Amazonia, Brazil. *Experientia* 43:234–241.
- Chave J, Andalo C, Brown S, et al (2005) Tree allometry and improved estimation of carbon stocks and balance

7. REFERENCES

- in tropical forests. *Oecologia* 145:87–99.
- Chave J, Norden N (2007) Changes of species diversity in a simulated fragmented neutral landscape. *Ecol Modell* 207:3–10. doi: 10.1016/j.ecolmodel.2007.03.025
- Chave J, Réjou-Méchain M, Búrquez A, et al (2014) Improved allometric models to estimate the aboveground biomass of tropical trees. *Glob. Chang. Biol.* 3177–3190.
- Chazdon RL (2003) Tropical forest recovery: legacies of human impact and natural disturbances. *Perspect Plant Ecol Evol Syst* 6:51–71. doi: 10.1078/1433-8319-00042
- Chazdon RL, Broadbent EN, Rozendaal DMA, et al (2016) Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. *Sci Adv.* doi: 10.1126/sciadv.1501639
- Chazdon RL, Colwell RK, Denslow JS (1999) Tropical Tree Richness and Resource-Based Niches. *Science* 285:1459a.
- Chazdon RL, Letcher SG, van Breugel M, et al (2007) Rates of change in tree communities of secondary Neotropical forests following major disturbances. *Philos Trans R Soc Lond B Biol Sci* 362:273–289. doi: 10.1098/rstb.2006.1990
- Clark DB, Kellner JR (2012) Tropical forest biomass estimation and the fallacy of misplaced concreteness. *J. Veg. Sci.* 23:1191–1196.
- Clark J, Silman M, Kern R (1999) Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* 80:1475–1494.
- Clark KE, West a. J, Hilton RG, et al (2015) Storm-triggered landslides in the Peruvian Andes and implications for topography, carbon cycles, and biodiversity. *Earth Surf Dyn Discuss* 3:631–688. doi: 10.5194/esurfd-3-631-2015
- Clement CR, Denevan WM, Heckenberger MJ, et al (2015) The domestication of Amazonia before European conquest. *Proc Biol Sci* 282:20150813. doi: 10.1098/rspb.2015.0813
- Cohen J, Cavalcanti I, Braga R, Neto L (2009) Squall lines along the north-northeast coast of South America. In: Cavalcanti I, Ferreira N, Silva M da, Dias M da S (eds) *Weather and Climate in Brazil*, 1st edn. Oficina da Textos, São Paulo, pp 75–93.
- Cole LES, Bhagwat S a, Willis KJ (2014) Recovery and resilience of tropical forests after disturbance. *Nat Commun* 5:3906. doi: 10.1038/ncomms4906
- Conrad O, Bechtel B, Bock M, et al (2015) System for Automated Geoscientific Analyses (SAGA).
- Costa MH, Pires GF (2010) Effects of Amazon and Central Brazil deforestation scenarios on the duration of the dry season in the arc of deforestation. *Int J Climatol* 30:1970–1979. doi: 10.1002/joc.2048
- Dale V, Joyce L, McNulty S, Neilson R (2001) Climate change and forest disturbances. *Bioscience* 51:723–734.
- Dalling J, Muller Landau H, Wright S, Hubbell S (2002) Role of dispersal in the recruitment limitation of neotropical pioneer species. *J Ecol* 90:714–727.
- Davidson EA, de Araújo AC, Artaxo P, et al (2012) The Amazon basin in transition. *Nature* 481:321–328. doi: 10.1038/nature10717
- de Oliveira AA, Mori SA (1999) A central Amazonian terra firme forest. I. High tree species richness on poor soils. *Biodivers Conserv* 8:1219–1244.
- Denslow J (1987) Tropical rainforest gaps and tree species diversity. *Annu Rev Ecol Syst* 18:431–451.
- Denslow J (1980a) Gap partitioning among tropical rainforest trees. *Biotropica* 12:47–55.
- Denslow J (1980b) Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia* 46:18–21.
- Denslow J, Ellison A, Sanford R (1998) Treefall gap size effects on above- and below-ground processes in a tropical wet forest. *J Ecol* 86:597–609.
- DeWalt SJ, Chave J (2004) Structure and Biomass of Four Lowland Neotropical Forest 1.-. *Biotropica* 36:7–19.

7. REFERENCES

- Don A, Bärwolff M, Kalbitz K, et al (2012) No rapid soil carbon loss after a windthrow event in the High Tatra. *For Ecol Manage* 276:239–246. doi: 10.1016/j.foreco.2012.04.010
- Duffy PB, Brando P, Asner GP, Field CB (2015) Projections of future meteorological drought and wet periods in the Amazon. *Proc Natl Acad Sci* 112:13172–13177. doi: 10.1073/pnas.1421010112
- Espírito-Santo F, Gloor M, Keller M, et al (2014) Size and frequency of natural forest disturbances and the Amazon forest carbon balance. *Nat Commun* 5:1–6.
- Espírito-Santo F, Keller M, Braswell B, et al (2010) Storm intensity and old-growth forest disturbances in the Amazon region. *Geophys Res Lett* 37:1–6.
- Everham EM, Brokaw NVL (1996) Forest damage and recovery from catastrophic wind. *Bot Rev* 62:113–185. doi: 10.1007/BF02857920
- Fauset S, Johnson MO, Gloor M, et al (2015) Hyperdominance in Amazonian forest carbon cycling. *Nat Commun* 6:6857. doi: 10.1038/ncomms7857
- Feldpausch TR, Banin L, Phillips OL, et al (2011) Height-diameter allometry of tropical forest trees. *Biogeosciences* 8:1081–1106.
- Feldpausch TR, Lloyd J, Lewis SLL, et al (2012) Tree height integrated into pantropical forest biomass estimates. *Biogeosciences* 9:3381–3403. doi: 10.5194/bg-9-3381-2012
- Felfili J (1995) Diversity, structure and dynamics of a gallery forest in central Brazil. *Vegetatio* 117:1–15.
- Figueiredo EO, Braz EM, Oliveira MVN de (2007) Manejo de precisão em florestas tropicais: modelo digital de exploração florestal. Embrapa Acre - Livros técnicos (INFOTECA-E), Rio Branco.
- Fine P, Ree R, Burnham R (2008) The disparity in tree species richness among tropical, temperate, and boreal biomes: the geographical area and age hypothesis. In: Carson W, Schnitzer S (eds) *Tropical forest community ecology*. Wiley-Blackwell, Chichester, pp 31–45.
- Finegan B (1996) Pattern and process in neotropical secondary rain forests: The first 100 years of succession. *Trends Ecol Evol* 11:119–124. doi: 10.1016/0169-5347(96)81090-1
- Fisher J, Hurtt G, Thomas R, Chambers J (2008) Clustered disturbances lead to bias in large-scale estimates based on forest sample plots. *Ecol Lett* 11:554–63.
- Food and Agriculture Organization of the United Nations (2010) *Global Forest Resources Assessment*.
- Food and Agriculture Organization of the United Nations and European Commission Joint Research Centre (2012) *Global forest land-use change 1990-2005*.
- Foster D, Knight D, Franklin J (1998) Landscape Patterns and Legacies Resulting from Large, Infrequent Forest Disturbances. *Ecosystems* 1:497–510.
- Franklin J, Spies T, Pelt R, et al (2002) Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For Ecol* 155:399–423. doi: 10.1016/S0378-1127(01)00575-8
- Fujita T (1976) Spearhead echo and downburst near the approach end of A.. John F. Kennedy Airport Runway, New York City. SMRP Res Pap 137:1–56.
- Fujita T (1990) Downbursts: Meteorological features and wind field characteristics. *J Wind Eng Ind Aerodyn* 36:75–86.
- Garstang M, Massie HL, Halverson J, et al (1994) Amazon coastal squall lines .1. structure and kinematics. *Mon. Weather Rev.* 122:608–622.
- Garstang M, White S, Shugart HH, Halverson J (1998) Convective cloud downdrafts as the cause of large blowdowns in the Amazon rainforest. *Meteorol Atmos Phys* 67:199–212. doi: 10.1007/BF01277510
- Garwood N (1989) Tropical Soil Seed Banks: a Review. In: Leck M, Parker T, Simpson R (eds) *Ecology of soil seed banks*. New York, Academic Press, New York, pp 49–210.
- Gee GW, Bauder JW (1986) Particle-size analysis. In: Klute A (ed) *Methods of Soil Analysis, Part 1. Physical and Mineralogical Methods*. Agronomy Monograph No. 9, 2nd edn. American Society of Agronomy/Soil

7. REFERENCES

- Science Society of America, Madison, WI, pp 383–411.
- Gibson L, Lee T, Koh L, et al (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478:378–81. doi: 10.1038/nature10425
- Gloor M, Phillips OL, Lloyd JJ, et al (2009) Does the disturbance hypothesis explain the biomass increase in basin-wide Amazon forest plot data? *Glob Chang Biol* 15:2418–2430.
- Goodman RC, Phillips OL, Baker TR (2014) The importance of crown dimensions to improve tropical tree biomass estimates. *Ecol Appl* 24:680–698.
- Google Earth Engine Team (2015) Google Earth Engine: A planetary-scale geo-spatial analysis platform.
- Gravel D, Canham C, Beaudet M, Messier C (2006) Reconciling niche and neutrality: the continuum hypothesis. *Ecol Lett* 9:399–409.
- Grubb P (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol Rev* 52:107–145.
- Guariguata M, Ostertag R (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. *For Ecol Manag* 148:185–206.
- Guariguata M, Pinard M (1998) Ecological knowledge of regeneration from seed in neotropical forest trees: implications for natural forest management. *For Ecol Manage* 112:87–99. doi: 10.1016/S0378-1127(98)00318-1
- Guimarães G (2007) Distúrbios decorrentes de blowdown em uma área de floresta na Amazônia Central. Dissertação, Mestrado. INPA, Manaus. M.Sc. Dissertation, Ciências de Florestas Tropicais (CFT), Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil.
- Hallé F (1974) Architecture of trees in the rain forest of Morobe District, New Guinea. *Biotropica* 6:43–50.
- Hallé F, Oldeman RAA, Tomlinson PB (1978) *Tropical trees and forests: an architectural analysis*. Springer-Verlag, Berlin, German Federal Republic.
- Hansen MC, Potapov P V, Moore R, et al (2013) High-resolution global maps of 21st-century forest cover change. *Science* 342:850–853. doi: 10.1126/science.1244693
- Harding K (2011) Thunderstorm formation and aviation hazards. *Front* 1–11.
- Harrison G (1979) Stability under environmental stress : resistance , resilience , persistence, and variability. *Am Nat* 113:659–669.
- Hérault B, Beauchêne J, Muller F, et al (2010) Modeling decay rates of dead wood in a neotropical forest. *Oecologia* 164:243–251. doi: 10.1007/s00442-010-1602-8
- Higuchi F (2015) Dinâmica de volume e biomassa da floresta de terra firme do Amazonas. Ph.D. Dissertation, Engenharia Florestal, Universidade Federal do Paraná (UFPR), Brazil.
- Higuchi N, Chambers JQ, Santos J dos, et al (2004) Carbon balance and dynamics of primary vegetation in the Central Amazon. *Floresta* 34:295–304.
- Higuchi N, Santos J dos, Lima A, et al (2011) A floresta amazônica e a água da chuva. *FLORESTA* 41:427–434.
- Higuchi N, Santos J dos, Ribeiro R, et al (1997) Crescimento e incremento de uma floresta amazônica de terra-firme manejada experimentalmente. In: Higuchi N (ed) *BIONTE - Relatório Final*. Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, pp 87–132.
- Higuchi N, Santos J dos, Ribeiro RJ, et al (1998a) Biomassa da parte aérea da vegetação da floresta tropical úmida de terra-firme da Amazônia brasileira. *Acta Amaz* 28:153–166.
- Higuchi N, Santos J dos, Sampaio P, et al (eds) (2003) *Projeto Jacaranda-Fase II: Pesquisas florestais na Amazônia Central*, 1st edn. Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus.
- Higuchi N, Santos J dos, Vieira G, et al (1998b) Análise estrutural da floresta primária da bacia do rio Cuieiras, ZF-2, Manaus-AM, Brasil. In: Higuchi N, Campos M, Sampaio P, Santos J dos (eds) *Pesquisas Florestais para Conservação da Floresta e Reabilitação de Áreas Degradadas da Amazônia*. Instituto Nacional de

7. REFERENCES

- Pesquisas da Amazônia (INPA), Manaus, pp 51–81.
- Holling C (1973) Resilience and stability of ecological systems. *Annu Rev Ecol Syst* 4:1–23. doi: 10.1146/annurev.es.04.110173.000245
- Holm JA, Chambers JQ, Collins WD, Higuchi N (2014) Forest response to increased disturbance in the central Amazon and comparison to western Amazonian forests. *Biogeosciences* 11:5773–5794. doi: 10.5194/bg-11-5773-2014
- Houghton RA, Lawrence KT, Hackler JL, Brown S (2001) The spatial distribution of forest biomass in the Brazilian Amazon: a comparison of estimates. *Glob Chang Biol* 7:731–746. doi: DOI 10.1046/j.1365-2486.2001.00426.x
- Hubbell S (2005) Neutral theory in community ecology and the hypothesis of functional equivalence. *Funct Ecol* 19:166–172.
- Hubbell SP, Fangliang H, Condit R, et al (2008) Colloquium paper: how many tree species are there in the Amazon and how many of them will go extinct? *Proc Natl Acad Sci U S A* 105 Suppl:11498–11504. doi: 10.1073/pnas.0801915105
- Hubbell SP, Foster RB, O'Brien ST, et al (1999) Light-Gap Disturbances, Recruitment Limitation, and Tree Diversity in a Neotropical Forest. *Science* 283:554–557.
- IBGE (2004) Mapa de Biomas do Brasil. Escala 1:5,000,000.
- INPE (2016) Projeto PRODES - Monitoramento da Amazônia Brasileira por satélite. São Paulo.
- IPCC (2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland.
- IPCC (2007) Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Intergovernmental Panel on Climate Change, Geneva, Switzerland.
- ISA (2016) Instituto Socioambiental (ISA). In: Inst. Socioambiental. <https://pib.socioambiental.org>
- ITT (2012) Environment for Visualizing Images software (ENVI).
- Jakovac C, Peña-Claros M, Kuyper T, Bongers F (2015) Loss of secondary-forest resilience by land-use intensification in the Amazon. *J Ecol* 103:67–77. doi: 10.1111/1365-2745.12298
- John R, Dalling JW, Harms KE, et al (2007) Soil nutrients influence spatial distributions of tropical tree species. *Proc Natl Acad Sci U S A* 104:864–9. doi: 10.1073/pnas.0604666104
- Johnson CM, Vieira ICG, Zarin DJ, et al (2001) Carbon and nutrient storage in primary and secondary forests in eastern Amazônia. *For Ecol Manage* 147:245–252. doi: 10.1016/S0378-1127(00)00466-7
- Johnson M, Galbraith D, Gloor E, et al (2016) Variation in stem mortality rates determines patterns of aboveground biomass in Amazonian forests: implications for dynamic global vegetation models. *Glob Chang Biol*. doi: 10.1111/gcb.13315
- Junk W, Piedade M, Shongärt J, et al (2011) A classification of major naturally-occurring amazonian lowland wetlands. *Wetlands* 31:623–640.
- Junqueira A, Almekinders CJM, Stomph T, et al (2016) The role of Amazonian anthropogenic soils in shifting cultivation : learning from farmers' rationales. *Ecol Soc*. doi: 10.5751/ES-08140-210112
- Kellner JR, Asner GP (2009) Convergent structural responses of tropical forests to diverse disturbance regimes. *Ecol Lett* 12:887–97.
- Kitajima K, Mulkey SS, Wright SJ (2005) Variation in crown light utilization characteristics among tropical canopy trees. *Ann Bot* 95:535–47. doi: 10.1093/aob/mci051
- Kramer MG, Sollins P, Sletten RS (2004) Soil carbon dynamics across a windthrow disturbance sequence in southeast Alaska. *Ecology* 85:2230–2244. doi: 10.1890/02-4098
- Kuo HL (1965) On formation and intensification of tropical cyclones through latent heat release by cumulus convection. *J Atmos Sci* 22:40–63. doi: 10.1175/1520-0469(1965)022<0040:OFAIOT>2.0.CO;2

7. REFERENCES

- Laurance WF (1997) Biomass Collapse in Amazonian Forest Fragments. *Science* 278:1117–1118. doi: 10.1126/science.278.5340.1117
- Leary C, Houze Jr R (1979) The structure and evolution of convection in a tropical cloud cluster. *J Atmos Sci* 36:437–457.
- Leibold MA, Holyoak M, Mouquet N, et al (2004) The metacommunity concept: A framework for multi-scale community ecology. *Ecol Lett* 7:601–613. doi: 10.1111/j.1461-0248.2004.00608.x
- Levick S, Asner G, Smit I (2012) Spatial patterns in the effects of fire on savanna vegetation three-dimensional structure. *Ecol Appl* 22:2110–2121.
- Lewis SL, Brando PM, Phillips OL, et al (2011) The 2010 Amazon drought. *Science* 331:554. doi: 10.1126/science.1200807
- Lewis SL, Edwards DP, Galbraith D (2015) Increasing human dominance of tropical forests. *Science* 349:827–832.
- Lewis SL, Phillips OL, Baker TR, et al (2004) Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. *Philos Trans R Soc B Biol Sci* 359:421–436. doi: 10.1098/rstb.2003.1431
- Lieberman M, Lieberman D, Peralta R (1989) Forests are not just Swiss cheese: canopy stereogeometry of non-gaps in tropical forests. *Ecology* 70:550–552.
- Lima AJN (2010) Avaliação de um sistema de inventário florestal contínuo em áreas manejadas e não manejadas do Estado do Amazonas (AM). Ph.D. Dissertation, Ciências de Florestas Tropicais (CFT), Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil.
- Lima AJN, Suwa R, Ribeiro GHM, et al (2012) Allometric models for estimating above- and below-ground biomass in Amazonian forests at São Gabriel da Cachoeira in the upper Rio Negro, Brazil. *For Ecol Manage* 277:163–172.
- Lima AJN, Teixeira LM, Carneiro VMC, et al (2007) Biomass stock and structural analysis of a secondary forest in Manaus (AM) region, ten years after clear cutting followed by fire. *Acta Amaz* 37:49–54.
- Lin K-C, Hamburg SP, Tang S, et al (2003) Typhoon effects on litterfall in a subtropical forest. *Can J For Res* 33:2184–2192. doi: 10.1139/x03-154
- Lindroth A, Lagergren F, Grelle A, et al (2009) Storms can cause Europe-wide reduction in forest carbon sink. *Glob Chang Biol* 15:346–355. doi: 10.1111/j.1365-2486.2008.01719.x
- Lloyd J, Gloor EU, Lewis SL (2009) Are the dynamics of tropical forests dominated by large and rare disturbance events? *Ecol Lett* 12:19–21. doi: 10.1111/j.1461-0248.2009.01326.x
- Longman KA, Jenik J (1974) *Tropical forest and its environment*, 1st edn. Longman Group Ltd., London
- Lugo A, Scatena F (1996) Background and catastrophic tree mortality in tropical moist, wet, and rain forests. *Biotropica* 28:585–599.
- Lunn DJ, Thomas A, Best N, Spiegelhalter D (2000) WinBUGS - a Bayesian modelling framework: concepts, structure, and extensibility.
- Magnabosco Marra D (2010) Sucessão florestal em área atingida por tempestade convectiva na região de Manaus, Amazônia Central. M.Sc. Dissertation, Ciências de Florestas Tropicais (CFT), Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil.
- Magnabosco Marra D, Higuchi N, Trumbore S, et al (2016a) Predicting biomass of hyperdiverse and structurally complex Central Amazon forests – a virtual forest approach using extensive field data. *Biogeosciences* 13:15537–15581. doi: 10.5194/bgd-12-15537-2015
- Magnabosco Marra D, Trumbore SE, Higuchi N, et al (2016b) Mechanisms of Amazon biomass resilience to windthrows. In preparation for *Ecol Monogr*.
- Malhi Y, Roberts JT, Betts RA, et al (2008) Climate change, deforestation, and the fate of the Amazon. *Science* 319:169–72. doi: 10.1126/science.1146961

7. REFERENCES

- Malhi Y, Wood D, Baker TR, et al (2006) The regional variation of aboveground live biomass in old-growth Amazonian forests. *Glob Chang Biol* 12:1107–1138. doi: 10.1111/j.1365-2486.2006.01120.x
- Marra DM, Chambers JQ, Higuchi N, et al (2014a) Large-scale wind disturbances promote tree diversity in a central Amazon forest. *PLoS One* 9:e103711. doi: 10.1371/journal.pone.0103711
- Marra DM, Pereira BA da S, Fagg CW, Felfili JM (2014b) Trees and environmental variables influence the natural regeneration of a seasonally dry tropical forest in Central Brazil. *Neotrop Biol Conserv* 9:62–77. doi: 10.4013/nbc.2014.92.01
- Marvin DC, Asner GP, Knapp DE, et al (2014) Amazonian landscapes and the bias in field studies of forest structure and biomass. *Proc Natl Acad Sci* 111:E5224–E5232.
- Mascaro J, Litton CM, Hughes RF, et al (2011) Minimizing Bias in Biomass Allometry : Model Selection and Log-transformation of Data. *Biotropica* 43:649–653.
- Mascaro J, Perfecto I, Barros O, et al (2005) Aboveground biomass accumulation in a tropical wet forest in Nicaragua following a catastrophic hurricane disturbance. *Biotropica* 37:600–608. doi: 10.1111/j.1744-7429.2005.00077.x
- Mazzei L, Sist P, Ruschel A, et al (2010) Above-ground biomass dynamics after reduced-impact logging in the Eastern Amazon. *For Ecol Manage* 259:367–373. doi: 10.1016/j.foreco.2009.10.031
- Mesquita R, Ickes K, Ganade G, Williamson G (2001) Alternative successional pathways in the Amazon Basin. *J Ecol* 89:528–537.
- Min S, Zhang X, Zwiers F, Hegerl G (2011) Human contribution to more-intense precipitation extremes. *Nature* 470:378–381. doi: 10.1038/nature09763
- Mitchard ETA, Feldpausch TR, Brienen RJW, et al (2014) Markedly divergent estimates of Amazon forest carbon density from ground plots and satellites. *Glob Ecol Biogeogr* 23:935–946. doi: 10.1111/geb.12168
- Mittermeier RA, Mittermeier CG, Brooks TM, et al (2003) Wilderness and biodiversity conservation. *Proc Natl Acad Sci U S A* 100:10309–13. doi: 10.1073/pnas.1732458100
- Molino J, Sabatier D (2001) Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. *Science* 294:1702–1704. doi: 10.1126/science.1060284
- Negrón-Juárez RI, Baker D, Chambers JQ, et al (2014) Multi-scale sensitivity of Landsat and MODIS to forest disturbance associated with tropical cyclones. *Remote Sens Environ* 140:679–689.
- Negrón-Juárez RI, Baker D, Zeng H, et al (2010a) Assessing hurricane-induced tree mortality in U.S. Gulf Coast forest ecosystems. *J Geophys Res* 115:1–11. doi: 10.1029/2009JG001221
- Negrón-Juárez RI, Chambers JQ, Guimaraes G, et al (2010b) Widespread Amazon forest tree mortality from a single cross-basin squall line event. *Geophys Res Lett* 37:1–5.
- Negrón-Juárez RI, Chambers JQ, Marra DM, et al (2011) Detection of subpixel treefall gaps with Landsat imagery in Central Amazon forests. *Remote Sens Environ* 115:3322–3328.
- Negrón-Juárez RI, Holm J, Magnabosco Marra D, et al (2016) Vulnerability of Amazon forests to storm-driven tree mortality. *Sci Adv* (in review).
- Nelson B (1994) Natural forest disturbance and change in the Brazilian Amazon. *Remote Sens Rev* 10:105–125.
- Nelson B, Kapos V, Adams J, et al (1994) Forest disturbance by large blowdowns in the Brazilian Amazon. *Ecology* 75:853–858.
- Nelson BW, do Amaral I (1994) Destructive wind effects detected in TM images of the Amazon basin. *Int Soc Photogramm Remote Sens* 30:334–343.
- Nelson BW, Mesquita RCG, Pereira JLG, et al (1999) Allometric regressions for improved estimate of secondary forest biomass in the central Amazon. *For Ecol Manage* 117:149–167.
- Nepstad D, Mcgrath D, Stickler C, et al (2014) Slowing Amazon deforestation through public policy and interventions in beef and soy supply chains. *Science* 344:1118–1123.
- Nepstad D, Stickler C, Filho B, Merry F (2008) Interactions among Amazon land use, forests and climate:

7. REFERENCES

- prospects for a near-term forest tipping point. *Philos Trans R Soc Lond B Biol Sci* 363:1737–46. doi: 10.1098/rstb.2007.0036
- Ngomanda A, Obiang NLE, Lebamba J, et al (2014) Site-specific versus pantropical allometric equations: Which option to estimate the biomass of a moist central African forest? *For Ecol Manage* 312:1–9.
- Nicotra A, Chazdon R, Iriarte S (1999) Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology* 80:1908–1926.
- Nogueira EM, Fearnside PM, Nelson BW, et al (2008) Estimates of forest biomass in the Brazilian Amazon: New allometric equations and adjustments to biomass from wood-volume inventories. *For Ecol Manage* 256:1853–1867. doi: 10.1016/j.foreco.2008.07.022
- Norden N, Chazdon R, Chao A, et al (2009) Resilience of tropical rain forests: tree community reassembly in secondary forests. *Ecol Lett* 12:385–394. doi: 10.1111/j.1461-0248.2009.01292.x
- Orville H, Farley R, Chi Y, Kopp F (1989) The primary cloud physics mechanisms of microburst formation. *Atmos Res* 24:343–357. doi: 10.1016/0169-8095(89)90054-9
- Pan Y, Birdsey RA, Fang J, et al (2011) A large and persistent carbon sink in the world's forests. *Science* 333:988–993. doi: 10.1126/science.1201609
- Penman J, Gytarsky M, Hiraishi T, et al (2003) Good practice guidance on land use, land-use change and forestry, prepared by the National Greenhouse Gas Inventories Programme. Institute for Global Environmental Strategies, Kanagawa, Japan.
- Peterson G, Allen C, Holling C (1998) Ecological resilience, biodiversity, and scale. *Ecosystems* 1:6–18.
- Phillips O, Aragão LE, Lewis SL, et al (2009) Drought sensitivity of the Amazon rainforest. *Science* 323:1344–1347.
- Phillips O, Baker T, Arroyo L, et al (2004) Pattern and process in Amazon tree turnover, 1976–2001. *Philos Trans R Soc Lond B Biol Sci* 359:381–407.
- Phillips O, Malhi Y, Higuchi N, et al (1998) Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science* 282:439–442. doi: 10.1126/science.282.5388.439
- Poorter L (2007) Are species adapted to their regeneration niche, adult niche, or both? *Am Nat* 169:433–42. doi: 10.1086/512045
- Poorter L (1999) Growth responses of 15 rain forest tree species to a light gradient; the relative importance of morphological and physiological traits. *Funct Ecol* 13:396–410.
- Poorter L, Bongers F, Aide TM, et al (2016) Biomass resilience of Neotropical secondary forests. *Nature*. doi: 10.1038/nature16512
- Poorter L, Bongers F, Sterck FJ, Wöll H (2003) Architecture of 53 Rain Forest Tree Species Differing in Adult Stature and Shade Tolerance. *Ecology* 84:602–608.
- Poorter L, Bongers L, Bongers F (2006) Architecture of 54 Moist-Forest Tree Species : Traits, Trade-Offs, and Functional Groups. *Ecology* 87:1289–1301.
- Poorter L, van de Plassche M, Willems S, Boot R (2004) Leaf traits and herbivory rates of tropical tree species differing in successional status. *Plant Biol* 6:746–54. doi: 10.1055/s-2004-821269
- Poorter L, van der Sande MT, Thompson J, et al (2015) Diversity enhances carbon storage in tropical forests. *Glob Ecol Biogeogr* 24:1314–1328. doi: 10.1111/geb.12364
- Popma J, Bongers F, Martinez-Ramos M, Veneklaas E (1988) Pioneer species distribution in treefall gaps in Neotropical rain forest; a gap definition and its consequences. *J Trop Ecol* 4:77–88.
- Pöschl U, Martin S, Sinha B, et al (2010) Rainforest aerosols as biogenic nuclei of clouds and precipitation in the Amazon. *Science* 329:1513–1516.
- Prance GT (1972) Ethnobotanical notes from Amazonian Brazil. *Econ Bot* 26:221–237.
- Putz F (1983) Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. *Ecology* 64:1069–1074.

7. REFERENCES

- QGIS (2016) Quantum GIS Development Team.
- Quesada C a., Phillips OL, Schwarz M, et al (2012) Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences* 9:2203–2246. doi: 10.5194/bg-9-2203-2012
- R Core Team (2014) R: A language and environment for statistical computing.
- Radam (1978) Programa de Integração Nacional- Levantamentos dos Recursos Naturais. Ministério das Minas e Energia, Brasil, Brasília.
- Rametsteiner E, Eichler L, Berg J (2009) Shaping forest communication in the European Union: public perceptions of forests and forestry. Rotterdam.
- Ranzani G (1980) Identificação e caracterização de alguns solos da Estação Experimental de Silvicultura Tropical. *Acta Amaz* 10:7–41.
- Ribeiro GHM, Chambers JQ, Peterson CJ, et al (2016) Mechanical vulnerability of Central Amazon tree species to windthrow in convective storms. *For Ecol Manage* (in review).
- Ribeiro GHM, Suwa R, Marra DM, et al (2014) Allometry for juvenile trees in an Amazonian forest after wind disturbance. *Japan Agric Res Q* 48:213–219.
- Ribeiro JELS, Hopkins MJG, Vicentini A, et al (1999) Flora da Reserva Ducke: Guia de Identificação das Plantas Vasculares de uma Floresta de Terra-firme na Amazônia Central. INPA, Manaus.
- Rice A, Pyle E, Saleska S, et al (2004) Carbon balance and forest dynamics in an old-growth Amazonian forest. *Ecol Appl* 14:S55–S71. doi: 10.1017/CBO9781107415324.004
- Rifai SW, Urquiza Muñoz JD, Negrón-Juárez RI, et al (2016) Landscape-scale consequences of differential tree mortality from catastrophic wind disturbance in the Amazon. *Ecol Appl*. doi: 10.1002/eap.1368
- Rizzini C (1997) Tratado de Fitogeografia do Brasil – aspectos ecológicos, sociológicos e florísticos, 2nd editio. Âmbito Cultural Edições, Rio de Janeiro, Brasil.
- Roosevelt T (1914) *Through the Brazilian Wilderness*, 1st edn. Charles Scribner's Sons, New York.
- Roxburgh S, Shea K, Wilson J (2004) The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. *Ecology* 85:359–371.
- Rozendaal D, Chazdon R (2015) Demographic drivers of tree biomass change during secondary succession in northeastern Costa Rica. *Ecol Appl* 25:506–516. doi: 10.1890/14-0054.1
- Rutishauser E, Baraloto C, Blanc L, et al (2015) Rapid tree carbon recovery in Amazonian logged forests. *Curr Biol* 25:R787–R788. doi: 10.1016/j.cub.2015.07.034
- Saatchi S, Harris N, S B, et al (2011) Benchmark map of forest carbon stocks in tropical regions across three continents. *Proc Natl Acad Sci U S A* 108:9899–9904.
- Saatchi SS, Houghton RA, dos Santos Alvalá RC, et al (2007) Distribution of aboveground live biomass in the Amazon basin. *Glob Chang Biol* 13:816–837. doi: 10.1111/j.1365-2486.2007.01323.x
- Saldarriaga JG, West DC, Tharp ML, Uhl C (1998) Long-Term Chronosequence of Forest Succession in the Upper Rio Negro of Colombia and Venezuela. *J Ecol* 76:938–958.
- Salo J, Kalliola R, Häkkinen I, et al (1986) River dynamics and the diversity of Amazon lowland forest. *Nature* 322:254–258. doi: 10.1038/322254a0
- Salomão R de P, Matos A de, Rosa N de A (2002) Dinâmica do sub-bosque e do estrato arboreo de floresta tropical primária fragmentada na Amazônia oriental. *Acta Amaz* 32:387–419.
- Salomão R, Nepstad D, Vieira I (1998) Biomassaeestoque de florestas tropicais primária e secundária. In: Gascon C, Moutinho P (eds) *Floresta Amazônica: Dinâmica, Regeneração e Manejo*. pp 99–119.
- Santos J dos (1996) Análise de modelos de regressão para estimar a fitomassa da floresta tropical úmida de terra-firme da Amazônia Brasileira. Ph.D. Dissertation, Universidade Federal de Viçosa, Minas-Gerais, Brazil.

7. REFERENCES

- Santos LT dos, Magnabosco Marra D, Trumbore S, et al (2016) Windthrows increase soil carbon stocks in a Central Amazon forest. *Biogeosciences* 13:1299–1308. doi: 10.5194/bgd-12-19351-2015
- Sawada Y, Suwa R, Jindo K, et al (2015) A new 500-m resolution map of canopy height for Amazon forest using spaceborne LiDAR and cloud-free MODIS imagery. *Int J Appl Earth Obs Geoinf* 43:92–101.
- Scatena F, Moya S, Estrada C, China J (1996) The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico. *Biotropica* 28:424–440.
- Schiatti J, Martins D, Emilio T, et al (2016) Forest structure along a 600 km transect of natural disturbances and seasonality gradients in central-southern Amazonia. *J Ecol*. doi: 10.1111/1365-2745.12596
- Schupp E (1990) Annual variation in seedfall, postdispersal predation, and recruitment of a neotropical tree. *Ecology* 71:504–515.
- Schupp E, Howe H, Augspurger C, Levey D (1989) Arrival and survival in tropical treefall gaps. *Ecology* 70:562–564.
- Sheil D, Burslem DFRP (2003) Disturbing hypotheses in tropical forests. *Trends Ecol Evol* 18:18–26. doi: 10.1016/S0169-5347(02)00005-8
- Shugart HH, West DC (1980) Forest Succession Models. *Bioscience* 30:308.
- Sileshi GW (2014) A critical review of forest biomass estimation models, common mistakes and corrective measures. *For Ecol Manage* 329:237–254.
- Silva R da (2007) Alometria, estoque e dinâmica da biomassa de florestas primárias e secundárias na região de Manaus (AM). Ph.D. Dissertation, Universidade Federal do Amazonas, Brazil.
- Silva RP da, Nakamura S, Azevedo C de, et al (2003) Use of metallic dendrometers for individual diameter growth patterns of trees at Cuieiras river basin. *Acta Amaz* 33:67–84.
- Silva RP da, Santos J dos, Tribuzy ES, et al (2002) Diameter increment and growth patterns for individual tree growing in Central Amazon, Brazil. *For Ecol Manage* 166:295–301.
- Silva Dias MAF, Rutledge S, Kabat P, et al (2002) Cloud and rain processes in a biosphere-atmosphere interaction context in the Amazon Region. *J Geophys Res* 107:1–39. doi: 10.1029/2001JD000335
- Silva A, Tamashiro J, Begossi A (2007) Ethnobotany of Riverine Populations From the Rio Negro, Amazonia (Brazil). *J Ethnobot* 27:46–72.
- Silvério DV (2015) Alterações na estrutura e funcionamento de florestas transicionais da Amazônia associadas à degradação florestal e transição do uso da terra. Ph.D. Dissertation, University of Brasília (UnB), Brasília, Brazil.
- Somers B, Asner G, Tits L, Coppin P (2011) Endmember variability in Spectral Mixture Analysis: a review. *Remote Sens Environ* 115:1603–1616. doi: 10.1016/j.rse.2011.03.003
- Sousa W (1984) The Role of Disturbance in Natural Communities. *Annu Rev Ecol Syst* 15:353–391.
- Sutherland WJ, Freckleton RP, Godfray HCJ, et al (2013) Identification of 100 fundamental ecological questions. *J Ecol* 101:58–67. doi: 10.1111/1365-2745.12025
- Swaine MD, Whitmore TC (1988) On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75:81–86.
- Tan J, Jakob C, Rossow WB, Tselioudis G (2015) Increases in tropical rainfall driven by changes in frequency of organized deep convection. *Nature* 519:451–454. doi: 10.1038/nature14339
- Teixeira L, Chambers J, Silva A, et al (2007) Projeção da dinâmica da floresta natural de Terra-firme, região de Manaus-AM, com o uso da cadeia de transição probabilística de Markov. *Acta Amaz* 37:377–384.
- Telles EC, Camargo PB, Martinelli LA, et al (2003) Influence of soil texture on carbon dynamics and storage potential in tropical forest soils of Amazonia. *Global Biogeochem Cycles* 17:1–12.
- ter Steege H, Pitman NCA, Sabatier D, et al (2013) Hyperdominance in the Amazonian Tree Flora. *Science* 342:1243092–1243092. doi: 10.1126/science.1243092

7. REFERENCES

- Terborgh J, Nuñez-Iturri G, Pitman NCA, et al (2008) Tree recruitment in an empty forest. *Ecology* 89:1757–1768.
- Toledo JJ de, Magnusson W, Castilho C (2013) Competition, exogenous disturbances and senescence shape tree size distribution in tropical forest: evidence from tree mode of death in Central Amazonia. *J Veg Sci* 24:651–663.
- Toledo JJ de, Magnusson WE, Castilho C V., Nascimento HEM (2011) How much variation in tree mortality is predicted by soil and topography in Central Amazonia? *For Ecol Manage* 262:331–338. doi: 10.1016/j.foreco.2011.03.039
- Trumbore S, Brando P, Hartmann H (2015) Forest health and global change. *Science* 349:814–818. doi: 10.1126/science.aac6759
- Turner M, Baker W, Peterson C, Peet R (1998) Factors Influencing Succession: Lessons from Large, Infrequent Natural Disturbances. *Ecosystems* 1:511–523.
- Uhl C, Clark K, Dezzeno N, Maquirino P (1988) Vegetation dynamics in Amazonian treefall gaps. *Ecology* 69:751–763.
- van der Sande MT, Arets EJMM, Peña-Claros M, et al (2016) Old-growth Neotropical forests are shifting in species and trait composition. *Ecol Monogr* 86:228–243. doi: 10.1890/15-1815.1
- Vandermeer J (1996) Disturbance and neutral competition theory in rain forest dynamics. *Ecol Modell* 85:99–111. doi: 10.1016/0304-3800(94)00152-9
- Vandermeer J, la Cerda I de, Boucher D, et al (2000) Hurricane Disturbance and Tropical Tree Species Diversity. *Science* 290:788–791.
- Vandermeer J, Mallona J, Boucher D, et al (1995) Three years of ingrowth following catastrophic hurricane damage on the Caribbean coast of Nicaragua: Evidence in support of the direct regeneration hypothesis. *J Trop Ecol* 11:465–471.
- Vandermeer J (1972) Niche theory. *Annu Rev Ecol Syst* 3:107–132. doi: 10.1146/annurev.es.03.110172.000543
- Vidal E, West TAP, Putz FE (2016) Recovery of biomass and merchantable timber volumes twenty years after conventional and reduced-impact logging in Amazonian Brazil. *For Ecol Manage* 376:1–8. doi: 10.1016/j.foreco.2016.06.003
- Vieira D, Scariot A (2006) Principles of natural regeneration of tropical dry forests for restoration. *Restor Ecol* 14:11–20. doi: 10.1111/j.1526-100X.2006.00100.x
- Vieira S, de Camargo PB, Selhorst D, et al (2004) Forest structure and carbon dynamics in Amazonian tropical rain forests. *Oecologia* 140:468–479.
- Vieira S, Trumbore S, Camargo P de, et al (2005) Slow growth rates of Amazonian trees: consequences for carbon cycling. *Proc Natl Acad Sci* 102:18502–7. doi: 10.1073/pnas.0505966102
- Vitousek P, Denslow J (1986) Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. *J Ecol* 74:1167–1178.
- von Humboldt A, Bonpland A (1907) Personal narrative of travels to the equinoctial regions of America, during the years 1799-1804. George Bell & Sons, London.
- Walker L (1991) Tree damage and recovery from Hurricane Hugo in Luquillo experimental forest, Puerto Rico. *Biotropica* 23:379–385.
- Wallace AR (1889) A narrative of travels on the Amazon and Rio Negro: with an account of the native tribes, and observations of the climate, geology, and natural history of the Amazon Valley, 2nd edn. Ward, Lock and CO., London, New York, and Melbourne.
- Werth D, Avissar R (2002) The local and global effects of Amazon deforestation David. *J Geophys Res* 107:1–8. doi: 10.1029/2001JD000717
- Wirth C, Messier C, Bergeron Y, et al (2009) Old-Growth Forest Definitions: a Pragmatic View. In: Wirth C, Gleixner G, Heimann M (eds) *Old-Growth Forests: Function, Fate and Value*. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 11–33.

7. REFERENCES

- Wirth C, Schumacher J, Schulze E (2004) Generic biomass functions for Norway spruce in Central Europe - a meta-analysis approach toward prediction and uncertainty estimation. *Tree Physiol* 24:121–139.
- Wright JS (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130:1–14. doi: 10.1007/s004420100809
- Wright SJ (2005) Tropical forests in a changing environment. *Trends Ecol Evol* 20:553–560. doi: 10.1016/j.tree.2005.07.009
- Zappi DC, Ranzato Filardi FL, Leitman P, et al (2015) Growing knowledge: An overview of Seed Plant diversity in Brazil. *Rodriguesia* 66:1085–1113. doi: 10.1590/2175-7860201566411
- Zeng H, Chambers J, Negrón-Juárez R, et al (2009) Impacts of tropical cyclones on U.S. forest tree mortality and carbon flux from 1851 to 2000. *Proc Natl Acad Sci U S A* 106:7888–92. doi: 10.1073/pnas.0808914106
- Zimmerman JK, Everham EM, Waide RB, et al (1994) Responses of tree species to hurricane winds in subtropical wet forest in Puerto-Rico: Implications for tropical tree life histories. *J Ecol* 82:911–922.
- Zimmerman JK, Mitchell Aide Bt T, Rosario M, et al (1995) Effects of land management and a recent hurricane on forest structure and composition in the Luquillo Experimental Forest, Puerto Rico. *For Ecol Manage* 77:65–76. doi: 10.1016/0378-1127(95)03575-U

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8. APPENDICES**8.1. Dissertation reviewers and defense committee**

1.	Name, date of birth	Daniel Magnabosco Marra, 08 October 1982
2.	Studies	M.Sc. Tropical Forest Science (2008-2010), Instituto Nacional de Pesquisas da Amazônia, Manaus, BR B.Sc. Forestry (2001-2007), University of Brasília, Brasília, BR
3.	Dissertation	Effects of windthrows on the interaction between tree species composition, forest dynamics and carbon balance in Central Amazon
4.	Host institutions	AG Spezielle Botanik und Funktionelle Biodiversität, Institut für Biologie, Universität Leipzig, Leipzig, DE Biogeochemical Processes Department, Max Planck Institute for Biogeochemistry, Jena, DE Laboratório de Manejo Florestal, Instituto Nacional de Pesquisas da Amazônia, Manaus, BR
5.	Supervisor	Prof. Dr. Christian Wirth
	Co-supervisor	Prof. Dr. Susan Trumbore
6.	Degree	<i>Doctor rerum naturalium (Dr. rer. nat.)</i>
7.	External reviewer	1. Prof. Dr. Lourens Poorter Wageningen University Forest Ecology and Forest Management Department Droevendaalsesteeg 3, 6708PB, Wageningen lourens.poorter@wur.nl +31-317486216
	Internal reviewer	2. Prof. Dr. Christian Wirth University of Leipzig AG Spezielle Botanik und Funktionelle Biodiversität
8.	Defense committee	1. Prof. Dr. Christian Wirth (cwirth@uni-leipzig.de) (Chair) 2. Prof. Dr. Susan Trumbore (Max Planck Institute for Biogeochemistry, Jena, trumbore@bgc-jena.mpg.de) 3. PD. Dr. Alexandra Weigelt (University of Leipzig, alexandra.weigelt@uni-leipzig.de) 4. Prof. Dr. Nico Eisenhauer (German Centre for Integrative Biodiversity Research [iDiv] Halle-Jena-Leipzig, nico.eisenhauer@idiv.de) 5. Prof. Dr. Christian Wilhelm (University of Leipzig, cwilhelm@rz.uni-leipzig.de)

8. APPENDICES

8.2. Author contributions statement

Paper 1

Dissertation

Daniel Magnabosco Marra

Effects of windthrows on the interaction between tree species composition,
forest dynamics and carbon balance in Central Amazon

Author Contributions Statement

Title:	Large-scale wind disturbances promote tree diversity in a Central Amazon forest
Journal:	PLoS ONE
Year of publication:	2014
DOI:	10.1371/journal.pone.0103711
Authors:	Marra DM, Chambers JQ, Higuchi N, Trumbore SE, Ribeiro GHPM, Santos J dos, Negrón-Juárez RI, Reu B and Wirth C

Daniel Magnabosco Marra

Designed research • Collected and processed data • Analyzed data • Contributed analytic tools • Conceptualized the paper • Wrote the paper • Edited the paper • Submitted the paper

Jeffrey Q Chambers

Designed research • Wrote proposal for grant • Edited the paper

Niro Higuchi

Designed research • Wrote proposal for grant • Edited the paper

Susan E Trumbore

Designed research • Wrote proposal for grant • Conceptualized the paper • Edited the paper

Gabriel HPM Ribeiro

Collected and processed data • Contributed analytic tools • Edited the paper

Joaquim dos Santos

Designed research • Wrote proposal for grant

Robinson I Negrón-Juárez

Contributed analytic tools • Edited the paper

Björn Reu

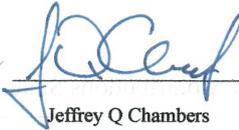
8. APPENDICES

Contributed analytic tools • Edited the paper

Christian Wirth

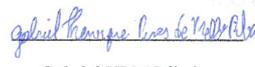
Designed research • Wrote proposal for grant • Contributed analytic tools • Conceptualized the paper • Edited the paper

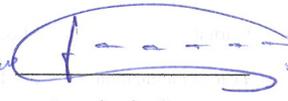

Daniel Magnabosco Marra


Jeffrey Q Chambers

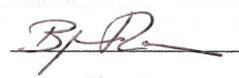

Niro Higuchi


Susan E Trumbore


Gabriel HPM Ribeiro


Joaquim dos Santos


Robinson I Negrón-Juárez


Björn Reu


Christian Wirth

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Paper 2

Dissertation

*Daniel Magnabosco Marra*Effects of windthrows on the interaction between tree species composition,
forest dynamics and carbon balance in Central Amazon**Author Contributions Statement**

Title:	Windthrows increase soil carbon stocks in a central Amazon forest
Journal:	Biogeosciences
Year of publication:	2016
DOI:	10.5194/bg-13-1299-2016
Authors:	Santos LT dos, Magnabosco Marra D, Trumbore S, Camargo PB de, Negrón-Juárez RI, Lima AJN, Ribeiro GHPM, Santos J dos and Higuchi N

Leandro Tavares dos Santos

Collected and processed data • Analyzed data • Contributed analytic tools • Conceptualized the paper • Wrote the paper

Daniel Magnabosco Marra

Designed research • Wrote proposal for grant • Analyzed data • Contributed analytic tools • Conceptualized the paper • Wrote the paper • Edited the paper • Submitted the paper

Susan Trumbore

Wrote proposal for grant • Conceptualized the paper • Edited the paper

Plínio Barbosa de Camargo

Designed research • Contributed analytic tools

Robinson I Negrón-Juárez

Contributed analytic tools • Edited the paper

Adriano José Nogueira Lima

Contributed analytic tools

Gabriel HPM Ribeiro

Contributed analytic tools • Edited the paper

Joaquim dos Santos

Designed research • Wrote proposal for grant

8. APPENDICES

Niro Higuchi

Designed research • Wrote proposal for grant • Conceptualized the paper • Edited the paper



Leandro T dos Santos



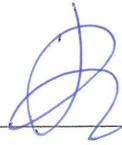
Daniel Magnabosco Marra



Susan Trumbore



Plínio B de Camargo



Robinson I Negrón-Juárez



Adriano JN Lima



Gabriel HPM Ribeiro



Joaquim dos Santos



Niro Higuchi

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Paper 3

Dissertation

Daniel Magnabosco Marra

Effects of windthrows on the interaction between tree species composition,
forest dynamics and carbon balance in Central Amazon

Author Contributions Statement

Title:	Predicting biomass of hyperdiverse and structurally complex Central Amazon forests – a virtual approach using extensive field data
Journal:	Biogeosciences
Year of publication:	2016
DOI:	10.5194/bg-13-1553-2016
Authors:	Magnabosco Marra D, Higuchi N, Trumbore SE, Ribeiro GHM, Santos J dos, Carneiro VMC, Lima AJN, Chambers JQ, Negrón- Juárez RI, Holzwarth F, Reu B and Wirth C

Daniel Magnabosco Marra

Designed research • Analyzed data • Contributed analytic tools • Conceptualized the paper •
Wrote the paper • Edited the paper • Submitted the paper

Niro Higuchi

Designed research • Wrote proposal for grant • Collected and processed data •
Conceptualized the paper

Susan E Trumbore

Conceptualized the paper • Wrote the paper • Edited the paper

Gabriel HPM Ribeiro

Contributed analytic tools • Edited the paper

Joaquim dos Santos

Designed research • Wrote proposal for grant • Collected and processed data

Vilany MC Carneiro

Collected and processed data • Contributed analytic tools

Adriano JN Lima

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Collected and processed data

Jeffrey Q Chambers

Collected and processed data

Robinson I Negrón-Juárez

Contributed analytic tools • Edited the paper

Frederic Holzwarth

Contributed analytic tools • Edited the paper

Björn Reu

Contributed analytic tools • Conceptualized the paper • Edited the paper

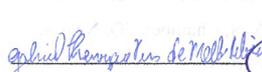
Christian Wirth

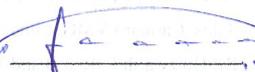
Designed research • Contributed analytic tools • Conceptualized the paper • Edited the paper


Daniel Magnabosco Marra

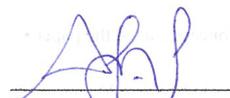

Niro Higuchi


Susan E Trumbore


Gabriel HPM Ribeiro


Joaquim dos Santos

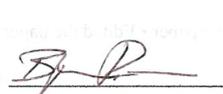

Vilany MC Carneiro


Adriano JN Lima


Jeffrey Q Chambers


Robinson I Negrón-Juárez


Frederic Holzwarth


Björn Reu


Christian Wirth

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Paper 4

Dissertation

Daniel Magnabosco Marra

Effects of windthrows on the interaction between tree species composition,
forest dynamics and carbon balance in Central Amazon

Author Contributions Statement

Title:	Functional diversity enhances biomass resilience of Amazon forests to windthrows
Journal:	To be submitted to PNAS as 'Research Reports'
Year of publication:	
DOI:	
Authors:	Magnabosco Marra D, Trumbore SE, Higuchi N, Ribeiro GHPM, Santos J dos, Carneiro VMC, Negrón-Juárez RI, Chambers JQ and Wirth C

Daniel Magnabosco Marra

Designed research • Wrote proposal for grant • Collected and processed data • Analyzed data
• Contributed analytic tools • Conceptualized the paper • Wrote the paper • Edited the paper

Susan E Trumbore

Designed research • Wrote proposal for grant • Conceptualized the paper • Edited the paper

Niro Higuchi

Designed research • Wrote proposal for grant

Gabriel HPM Ribeiro

Designed research • Collected and processed data • Contributed analytic tools

Joaquim dos Santos

Designed research • Wrote proposal for grant

Vilany MC Carneiro

Contributed analytic tools

Robinson I Negrón-Juárez

Designed research • Contributed analytic tools

*Note that the title of this paper and intended journal for submission have been modified

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Jeffrey Q Chambers

Designed research • Wrote proposal for grant

Christian Wirth

Designed research • Wrote proposal for grant • Conceptualized the paper • Edited the paper


Daniel Magnabosco Marra

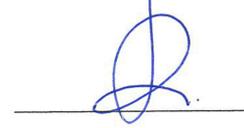

Susan E Trumbore


Niro Higuchi


Gabriel HPM Ribeiro


Joaquim dos Santos


Vilany MC Carneiro


Robinson I Negrón-Juárez


Jeffrey Q Chambers


Christian Wirth

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8.3. Topic-related publications/activities*Topic-related publications contributed within the doctorate period*

Negrón-Juárez RI, Holm JA, **Magnabosco Marra D**, Rifai SW, Riley WJ, Chambers JQ, Koven CD, Knox RG, McGroddy ME, Di Vittorio AV, Urquiza-Munoz JD, Tello-Espinoza R, Alegria-Munoz W, Ribeiro GHPM, Higuchi N (2016): Vulnerability of Amazon forests to storm-driven tree mortality. *Science Advances* (in review).

Ribeiro GHPM, Chambers JQ, Peterson CJ, Trumbore SE, **Magnabosco Marra D**, Wirth C, Cannon JB, Negrón-Juárez RI, Lima AJN, de Paula EVC, Santos J dos, Higuchi N (2016): Mechanical vulnerability of Central Amazon tree species to windthrow in convective storms. *Forest Ecology and Management* (in review).

Marra DM, Pereira BSA, Fagg CW and Felfili JM (2014): Trees and environmental variables influence the natural regeneration of a seasonally dry tropical forest in Central Brazil. *Neotropical Biology and Conservation*, 9(2), 62-77.

Ribeiro GHPM, Suwa R, **Marra DM**, Lima AJN, Kajimoto T, Ishizuka M and Higuchi N (2014): Allometry for juvenile trees in an Amazonian forest after wind disturbance. *Japan Agricultural Research Quarterly*, 48(2), 213-219.

Chambers JQ, Negrón-Juárez RI, **Marra DM**, Di Vittorio A, Tews J, Roberts D, Ribeiro GHPM, Trumbore S and Higuchi N (2013): The steady-state mosaic of disturbance and succession across an old-growth Central Amazon forest landscape. *P. Natl. Acad. Sci. USA*, 110, 3949-3954.

Menger JS, **Marra DM** and Salimon, CI (2013) Forest management effects on the abundance and species composition of ferns in South West of Brazilian Amazon. *Neotropical Biology and Conservation*, 8(1), 25-30.

Silva RP, Souza CAS, Amaral MRM, Carneiro VM, Barros PC, **Marra DM**, Santos J dos and Higuchi N (2012): Árvore - crescimento, desenvolvimento e sua identificação, p. 71-99, In: Higuchi MIG and Higuchi N (org.) *A floresta amazônica e suas múltiplas dimensões: uma proposta de educação ambiental*. 2ed., Manaus, Brasil, 424p. Available at: https://www.researchgate.net/publication/294873422_Arvore_crescimento_desenvolvimento_e_identificacao, last access: 10.03.2016.

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Negrón-Juárez RI, Chambers JQ, **Marra DM**, Ribeiro GHPM, Rifai SW, Higuchi N and Roberts D (2011): Detection of subpixel tree fall gaps with Landsat imagery in Central Amazon forests. *Remote Sensing of Environment*, 115(12), 3322-3328.

Additional topic related publications

Negrón-Juárez RI, Chambers JQ, Guimarães G, Zeng H, Raupp CFM, **Marra DM**, Ribeiro GHPM, Saatchi SS, Nelson BW and Higuchi N (2010): Widespread Amazon forest tree mortality from a single cross-basin squall line event. *Geophysical Research Letters*, 37, L16701.

Chambers JQ, Negrón-Juárez RI, Hurtt GC, **Marra DM** and Higuchi N (2009): Lack of intermediate-scale disturbance data prevents robust extrapolation of plot-level tree mortality rates for old-growth tropical forests. *Ecology Letters*, 12, E22-E25.

Grant

Succession after Windthrows (SAWI). Project funded by the *Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq)*, Brazil, Chamada Universal (MCTI/CNPq 14/2012), No. 473357/2012-7, 2012-2015. Budget: R\$120,000.

Talks and lectures

Magnabosco Marra D et al. (Jun/2016): Windthrows affect biomass stocks and balance in Central Amazon forests. *53rd Annual Meeting of the Association for Tropical Biology and Conservation (ATBC)*, Montpellier, France.

Magnabosco Marra D et al. (Jul/2015): Predicting biomass of hyperdiverse and structurally complex Central Amazon forests – a virtual approach using extensive field data. *52nd Annual Meeting of the Association for Tropical Biology and Conservation (ATBC)*, Honolulu, Hawaii, USA.

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Magnabosco Marra D et al. (Sep/2014): Large wind-throw events affect biomass dynamics of Central Amazon forests. *44th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland (GfÖ), Hildesheim, Germany.*

Magnabosco Marra D et al. (Jul/2014): The effects of large-scale wind disturbances on forest structure and species composition in Central Amazon. *51st Annual Meeting of the Association for Tropical Biology and Conservation (ATBC), Cairns, Australia.*

Magnabosco Marra D et al. (Mar/2014): Large-scale wind disturbances affect forest structure and species composition in the Central Amazon. *1st PhD-Conference on Earth System Science, Max Planck Institute for Biogeochemistry, Jena, Germany.*

Magnabosco Marra D (Jun/2013 and 2014): Tropical forest dynamics. Tropical Forest Ecology Module, M.Sc. Forest Sciences, *Albert-Ludwigs University Freiburg, Germany.*

Magnabosco Marra D (Jun/2013): Wind-throw disturbance affects structure and species composition of a Central Amazon forest. Tropical Forest Ecology Module, M.Sc. Forest Sciences, *Albert-Ludwigs University Freiburg, Germany.*

Magnabosco Marra D (Jul/2011-2014): Dendrology and identification of Amazon tree species. *Curso Noções Básicas sobre Manejo Florestal, Laboratório de Manejo Florestal, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil.*

Posters

Magnabosco Marra D, Trumbore SE, Chambers JQ, Higuchi N, Ribeiro GHPM, Negrón-Juárez RI, Holzwarth F and Wirth C (2015): Functional diversity enhances resilience of wind-disturbed Amazon forests. *iDiv Annual Conference, Leipzig, Germany.*

Santos LT dos, ***Magnabosco Marra D**, Camargo PB de, Trumbore SE, Ribeiro GHPM, Chambers JQ, Santos J dos and Higuchi N (2015): Large-scale wind disturbances change soil attributes in a Central Amazon *terra firme* forest. *52nd Annual Meeting of the Association for Tropical Biology and Conservation (ATBC), Honolulu, USA.*

*Presenter

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Magnabosco Marra D, Pereira BAS, Fagg CW and Felfili JM (2014): The natural regeneration in a seasonally dry tropical forest on limestone outcrops. *51st Annual Meeting of the Association for Tropical Biology and Conservation (ATBC)*, Cairns, Australia.

Interview

Magnabosco Marra D (2011): Amazônia e o ano da floresta. *Ciência para todos*, 7(3), 28-33. Available at: https://www.inpa.gov.br/arquivos/revistas/revista_ciencia_para_todos_n7-2.pdf, last access: 8 March 2016.

Botanical collection

During the execution of the Succession After Windthrows (SAWI) project, I collected and identified botanical samples from all the *ca.* 8,000 trees recorded in the 344 blowdowns subplots I monitored between 2011 and 2015. In total, I prepared *ca.* 2,100 botanical exsiccates, which were incorporated to the collection of the herbarium of the IFAM, Manaus, Brazil. This collection is currently being used in different studies within the SAWI project and will support future research in different topics.

Field campaigns

Jun/2015: *Central Amazon, Brazil*. Field campaign undertaken within the projects SAWI (PI: Joaquim dos Santos) and TACAPE (PI: Susan E. Trumbore), funded by the Brazilian Council for Scientific and Technological Development (CNPq), the Biogeochemistry Department from the Max Planck Institute for Biogeochemistry (Head: Susan E. Trumbore) and the Functional Biogeography Group from the Max Planck Institute for Biogeochemistry (Head: Christian Wirth). Team: Daniel Magnabosco Marra, Gabriel H.P.M. Ribeiro, Frank A. dos Santos and Ivan C.A. dos Santos.

Jul-Sep/2014: *Central Amazon, Brazil*. Field campaign undertaken within the projects SAWI (PI: Joaquim dos Santos) and the TACAPE (PI: Susan E. Trumbore), funded by the Brazilian Council for Scientific and Technological Development (CNPq), the Biogeochemistry Department from the Max Planck Institute for Biogeochemistry (Head: Susan E. Trumbore)

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and the Functional Biogeography Group from the Max Planck Institute for Biogeochemistry (Head: Christian Wirth). Team: Daniel Magnabosco Marra, Gabriel H.P.M. Ribeiro, Farcinilson M. Araújo and Fabiano Emmert.

Jul-Nov/2013: *Central Amazon, Brazil*. Field campaign undertaken within the projects SAWI (PI: Joaquim dos Santos) and the TACAPE (PI: Susan E. Trumbore), funded by the Brazilian Council for Scientific and Technological Development (CNPq), the Biogeochemistry Department from the Max Planck Institute for Biogeochemistry (Head: Susan E Trumbore) and the Functional Biogeography Group from the Max Planck Institute for Biogeochemistry (Head: Christian Wirth). Team: Daniel Magnabosco Marra, Alberto F. Neves, Izaías G. de Souza, Sidnei L. Pereira and Gabriel H.P.M. Ribeiro.

Apr/2013: *Finland*. Field campaign undertaken within the project Functional Significance of Forest Biodiversity (FunDivEUROPE) (PI: Christian Wirth and Christian Messier). Team: Ian Seiferling and Daniel Magnabosco Marra.

Jul-Oct/2012: *Central Amazon, Brazil*. Field campaign undertaken within the project TACAPE (PI: Susan E. Trumbore) and the Brazilian Institute for Science and Technology (INCT) Madeiras da Amazônia (PI: Niro Higuchi), funded by the Biogeochemistry Department from the Max Planck Institute for Biogeochemistry (Head: Susan E. Trumbore), the Brazilian Council for Scientific and Technological Development (CNPq) and the Functional Biogeography Group from the Max Planck Institute for Biogeochemistry (Head: Christian Wirth). Team: Daniel Magnabosco Marra, Alberto F. Neves, Izaías G. de Souza and Gabriel H.P.M. Ribeiro.

Apr/2012: *Poland and Romania*. Field campaign undertaken within the project Functional Significance of Forest Biodiversity (FunDivEUROPE) (PI: Christian Wirth and Christian Messier). Team: Ian Seiferling and Daniel Magnabosco Marra.

April/2012: *Germany*, Nationalpark Hainich. Field campaign undertaken within the Biodiversity Exploratories Project - FUNWood 2 (PI: Jürgen Bauhus), funded by the Deutsche Forschungsgemeinschaft (DFG). Team: Peter Otto, Kristin Baber and Daniel Magnabosco Marra.

Jun-Oct/2011: *Central Amazon, Brazil*. Field campaign undertaken within the National Aeronautics and Space Administration (NASA) Biodiversity Project (PI: Jeffrey Q.

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Chambers), funded by the NASA, the Biogeochemistry Department from the Max Planck Institute for Biogeochemistry (Head: Susan E. Trumbore), the Brazilian Council for Scientific and Technological Development (CNPq), and the Functional Biogeography Group from the Max Planck Institute for Biogeochemistry (Head: Christian Wirth). Team: Daniel Magnabosco Marra, Gabriel H.P.M. Ribeiro, Farcinilson M. Araújo, Alberto F. Neves and Izaias G. de Souza.

Co-supervision/mentoring

Ramiris Morais (2014 – to date): Tree biomass and nutrients in a mosaic of fragmented landscapes, Bahia, Brazil. *Ph.D. Dissertation*, Universidade Estadual de Santa Cruz, Bahia, Brazil.

Leandro Tavares dos Santos (2012 -2014): Estoque de carbono no solo em área de blowdown na floresta tropical úmida da Amazônia Central. *M.Sc. Dissertation*, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil.

Klinger Renasson Pereira Leitão (2013 -2015): Dinâmica da população de *Scleronema micranthum* Ducke em uma floresta de terra firme, Manaus - Amazonas. *M.Sc. Dissertation*, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil.

Reviewer for journals

Journal of Vegetation Science (since Oct/2014)

Neotropical Biology and Conservation (since Dez/2014)

Oecologia (since Mar/2015)

FLORESTA (since Nov/2015)

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International Max Planck Research School for Global Biogeochemical Cycles (IMPRS-gBGC) certificate**Certificate Supplement****Mr. Daniel Magnabosco Marra**

born on October 08, 1982 in Uberaba, Brazil

At the International Max Planck Research School high potential students have the opportunity to work on their Ph.D. theses in the framework of a structured programme providing excellent research conditions.

He carried out (amongst others) the following curricular activities in the respective categories and earned in total 44.4 credit points (1 CP = 25-30 hours of work ≈ 5-day block course).

	CP
Courses related to global biogeochemical cycles - Biogeochemical cycles in the earth system - an overview - Biodiversity and Ecosystem Function - Terrestrial Biosphere & Ecoystems	3.0
Transferable skill courses - Data visualisation - Scientific Writing - Structural Equation Modelling (SEM) in the context of the Jena Experiment	1.2
Skill & elective courses - R course: The basics - An introduction to data analysis in R - Introduction to LaTeX - Tanguro workshop - Workshop on installation of time-lapse camera units and acquisition of in-situ imagery data using 'side-view' and 'snap-shot' technics - Workshop on Succession After Windthrows [SAWI], Forest Management Lab from the National Institute of Amazonian Research, Manaus, Brazil	3.7
Outreach activities - Research stay at Lawrence Berkeley National Laboratory (Oct-Dec 2011), Earth and Sciences Division, Climate Science Department, Berkeley, CA, USA, PhD Jeffrey Quintin Chambers - Oral presentation at the PhD Conference on Earth System Science 2014, Jena, Germany - Poster presentation at the 49th ATBC Meeting, 2013. Bonito, Brazil - Oral and poster presentation at the 51st ATBC Meeting, 2014. Cairns, Australia - Oral presentation at the 44th GfÖ Annual Meeting, 2014. Hildesheim, Germany - Oral and poster presentation at the 52nd ATBC Meeting, 2015. Honolulu, US - Oral presentation at the 53rd ATBC Meeting, 2016, Montpellier, France - Oral presentation at the iDiv Conference, 2015. Leipzig, Germany - Oral presentation at the I Latin American Meeting of Environment Engineer, 2011. Quibdó, Colombia - Oral presentation at the 101st ESA Annual Meeting, 2016. Fort Lauderdale, US	10.5
Other scientific activities - Succession after wind-disturbance (SAWI). Funded by the Brazilian Council for Scientific and Technological Development (CNPq), Brazil, Chamada Universal - Teaching of the modules 'Tropical Forest Dynamics' and 'Wind-throw disturbance affects structure and species composition of a Central Amazon forest', Tropical Forest Ecology, Albert-Ludwig University Freiburg - Teaching of the course 'Dendrology and identification of Amazon tree species', Forest Management Department of the National Institute of Amazonian Research, Manaus, Brazil	13.0

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8.4. Curriculum vitae

 Daniel Magnabosco Marra

- Birth date and place October 8, 1982, Uberaba, Brazil
 Address Blümnerstraße 23, 04229, Leipzig, DE
 Email daniel.marra@uni-leipzig.de
 dmarra@bgc-jena.mpg.de
 Phone 0151 22077370
 Since 2016 Postdoctoral research fellow
 Biogeochemical Processes Department, Max Planck Institute for
 Biogeochemistry, Hans-Knöll-Straße 10, 07745, Jena, DE
 AG Spezielle Botanik und Funktionelle Biodiversität, Universität Leipzig,
 Johannisallee 21, 04103, Leipzig, DE
 PIs: Prof. Dr. Susan Trumbore and Prof. Dr. Christian Wirth
 2011 Research visit
 Climate Science Department, Lawrence Berkeley National Laboratory,
 Berkeley, US
 PI: Dr. Jeffrey Quintin Chambers
 2011-2016 Doctorate-candidate (*Dr. rer. nat.*)
 Universität Leipzig, Fakultät für Biowissenschaften, Pharmazie und
 Psychologie, Leipzig, DE
 Student fellowship at the International Max Planck Research School for Global
 Biogeochemical Cycles (IMPRS-gBGC), Max Planck Institute for
 Biogeochemistry, Jena, DE
 Supervisors: Prof. Dr. Christian Wirth and Prof. Dr. Susan Trumbore
 2010-2011 Research assistant
 University of Tulane, New Orleans, US
 PI: Dr. Jeffrey Quintin Chambers
 Since 2010 Research collaborator
 Laboratório de Manejo Florestal (LMF), Instituto Nacional de Pesquisas da
 Amazônia, Manaus, Brazil
 PI: Prof. Dr. Niro Higuchi
 2008-2010 Master of Science in Tropical Forest Sciences
 Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil
 Dissertation: *Forest succession over a blowdown area in Central Amazon*
 (approved with distinction)
 Supervisors: Prof. Dr. Joaquim dos Santos and Prof. Dr. Niro Higuch
 2004 Visitor student

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Facultat Biologia, Ciències Ambientals, Universitat de Barcelona, Barcelona,
Spain

2001-2007 Bachelor of Science in Forestry

Faculdade de Tecnologia, Universidade de Brasília, Brazil

Monograph: *Natural regeneration and seed bank in a tropical dry forest*
(approved with distinction)

Supervisor: Prof. Dr. Maria Jeanine Felfili
