

Selection and adaptation in human migration

Adrian Viliami Bell^{1,2} 

¹Department of Anthropology, University of Utah, Salt Lake City, Utah, USA

²Department of Human Behavior, Ecology and Culture, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

Correspondence

Adrian Viliami Bell, Department of Anthropology, University of Utah, Salt Lake City, UT, USA.

Email: adrian.bell@anthro.utah.edu

Abstract

This article reviews the ways migration shapes human biology. This includes the physiological and genetic, but also socio-cultural aspects such as organization, behavior, and culture. Across disciplines I highlight the multiple levels of cultural and genetic selection whereby individuals and groups adapt to pressures along a migration timeline: the origin, transit, and destination. Generally, the evidence suggests that selective pressures and adaptations occur at the individual, family, and community levels. Consequently, across levels there are negotiations, interactions, and feedbacks that shape migration outcomes and the trajectory of evolutionary change. The rise and persistence of migration-relevant adaptations emerges as a central question, including the maintenance of cumulative culture adaptations, the persistence of “cultures of migration,” as well as the individual-level physiological and cognitive adaptations applied to successful transit and settlement in novel environments.

KEYWORDS

culture, evolution, human biology, migration

1 | INTRODUCTION

Accounts of *Homo sapiens* after their appearance are essentially migratory. Out of Africa and the subsequent expansions across Arabia, Eurasia, the Pacific, and the Americas characterize the early human experience. The late Holocene expansions enabled by domesticates leave cultural and genetic legacies that persist to the present, while the more recent European colonial period from the 15th century has shaped the genetic, social and political landscape lived today.^{1–3} Migration often causes greater local demographic change than birth and death processes, and thus can exert tremendous change especially when involving distinct regions. While present in most evolutionary mechanisms and models, if placed into greater focus then fundamental features and novel questions about genetic and cultural variation will be made clear.

1.1 | The evolutionary forces around migration

Migration is individual or group movement across a boundary. Boundaries and the spatio-temporal scale of movement are defined

by the trait of interest. Food preferences may involve both ecological and sociocultural boundaries, while language will primarily involve the latter. Genetic variation is likewise influenced by ecological gradients and population structure that leads to admixture events. Thus, salient boundaries incorporate combinations of ethnolinguistic, demographic, ecological, and political features. In cultural anthropology most work centers around ethnolinguistic traits or traits closely aligned with ethnic groups, thus sociocultural boundaries along generational timescales are often the focus of study.⁴ Interest in the political economy, labor markets, and policy place national boundaries on legislative timescales as the primary focus.⁵ Because selective pressures on cultural and genetic variation may operate at political, ethnic, ecological and other dimensions, a variety of boundaries are described in this review.

Migration introduces several mechanisms that influence genetic and cultural evolution. These mechanisms operate along three fundamental demographic components of migration: the origin, transit, and the destination (Figure 1). To identify what is evolving or under selective pressure, we can assume there are costs and benefits to migration, and that selection has shaped ways to mitigate against the costs and enable the benefits. Whether to shape decision-making on

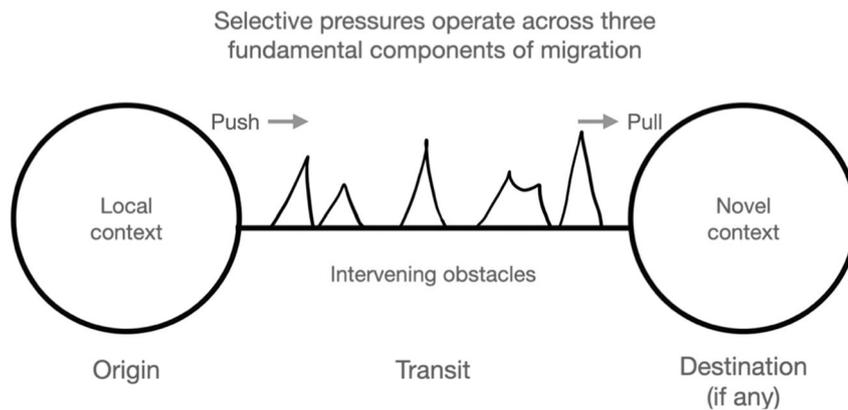


FIGURE 1 Three contexts within which selection may operate on genetic and cultural variation. *Local context* includes ecological, economic, social and cultural circumstances centered around the origin that affect the probability of migration events. These may be labeled as *push* factors. *Novel context* includes features of the destination, including levels of uncertainty. These may be labeled as *pull* factors. Migration without destination, or exploration, is primarily driven by the origin. *Transit* includes risks that may be mitigated by technology and strategy. Adapted from Lee.⁶

whether to migrate, reduce risk during travel, or access resources after arrival, there is assumed enough genetic and/or cultural mechanisms that generate variation whereby selection can act on to enable and promote mitigation measures. Along this timeline we can ask how the responses to conditions at the origin, destination, and the intervening obstacles are shaped by inherited traits (Figure 1).

Some mechanisms are especially relevant to migration. As migration often involves crossing environmental boundaries, key questions revolve around both genetic and cultural responses to contrasting contexts. In general, the response to environmental variation is flexibility,⁷ and thus migration encourages plasticity to navigate the complexities of migration before, during, and after arrival.^{8,9} A genetic basis for plasticity via DNA methylation enables generational feedbacks,¹⁰ such that contrasting environmental states—such as might be experienced between mother and fetus¹¹—will cause epigenetic mechanisms to respond to selective pressures around migration.¹² This short-term plasticity occurs within somatic responses to temporally longer selective environmental pressures such as climate.¹³ Migration also introduces socio-cultural gradients and hence pressures to navigate intergroup contact and the acquisition of cultural knowledge through learning. Cultural evolutionary mechanisms may become the dominant form whereby individuals can quickly adapt to novel environments,¹⁴ including social and individual learning strategies that generate innovations through “guided variation,”¹⁵ that make use of social cues and cultural content,¹⁶ and that account for demographic complexity common to migration^{17,18} and its impacts on cultural adaptation.^{19–21}

As migration involves both selective pressures on individual and group traits, I frame the evolutionary forces within multilevel selection theory. This allows us to consider the genetic and cultural timescales relevant to both levels, and integrate the deeper history of directed change over time along with shorter timescales of individual and group action. In Box 1 I provide a basic mathematical representation of two levels of selection, asking how the prevalence of migration may change depending on a cost-benefit calculation at each level. Note that in additive fashion it shows the interplay between individual and group adaptation, with the timescales of evolution implicit in the fitness function. Not every scenario requires an appeal to group-level selection, as the

illustration states, yet in many cases below the negotiation between the two is inescapable.

This formulation also may be used to conceptualize evolutionary mechanisms that modify the individual and group-level costs and benefits to migration. For example, selective pressures around migration may involve the opposing factors of energy, risk, and acquisition. The former two factors act as constraints on individuals seeking to gain access to food, mates, materials, and favorable social circumstances. As I review below, genetic and cultural processes reduce energetic costs and risk and aid resource acquisition thus increasing the scope for migration to be favored. Sometimes individuals and groups appear to have deliberate strategies that alter these cost-benefit parameters. Uncertainties along the migration timeline also means individuals address contingencies by maintaining a set of possible actions. We can imagine these strategies and actions as being the objects of cultural inheritance as they spread or decline in a population at each particular time point—before, during, or after migration.

Finally, the temporal dynamics for some traits described in this review are inherently complex, and it is important to distinguish between selection *for* migration-relevant traits and selection *of* migration-related traits, taking Sober's²² distinction. Other selective forces may be favoring or not, for example, efficient mobility, and the net effects of migration on the focal trait may be small. During migration events the advantages to a trait—represented by parameters k and h in Box 1—may be driving selection, while in-between migration events the background fitness of a trait may dictate the direction of selection. This occurs when the background fitness covaries with the expression of the focal trait, in which case we add $E[\text{Cov}(w_0, x_{ig})]$ to the migration terms in Equation (1). It is also the case that background fitness may always drive selection. In either scenario, selection of migration-related traits remains despite not dictating the outcome because k and h are not zero. This complexity begs further investigation into the temporal nature of migration events, such as when movement across boundaries is common, and inquiry into the strength of selection, such as when there are strong environmental or social bottlenecks across the migration timeline (Figure 1). By isolating and decomposing the pressures specifically around migration, we may explore the scope of selection and motivate inquiry into the nature of migration events.

BOX 1. Selection for migration at multiple levels

Applying a mathematical expression of multilevel selection by Price²³ can show how individual and group-level processes influence migration. Let's define x_{ig} as the probability of individual i in group g migrating to a destination, and x_g is the average propensity to migrate in group g . For individuals there is an associated fitness value to migration w_{ig} as well as a group fitness value w_g . This yields the equation for the change in migration rate as a function of covariance terms at the group and individual level:

$$\bar{w} \Delta x = \text{Cov}(w_g, x_g) + E[\text{Cov}(w_{ig}, x_{ig})].$$

We can break down fitness in terms of individual and group-level costs and benefits. For any individual with behavior x_{ig} , there is a baseline individual net benefit-cost value of k to an individual, where k can take on negative or positive values. An individual may also experience benefits or costs from interacting with co-migrants with value h . There may be group-level benefits or costs to having more migrants in a group, which we represent with b . Assuming unbiased (random) interactions the individual fitness in the population becomes $w_{ig} = w_0 + x_{ig} k + x_{ig} x_g h$. Lets assume that group-level benefit/cost changes linearly with more migrating individuals in the group, or $w_g = b x_g$. We can insert these expressions into the two covariance expressions and simplify using properties of covariance:

$$\text{Cov}(w_g, x_g) = \text{Cov}(b x_g, x_g) = b \text{Var}(x_g),$$

$$E[\text{Cov}(w_{ig}, x_{ig})] = E[\text{Cov}(w_0 + x_{ig} k + x_{ig} x_g h, x_{ig})] \\ = k E[\text{Var}(x_{ig})] + h E[x_g \text{Var}(x_{ig})].$$

After we substitute these expressions into the Price equation we ask when migration is favored by setting $\Delta x > 0$, yielding the condition:

$$b \text{Var}(x_g) + k E[\text{Var}(x_{ig})] + h E[x_g \text{Var}(x_{ig})] > 0. \quad (1)$$

There are two components to this condition for migration to evolve and persist. The first term to the left is selection among groups and the second and third terms are the individual-level costs and benefits. If the individual-benefit parameters k and h are both positive, then the condition is always satisfied as variances are by definition greater than or equal to zero. No group-level process required. However, if there are any individual-level net costs either alone ($k < 0$) or in a co-migrant interaction ($h < 0$), then the condition depends on whether the group-benefits to migration are high enough to offset any costs at the individual level. Group-level processes are required in this circumstance. Though not explicitly described here, selection or exogenous environmental factors may also change the values of b , k , and h making migration more or less favored.

The review of evidence follows the three contexts of migration outlined in Figure 1—the origin, transit, and destination. I review how each context has shaped genetic and cultural evolution, noting the emphases of the diverse literatures, for example, genetic studies have more to say about the pressures around transit. As the focus is on the biological evolution of humans—where human biology includes cognition, behavior, and culture—the level of analysis flows between individual and group-level adaptations.

2 | ORIGIN

Migration is rarely a benign activity. Sometimes there are substantial sunk costs, such as leaving socioeconomic resources and potentially becoming objects of resentment and envy in their origin communities.²⁴ The destination may be unknown and even if it is, the road could be dangerous and the reception unwelcoming. However, migration may also be expected, even preferred in a society to meet cultural obligations.²⁵ Resources to obtain marriage partners, build a home, or fund next-generation activities may rely heavily on migration or a migrant network. Given the gravity around migration outcomes, individuals are likely to have mitigating strategies around the information about migration and the context of leaving. I view the evaluation of information as the central problem that individuals face when deciding to migrate or how to go about it.

2.1 | Knowledge

In rural Thailand, Garip²⁶ observes that the immediate benefit to migrating to the city depended on the initial resource level of the household or individual. It is detrimental if migration leads to loss of human capital among land-rich families who need workers and managers, while resource-poor families lacking land have greater marginal gains. However, continued migration may still yield a net beneficial act, even for resource-rich families, as one type of resource—agricultural yields—may be transferred to a more profitable resource across generations. Further, in general most migrants do not know whether food, medicine, social norms, finding mates, or access to resources will be more challenging to confront. This uncertainty is inherent in the migration narrative and can only be addressed with the transmission of knowledge and know-how. How do rural Thai and other groups confront the complexity of migration outcomes? How is gaining knowledge to inform decisions achieved?

The amount of information held by individuals is one of the more highly varied dimensions in models of migration flows.²⁷ Since uncertainties increase with greater effective distance from home, individuals and groups pay special attention to the types of information available. This information may be divided into one of the more salient metaphors around the flow of migration: knowledge that *pulls* and knowledge that *pushes*. Solely considering the latter allows us to discuss migration without a destination (exploration) and also consider local context of origin. The former involves features of a specific destination. In both cases, the

overarching questions is how potential migrants respond to prior information.

2.1.1 | Knowledge that pushes

The local context contains information that may lead to individuals or groups migrating from an origin. While extreme circumstances such as violent conflict or resource collapse clearly predict emigration, more often individuals and groups use combinations of sociocultural and environmental information to make decisions. Given the presence of an information field, what may evolve are strategies to access information, make inferences, and build social norms that improve the outcomes of migration.

Consider the transmission of information between a potential migrant and an experienced migrant. Often migration leads to resource acquisition that is displayed in the origin community by the return migrant or indirectly through remittances. For this reason, being able to migrate is a metaphor of “power and advancement,”²⁸ because it symbolizes the expectation of significant wealth gains. The migrant's gains stimulate comparisons among nonmigrant and migrant neighbors and further causal reasoning around access to goods. This oft-cited mechanism, called relative wealth deprivation, is thought to heavily influence migration decisions even in places where absolute wealth has not changed.²⁹ By seeing the resource gains of others, or hear from them postmigration even from afar, then migration is inferred as a direct route to greater prosperity.

There are good theoretical reasons as to why individuals should pay attention to the behaviors of others who are successful. When environments are fairly stable copying successful others is a shortcut to making correct inferences on expected gains from an activity.¹⁵ Even when environments do shift occasionally, learning from others effectively leads individuals to a best response.³⁰ Thus the strategy “migrate when wealthier others migrate” will lead to broader migration waves as returnees show significant wealth gains.

However, success-biased imitation has its limitations, primarily from false signals. Individuals in the homeland often perceive the gains but not the costs of living abroad experienced by their migrant family members. Another common modern observation is that migrants give unrepresentative reports of well-being and resource acquisition while abroad or when returning home. Emotions of shame and embarrassment among migrants who did not meet expectations lead to false signals that accumulate into biased expectations of migration outcomes. This is a problem when migration actually leads to fewer resource gains than staying. If common enough then the relative deprivation mechanism is inherently misleading. Do potential migrants correct for this bias by considering the wealth signaling bias, or does this inevitably lead to accumulated bad migration decisions? A quick literature search yields no work on whether potential migrants correct for biases in the signals of current or return migrants.

As potential migrants evaluate options the calculus is often embedded within a larger social context that itself evolved through a

response to a history of migration. Cultural norms respond to migration that may enable its continuation. The concept *culture of migration* develops this idea, highlighting how areas of material culture, marriage, schooling, learning, and other domains of life celebrate and encourage migration.³¹ Whether through an incremental range expansion, individual-level emigration, or complete translocation of a community, cultural norms and expectations evolve to reflect success derived from movement.

Syed Ali²⁵ documents a culture of migration in Hyderabad, India where labor migration to prominent destinations increases social status significantly, such that the returning migrant laborer may be viewed as equivalent to a local medical doctor. Over time the concept of the “migrant-hero” arose as remittances and wealth acquired overseas became the definer of high status at the expense of an ascribed status derived from a prestigious family lineage. This remained the case for Ali's study even as Hyderabad experienced an economic boom in professional-level occupations. More generally, as movement often happens at the borders of life stages it becomes a part of a cultural life history, such as a transition to adulthood.³² As globalization adds new stages of life—for example, formal schooling and wage labor—for some communities, migration becomes the more pervasive stage of all.

However, what constitutes a culture of migration can vary widely since they reflect the socioecology of the migration process. Kandel and Massey³¹ discuss how attitudes toward US migration among school children from the Mexican state of Zacatecas is shaped by a family's prior experience with migration. This effect appears stronger than community-level migration rates, and potential migrants have reduced local educational aspirations. Contrast this with the Hyderabad study discussed above where gaining education and specialized training are prime strategies for prospective migrants. These differences reflect the means to access a destination. The US-Mexico land border presents the major obstacle to migration in contrast to cross-continent labor migration from Hyderabad, motivating potential migrants in the latter case to specialize in transferable skills.

This is one of the more unexpected outcomes of continued migration, as demands for transferable skills has led to the build-up of language education, specialized training to fill specific demands in the migrant labor market, and expectations at all levels from the individual and family to bring earnings back home.^{33,34} Thus the *brain drain* commonly observed as the emigration of the best and the brightest is sometimes accompanied by a buildup of educational endeavors at home or through return migration, or *brain gain*.³⁵ In other words, formal school or training is developed to prepare individuals for successful migration.

2.1.2 | Knowledge that pulls

Centered around the features of the destination, knowledge of this type ranges from error prone rumor to the calculated divulgences of return migrants, guides, traders or recruiters. Here, the primary

challenge for the potential migrant is calibrating the uncertainty about the destination, given biased transmission of information sometimes as the result of conflicts of interest between transmitters and receivers. Other mechanisms are less intentional, such as *information cascades* that may lead to migrants clustering in locations with other co-ethnics despite increasing costs with higher co-ethnic density.³⁶ The contemporary media representation of potential destinations shares the same challenges of information shared through an in-person network. The reliability of information is tied to shared interests between the transmitter and receiver, thus while the manifestation of knowledge can be qualitatively different, the same challenges of uncertainty apply.

The information challenge can be summed-up by a short story by the famed Samoan writer Albert Wendt.³⁷ A young Samoan man migrates to New Zealand and subsequently returns with a suitcase full of European clothes and other adornments. The daily opening up of the suitcase was an impressive affair among his family and friends, and gave enviable status to the young man. One day, however, the suitcase disappeared and the young man “crumpled on to the floor and wept bitterly, all the time saying, ‘What am I going to do now? I've lost everything!’....” In response, the young man's benefactor proclaimed,

From now on, you're just like us; you've got to pay your own way. There're no mosquitoes in this family!

Unable and unwilling to return to the labors of life before migration, the young man becomes nearly destitute.

Wendt's story humanizes the inferential problem. Given the fragility of the young man's wealth, we may conclude that the status advantages brought by migration were highly exaggerated. Further, the suitcase adds an element of mystery and uncertainty about the origins of foreign wealth. What is constant throughout the story is the young man's desire to signal status and adopt the higher life expectations consistent with his migration experience, however misleading it might be to the local observer.

On the other hand, accurate information may be embodied in others when there is enough shared common interest between individuals. Migration brokers are those that act as intermediaries between locations, resolve conflicts of interest, and enable a migrant into a favorable position in the destination. Pertinent ethnographic examples include *kijaji*, religious teachers in Indonesia that bridge local and national interests,³⁸ middlemen “ethnic” entrepreneurs operating travel agencies in Toronto's Portuguese diaspora,³⁹ or the hacienda owners in village communities in early Mexican statehood.⁴⁰ Brokers help migrants find housing and jobs, fill government forms, and navigate the foreign world. Family networks and/or community networks are also key brokers, as their increasing participation with migration greatly increases the probability of a potential migrant within their network to also go.⁴¹

Along controlled borders, brokers become indispensable to potential migrants as they engage in negotiations and preparations to navigate the segments of precarious migration routes, acting

essentially as “transit-knowledge brokers as well as intermediaries who mitigate migrants' risks along their journeys.”⁴² While brokers operate across the full range of ethical considerations—from labor recruiters, humanitarian advocates, to scammers and human traffickers⁴³—they are the most familiar to the conditions during transit and at the destination and are thus vital to the migration event.

The empirical lessons about brokers and intermediaries corroborate theoretical work on the evolution of learning strategies in changing or uncertain environments.¹⁵ When confronting uncertainty, seeking out and/or observing common practices of the majority or of prestigious, successful individuals can be adaptive in low or moderately changing environments. This strategy is named *context bias*, and prescribes that individuals pay particular attention to the environment in which the information is being presented.¹⁶ As with any socially-learned information, however, the quality of the information is tied to the nature of environmental shifts, assuming that local knowledge is only useful given enough time to develop.

3 | TRANSIT

3.1 | Physiology and morphology meet the demands of movement

Flexibility is one of the primary modes of adaptation as individuals cross boundaries that exert pressure on the human body. We therefore expect the body to respond to varying environmental pressures, such as distinct terrain or ecological gradients, which varies widely among human groups and even within an individual's lifetime. If we account for these varying pressures and consider possible endpoints of selection, we can gain an understanding of the selection of migration-relevant traits *sensu* Sober²² along the migration timeline.

The daily distance covered by an individual, or mobility, is reflective of how resources are distributed across space, thus prescribing pressures on the body. A simple energetics expression of this principle relates metabolism and the environment⁴⁴:

$$\text{Day range} \propto \frac{\text{Metabolic needs}}{\text{Resource density}}$$

While resource density has been manipulated by humans in some cases,^{45,46} for many foragers meeting metabolic needs is tied to mobility across a landscape.⁴⁷ For modern day foragers in northern Tanzania, Wood et al.⁴⁸ documents individual travel on foot on average 10 km per day with substantial variation across individuals and genders. Foraging activities may coincide with migration events if they cross environmental or social boundaries that are relevant to a specific trait. Thus, selection of migration-relevant traits may coevolve with adaptations to mobility for foraging activities, as might be found among early *Homo*.

Shortly after *Homo erectus* appeared in Africa it was found across Eurasia, including Georgia, Indonesia and possibly China.⁴⁹ As likely the first *Homo* out of Africa, the range expansion is attributed to

larger brain and body sizes that supported sufficient developmental plasticity, broad diets, and higher cognitive capacity. The later arriving *H. sapiens* were similar in morphology, and likely exhibited similar levels of plasticity in mobility. For these populations the morphological adaptations for efficient mobility centered around the postcranium and its efficient forms for load carrying, traversing specific types of terrain, and distance.⁵⁰ Efficient walking speeds, for example, are closely tied to body morphology⁵¹ and conversely body morphology—such as the lower limbs and breadth of the pelvis—will respond to subsistence strategy and terrain.^{52,53} A wider pelvis reduces costs to walking, both on level terrain and on an incline as it lowers the center of gravity. Further if there is a load burden a wider pelvis will support a wider variety of optimal speeds at reduced cost than a narrow pelvis. Longer lower-limbs reduce the cost of walking for a range of speeds and increases heat dissipation so that higher speeds can be maintained. The tibia gives a higher predicted optimal speed for anatomically modern humans than for Neanderthals. However, the advantage of longer-lower limbs decreases with increasingly inclined terrain. Lastly, another key feature of bone plasticity is that more mechanical stress leads to greater rigidity, robusticity, and supportive mechanical shape.⁵⁴

However, morphology is likely influenced by a variety of other forces common to migration other than terrain, making Sober's²² distinction here quite pertinent. These may stem from ecological or social influences, such as climatic influences and sociality. Thermoregulation has been shown to influence limb proportions—more surface area to body mass in warm areas, less in the cold^{55,56}—that may influence the direction of selection as individuals experience weather or climate boundaries or bottlenecks. On another tack, as migration may occur in groups, experimental studies show that in sexually dimorphic species we see collective transit costs of mixed group travel.⁵⁴ If larger males or females walk with their mate then it imposes energetic costs, unless the smaller mate has long lower-limbs compared with its size. Traveling in mixed groups, which may be favored for other reasons, may act as a leveling mechanism across morphologies. These complexities suggest strong selection for bone phenotypic plasticity to accommodate the highly varied boundaries and ecological gradients encountered by a geographically dispersed and social species.

The ability to cross ecological boundaries, however, also has a strong metabolic component. Gene scans that link ecological and subsistence history suggests positive selection on alleles that relate to energy metabolism.^{57,58} Selection due to diet is one of the clear findings for these studies, documenting the ability to metabolically adapt to different nutritional environments, as the genus *Homo* likely experienced before its continental-scale range expansion.⁴⁹ The relationship between amylase production and starchy foods is one example,⁵⁹ which generally relates to the scope for local genetic adaptation driven by cultural or ecological pressures.^{60,61}

One hypothesis that is especially relevant to migration is the thrifty-genes hypothesis. This idea posits that human populations exposed to episodes of famine will evolve adaptations to more efficiently process sugars and starches for storage.⁶² For migrants

this occurs during acute population bottlenecks during transit (Figure 1). This attractive idea has been applied to the first settlers of the Pacific Islands, where people may have experienced periods of scarcity when moving across the seascape onto islands with precarious environments. Due to the current differences in traditional and modern diet, this theory aims to explain the prevalence of Type II diabetes, obesity, and other ailments currently burdening many of Pacific ancestry.^{63,64} However, the selective pressure of famine episodes for the Pacific case are weak or underdeveloped at best^{65,66} and other potential mechanisms such as genetic drift may play a role.⁶⁷ We are also limited methodologically in detecting true signals in selection in what is clearly a polygenic trait.⁶⁸

Despite the lack of evidence for thrifty genes, the case is instructive in clarifying the difficulty in gene studies of adaptation in migrating populations. We usually research events in the past that are not directly observed and environmental shifts and small serial founder events make it difficult to disentangle shifting selective pressures and other processes such as kin-structured migration,⁶⁹ drift, or any process that introduces statistical sampling biases along the timeline of migration.⁷⁰ This makes most thrifty-gene-like case studies reach an immediate inferential problem.

3.2 | Cognitive foundations

Migration exposes individuals to unfamiliar terrain, new fauna, and possibly other humans. What type of cognition prompts individuals to seek out, navigate to, and thrive in novel environments? Evidence suggests the rate and nature at which individuals cross boundaries is highly variable,⁷¹ suggesting we should expect high levels of developmental plasticity around cognitive adaptations that mitigate the costs of migration. Further, as there are significant population differences in migratory behavior, we might expect group-level variation in migration-related traits. The examples in this section discuss both individual developmental mechanisms and population processes that may enable a cognition amenable to the migration timeline.

Developmental studies among adolescents document age-structured patterns, with changes in brain, cognition, and behavior during the teenage years that result in heightened risk-taking and novelty seeking.^{72,73} While much of this work asks questions of substance abuse and other preventable causes of injury or harm, it also presumes that this suite of behaviors enables skill development in preparation for adulthood. For example, individuals experiencing unpredictability in childhood may thrive in such environments as adults.⁷⁴ If in fact there is flexible development of *cognitive gadgets* such as imitation, causal understanding, memory and so on (*sensu Heyes*⁷⁵), a more general process may also be at play here promoting a more plastic, and thus migration-friendly, cognition.

One especially relevant domain is spatial cognition, where there are often observed sex-differences. Seeking to explain wide differences in performance in spatial cognition tasks, Cashdan and Gaulin⁷⁶ place the demands of the socio-ecological environment, such as

seeking mates and caring for offspring, as mediating spatial navigation and ability. This means that the sex who travels more widely to seek mates, engages in parental and alloparental care effort, or other reasons performs more accurately in spatial cognition tasks during the life stage of such exploration.^{77,78} Thus, cultural and environmental variation may shape spatial navigational ability, further supporting cognitive plasticity that enables migratory behavior.

However, there is also evidence of population-level genetic variation associated with both novelty-seeking and migration history. The dopamine D4 receptor (DRD4) with seven-repeat (7R) VNTR polymorphism is associated with novelty-seeking behaviors—exploratory, impulsive, excitable, quick-tempered, and extravagant—while the DRD4 variant 4R is associated with lower expression of this behavior.⁷⁹ Populations with longer migratory histories have greater expressions of the 7R (and 2R) variant,^{80,81} which holds after accounting for biogeographic features.⁸² Does novelty-seeking promote exploration and founding of a population, or does it enable a successful adaptation after arriving in a new space? This is an open question with some efforts affording very preliminary insights.⁸⁰ In one case nutritional status among Kenyan pastoralists with the 7R allele measured a higher nutritional status only in the migratory/nomadic subgroup, and a lower status in the sedentary group.⁸³ Thus, while some clues behind DRD4 are promising, and there are questions as to what variant of DRD4 is in fact more relevant,⁸⁴ its effects on migration may be best viewed as in combination with other personality traits such as extraversion, neuroticism and drive which are influenced by other dopaminergic genes.⁸⁵ Further, any genetic mechanism will likely have coevolved with cultural and environmental feedbacks.^{9,60}

3.3 | Bodies of transport and tools of movement

The vehicles of movement and the technology behind navigation are often the primary means of cultural adaptation between origin and destination. Humans occupied the islands around New Guinea for at least 40 thousand years before a later expansion led to the occupying of nearly all places of land and sea in the Moana Pacific.^{86,87} Occurring too quickly to be explained by ecological constraints or population pressure,⁸⁸ the Austronesian expansion was likely culturally driven, in that the culturally-inherited means and strategies of movement were key to the settlement chronology.^{89,90} The Caroline islands asymmetric hull and outrigger canoe described ethnographically is a formidable example. Larger-hulled canoes created by sewn-planks was an especially poignant innovation that allowed canoes to increase in size, comparable to contact-era European ships. The outrigger and double-hull innovations in particular are thought to have propelled populations from the close-clustered islands around New Guinea to the dispersed islands of the entire Pacific and the coasts of the Americas.⁹¹ Tacking and shunting technologies appear also to be regionally developed. While the canoe designs likely diverged after populations settled and adapted across the Pacific,⁹² some designs appear to be conserved as key functional features of canoe performance.^{93,94}

The success of the Austronesians in the Moana Pacific mirrors successes on land by many others before the industrial era. The use of horses is perhaps one of the most studied examples. Mitchell⁹⁵ discusses how horses were readily adopted by several indigenous groups ahead of the European colonial expansion, resulting in quick changes in society. The horse created a “kinetic empire” characterized by long-distance trade and raiding among the Comanche of the American Southwest, the Guaykukú of the Gran Chaco, and the Bushman raiders of South Africa, to name a few. The expanded mobility transcended “previous limits on human existence” (381). The broader adoption of horses, donkeys, and a suite of other animals associated with mobility attests to their effectiveness.^{96,97}

However, the development of transport technology is not always sufficient. The cognitive development of spatial navigation⁷⁶ combined with a large corpus of culturally inherited elaborations appear to be vital for successful transit.⁹⁸ Ethnographic studies of traditional seafaring navigation,⁹⁹ combined with modern experimental voyaging¹⁰⁰ and computer simulations⁸⁹ provide evidence of a complex knowledge set around traditional voyaging that included not just the use of stars but also the use of reflected and refracted wave patterns.¹⁰¹ Wayfinding instruments such as the compass along with mapping tools and techniques, oral traditions and written work about landmarks and cues appear to have required generations of development, intergroup adoption, and adaptation to become useful for both land and sea navigation.^{102,103} Aporta and Higgs¹⁰⁴ provide a revealing account of the mixed use of GPS technology with Inuit wayfinding methods to traverse challenging land and seascapes. Traditional methods that used wind direction, snowdrifts, environmental features, and memorized routes aided Inuit hunters of Igloodik to find waypoints and destinations. GPS receivers, however, provided help when cues were obscured, especially in heavy fog. The combination of the two allowed the hunters to move more effectively across the landscape than previously known. Most accounts about navigation similarly stress that success relies on a large set of tools and knowledge that tracks the complex, shifting signs during transit.

3.4 | Social organizations that move

Early Hawaiian society has been called the society of the canoe (Kirch in Low¹⁰⁵), where the hierarchical features of canoe leadership and knowledge were presumably important requirements for successful crossings and navigation of the vast ocean. This conjecture also prescribes the more intriguing hypothesis that features of early Pacific societies were shaped by the migration process itself. Here, social life may be necessarily hierarchical because of the specialized nature of canoe manufacture and navigation that reflected on society as it developed on land. In this case, the migration process leaves an imprint on society after migration has stopped. One might argue that the relatively rapid settlement of the Moana Pacific is a consequence of this effect. Given supposed hierarchical features of the migrating group, individuals or groups with the incentive and means to explore are driven forward by the

rewards of being founders. This concept of founder-focused ideology imagines, for example, lower-level chiefs or chiefly families who seek the advantages of an unoccupied resource base.¹⁰⁶

More generally, specific institutions of knowledge production, labor management, and other group features may lead to greater representation through expansion or migration.¹⁰⁷ Systems of expansion may feature norms that mediate resource demands such as the acceptance of credit,¹⁰⁸ agricultural demands,¹⁰⁹ and warfare.¹¹⁰ Frontier culture is a well-illustrated concept aimed at capturing the selective process by which individuals adapt to propel themselves beyond a society's well-worn pathways.¹¹¹ The primary observation is that at the margins of society people house greater individualistic attitudes than in the interior. Individualism in this context means high values placed on self-sufficiency and opposition to redistribution of wealth. The legacy of individualism is reflected at higher social units, and well-documented in the American West and much of the United States,¹¹² holding vestiges of the frontier in contrast to Europe from where many of the occupants hold ancestry. Both self-selection and the "you reap what you sow" attitudes carried individualism to new heights as the self-sufficient, hard-working individual operated outside of the social constraints to mobility found in the interior of society. Supposedly given the fleeting nature of dyadic reciprocal relationships and lower population density, trailblazers emphasize self-sufficiency at greater levels than in the interior.¹¹³

In the Moana Pacific and the American West there is little doubt that migration shaped the way social organization evolved. However, the comparison between the two – hierarchically-dependent versus individualistic—shows there is no satisfactory formal theory coupling social organization and migration. Perhaps there is a relationship between individualism, frontier culture and novelty-seeking behaviors, but we have not seen an explicit individual and group-level analysis behind the benefits and costs of the novelty-seeking strategy on a frontier. Does seeking and thriving in new lands require strict hierarchical organization to be successful, or do bands of self-sufficient explorers with fleeting reciprocal relationships move at a faster pace? Not knowing the scope of possibilities makes the empirical work difficult to interpret.

4 | DESTINATION

The novel context presents several problems to solve for individuals and groups. The presence of an existing population will require establishing ties, otherwise an empty landscape may require adjusting to a new ecology. These two forces create formidable challenges in many cases, with the former requiring more immediate socio-cultural adaptations. For both, however, the *context of reception* is one of the more highly variable dimensions of migration, a major driver of outcomes, and a large focus of research.¹¹³ Hence strategies to mitigate costs and raise benefits are sensitive to the detailed features of the environment recent migrants navigate.

A key feature shaping the selective forces at the destination is the nature of in-group and out-group interactions.^{113,114} The rate of

intergroup contact in history suggests a large scope for behaviors that mediate coordination,^{115–117} cooperation,¹¹⁸ and threat.^{119–121} Among smaller societal scales the endogamy rates of ethnolinguistic groups range from 92% linguistic and 84% territorial lineage-unit endogamy for agro-pastoralists of highland Peru¹²² to 0% for Tukanoan language speakers of Venezuela and Brazil, who endorse linguistic and regional exogamy.¹²³ Among groups in the United States, 95% of blacks, 75% of Asian subgroups, 65% of Hispanic subgroups, 45% of American Indians, 25% of (unmixed) European subgroups are endogamously married. This level of variation continues for religion in the late 1970s, where 62% of Catholics, 84% of Protestants, and 80% of Jews were married endogamously.⁷¹

For hunter-gatherer populations, Tindale reports on various aboriginal Australian tribes a range of endogamy rates from 79% to 94% with average of 15% marital exogamy (1953).¹²⁴ This large variation may be expected given demographic models predict larger adult sex ratios imbalances in smaller populations.¹²⁵ A 25-year demographic record of two Savannah Pumé hunter-gather groups show large fluctuations in the adult sex ratio throughout,¹²⁶ suggesting episodes of marital exogamy as a common phenomenon in small groups. Finally, much earlier in human evolutionary history, Reich¹²⁷ summarizes ancient DNA studies suggesting constant migration and admixture among highly differentiated groups of anatomically modern humans and related groups—from the Pleistocene to the Holocene.

When crossing social boundaries, the theory and empirical evidence suggest pressures for greater inferential skills, cross-cultural competence²⁰ and an ability to account for relationships about partners, groups, and sensitivity to social cues. In small-scale fission-fusion dynamics, tools would be needed to track information about individuals, whereas in larger scale migration dynamics it would require information about groups or categories of individuals.¹²⁸ Moya and Boyd¹²⁹ show that the cues used to categorize others may vary according to context, with culturally derived markers bolstered by a cognitive sensitivity to social categories. Evidence suggests strategies evolve among migrants to navigate toward beneficial outcomes when interacting with unfamiliar groups.

Consequently, two broad categories of interaction shape the adaptive strategies of migrants within the novel context. The first is coordinating and establishing cooperative ties among migrants and locals if present, and the second is gaining local adaptive knowledge. These two processes drive much of the observed shifts in culture, language, and identity. It also outlines efforts to gain local knowledge through formal or informal means, and outlines the scope for religious, political, and civic membership.

4.1 | Coordinating and establishing cooperative ties

Across four prominent immigrant groups entering the United States in the 1930s—the Irish, Italians, Germans, and Polish—Goldstein and Stecklov¹³⁰ found that children of immigrants with more common

American first-names earned 2%–5% more annually than those with common first-names in their parent's country of origin. For this new second-generation, parents likely signaled their child's place in society hoping for acceptance and economic mobility. This interpretation has basis as names have consequences ranging from acceptance to discrimination.¹³¹ Not surprisingly name changing or the adoption of an alias is also common when crossing ethnic lines.

Several domains of culture and behavior follow this pattern. Language and religion, for example, are often the focus of cultural shifts. Crossing boundaries inevitably leads to a search of common ground on which to coordinate beliefs, interests, and behaviors, which migrants often show great eagerness to accommodate. Dialect leveling, multilingualism, and the spread of *lingua francas* accompany the contact of increasingly more distinctive linguistic groups. For example, Dillard¹³² argues that the forced migration of African slaves of (intentionally) different language groups led to creoles to communicate with slave owners and among themselves. Driven by the children and adolescents of the groups in contact, simpler forms developed and were eventually shared by the population. However, the linguistic variants found among the majority at the early stages of leveling usually become the center of linguistic accommodation and become more widely adopted.¹³³ The legacies of language forms follow the struggle to communicate across initially multilingual contexts.

Religion is another primary center of adaptation. While religion may intersect at all parts of the migration process,¹³⁴ at the destination it may be vital to immigrant adaptation. Religions operate as mobile reproductions of sub-cultures, with members sharing norms and traits. The “refuge, respect, and resources” offered by religious institutions includes protection from hostilities, mediating collective political action, and allows the building of beneficial social networks.¹¹³ For this reason, religious affiliations are reportedly heightened among immigrants who arrive at societies with religious freedoms or leanings, as they build houses of worship or convert to an established belief system.¹³⁵ In fact, over time national identities may be tied to, or even replaced by, the religious community to which they belong.

4.1.1 | Enclaves

In the same study of immigrant first-names by Goldstein and Stecklov¹³⁰ discussed above, I did not mention the fifth group in the study—Russians of mostly Jewish heritage. In this group we see an opposite effect of all the other groups: those with names more common in their origin country experienced higher annual earnings. The current hypothesis is that this is tied to the advantages of mutual aid among co-ethnics in an ethnic enclave economy.¹³⁶ These migrants gained the benefits of a previous wave of Jews from Germany that became economically successful, and the later wave from Russia contributed to the growing enclave in East Manhattan.¹³⁷ While they learned English and other requirements for business and trade, the Jewish enclave became the focus of adherence to religion, language, and culture.

Despite the wider incentives for a cultural shift to the majority, a large number of migrants have incentives to maintain cultural beliefs and behaviors.¹³⁸ Once formed, enclaves provide services akin to religious institutions in the form of resource acquisition, political action, and protection.¹³⁹ Enclaves also introduce new traits as individuals occupy new spaces, resources, and opportunities.³⁸

However, not all significant movements result in a cultural or enclave economy. The comparative ethnographic study by Brettell¹⁴⁰ highlights the contingencies, comparing the outcomes of Portuguese immigration to Toronto, Canada and Paris, France. The influx of Portuguese resulted in a vibrant enclave in Toronto but not Paris. A compelling explanatory factor are the contrasting residence patterns. The segregated neighborhoods of Toronto lent to enclave formation while the live-in Portuguese workers residing in traditional Parisian apartments made difficult the interactions needed for a co-ethnic network to be built. While religious communities may help build co-ethnic networks, no ethnic religious institutions were supported well in France at the time of study.

Not all top-down pressures for assimilation or exclusion will suppress an enclave. In fact, individuals may mobilize political reactions and build co-ethnic networks in reaction to exclusionary and discriminatory measures by the majority.^{113,141} One of many examples is the formation of Japanese enclaves in San Francisco and other Western cities. In the early 20th century Japanese immigrants were effective independent farmers and posed unwanted economic competition to white farmers.¹⁴² California laws were passed that led to the loss of land by Japanese farmers and their eventual exit from agriculture. However, they entered urban areas in the form of small shops along Western cities supported by mutual-aid organizations and ethnic credit networks set up by the Japanese themselves, leading to substantial economic mobility in subsequent generations.¹³⁷

Among the Japanese, the felt political power differences likely led to the formation of an enclave that mitigated the plight of the persecuted. This is similar to the Black Power and Red Power movements most prominent in the Civil Rights Era in the United States that respectively celebrated African American and Native American peoples in reaction to actions of the predominant European-derived culture.¹⁴³ While co-ethnic exploitation also exists,¹⁴⁴ the ubiquity of enclaves attests to the overall advantage of co-ethnic ties.

4.1.2 | In-betweeners

Between the space occupied by enclaves and the out-group majority is a strategically important *third-space* where individuals interact frequently across two or more groups. Individuals that primarily occupy this space are *in-betweeners*, conceptually similar to brokers mentioned above, though they need not participate in the specialized activities of brokers. Rather the strategies employed by this group help them navigate multiple social settings with little aid from others. While important to today's experiences as national boundaries are blurred by fast travel of those with multi-state affiliations,¹⁴⁵ the

strategy is also key for traders, labor migrants, cultural proselytizers, forced migrants and others.

Maintaining high levels of cross-cultural competence help in-betweeners occupy and support the third-space.²⁰ For instance, Kiliç et al.¹⁴⁶ discuss how Turkish-German second-generation return migrants find a space in tourism hubs to not only use their transcultural capital but also their experienced shared norms, even if it is divided among interactions between visiting Germans, expat Germans, or locals. Tongan-Americans navigate spaces of family and religious obligations that span multiple countries, while navigating the realities of work and family life in the United States.^{147,148} While common among children of migrants, the strategy of in-betweeners can persist if individuals remain situated between prominent groups.

In principle coordinating behaviors and exclusions among the confluence of larger numbers of groups can lead to an infinite regress of layered identities. Thus in-betweeners that occupy the third-space can occupy a fourth, fifth, or *N*th space. The number of spaces derive from the segmentations already present in society such as wealth or religion, and the multiple groups that may correlate with some of these. An individual from ethnic group A that is wealthy may occupy a separate space from a poorer co-ethnic. The combinatorics suggest that the spaces for which cross-cultural competency is needed increases quickly with more groups and traits associated with the groups. That is, one ethnic group with a rich-poor distinction is two groups, two groups with rich-poor is four groups, add another binary distinction (e.g., religion) and the number is eight. If *g* is the number of groups and *n* is the number of non-exclusionary binary distinctions, then there are $g2^n$ possible spaces. For example, four groups with three binary distinctions has $4 \times 2^3 = 32$ spaces! Thus, in multicultural environments with divisions by wealth or other categories, the dominant mode of interaction is occupying the in-between spaces. Those that better navigate across spaces experience higher well-being.^{149–151}

4.2 | The frontier again

The concept of *frontier culture* discussed above was used to describe the evolution of a mobility-enhancing cultural norm in response to the boundary between settled and unsettled land. It may also be viewed as a strategy taken up by individuals in the absence of strong norms. As famously argued in 1893 by Frederick Jackson Turner,¹¹¹ the frontier attracted individualistic migrants who sought upward mobility. Once there, the harsh life further selected for individuals to be self-sufficient and more individualistic, as extended reciprocity arrangements were difficult among these highly mobile populations. With cooperation via reciprocity limited, the importance of “rugged-individualism” allegedly became the favored adaptation along the European frontier. (Emphasis on European frontier given the prior and established presence of Native Americans.) There are exceptions to strict individualism, such as the migration of religious groups that integrated a communal ethos across North America in the 19th century such as the Hutterites of North America and Canada, and

members of the Church of Jesus Christ in Utah and surrounding states.

Turner's explanation predicts that individualism becomes more prevalent with increasing exposure to a frontier. A test of this hypothesis by Bazzi et al.¹¹² looked at naming conventions as a proxy of individualism. Using the prevalence of uncommon names, their analysis showed that the longer time spent on the frontier, the more likely a family will name children with infrequent names—a sign of individualism. Other support for the hypothesis using different methods included a contemporary study of Hokkaido residents on the “frontier” of Japan¹⁵² and a historical study of emigration out of Scandinavia.¹⁵³ In all these studies there is the claim that the effects of migration are long-lasting after it has slowed or stopped. In other words, the cultural norm of rugged-individualism remains for some time after the pressure for its selection has disappeared, suggesting that other mechanisms act to maintain them (e.g., conformity).

4.3 | Gaining, creating, and maintaining local adaptive knowledge

Increasing resource benefits from an environment often requires costly experiences or strategies developed over generations. One strategy is to acquire knowledge maintained by locals. Another is to transform an environment to suit the knowledge and objects brought by migrants. These two strategies cover many examples of ecological adaptations of migrants, though the former is more subtle, while the latter is more easily observed.

Acquiring local adaptive knowledge is a high dimensional task given the cues from (migrant) co-ethnics, locals, and the environment. Theory suggests individuals should pay attention to markers signaling the categorical affiliation of individuals that house different knowledge bases, especially in heterogeneous environments.¹⁵⁴ The large literature on assimilation and cultural shifts attest to the power of this strategy,¹⁵⁵ which plays rival to the positive assortment mechanism that enclaves provide. In a rain-forest habitat in Guatemala, for example, Atran et al.¹⁵⁶ document how immigrant Ladino communities have learned to think and do as the native Maya group, the Itza', housing the greatest sustainable ecological knowledge around agriculture and the forest. Well-connected Ladinos attend to individual Itza' that are recognized holders of knowledge, who in turn become a source of knowledge for other Ladinos. Learning from native knowledge holders, however, is complex, as another immigrant group to the same region, the Q'eqhi' Maya, do not attend to Itza' ecological practices and consequently practice agriculture that is less sensitive to forest survival.

In general, not all cultural shifts and knowledge gains are inevitable, as groups may retain their norms if spheres of contact are protected from influence of outside others.¹³⁸ This may explain why heritage language and culture retention among second generation immigrants varies according to residence patterns and the segmented nature of the labor market.^{19,137,140,157} The acculturation factors and outcomes reviewed by Berry^{158,159} provides further evidence that

origin and destination norms and institutions, along with individual-level variation such as time since migration, affect whether individuals (prefer to) shift to the majority (assimilate), integrate, or remain separate as potentially marginalized members of a population.

A relatively visible second strategy made by migrants is the transformation of the environment.¹⁶⁰ This is important for migrants to an unoccupied space, at least initially. Anderson¹⁶¹ shows how this tendency plays out among wild plants and cultigens—coined “transported landscapes”—with the deliberate translocation of plants significantly altering the biota of the new space. This concept has been adapted to describe the dozens of species of plants and animals that were brought across the Pacific Islands for cultivation by its First Peoples.^{162,163} Taro, yam, breadfruit, Tahitian chestnut, dogs, pigs, chickens, and other biota were introduced. On the larger islands food production strategies changed over time as the introduced domesticates became more prominent sources of food relative to fishing, foraging along the reef, and hunting native species.¹⁶⁴ There are a few instances of island abandonment but the cultivation strategy was so successful that these are rare compared to the continued settlement of hundreds of islands across the Pacific. In the Americas there is also work on reconstructing the suite of biota introduced by migrants, demonstrating deliberate ecological strategies employed by migrants in the early historical period in California¹⁶⁵ and the Bahamas¹⁶⁶ in the use of translocated plant and animal domesticates.

4.3.1 | Knowledge loss

Migration alters the composition of a community at the origin and destination. Because this affects the community knowledge base that individuals may draw from, strategies may evolve to mitigate the loss of knowledge and navigate the introduction of new knowledge.

The knowledge or traits most susceptible to loss are those that are hard or take time to learn, such that there is a skewed distribution of those with high and low proficiency.¹⁶⁷ This includes language, manufacture of objects with multiple steps, and activities that require a critical mass of participants like hunting cooperatives, fish-trapping, and musical groups. Any loss of an individual may lower the knowledge base significantly, which may be more the case in smaller populations.^{21,168} In an ethnographic study of basket weavers in Tonga, Bell¹⁶⁹ found that among women who were introduced to a new method, there was a wide variety of weaving rates and elaborations on the method. The distribution of proficiencies suggested this particular mode of material culture, which had been lost after European contact, remained highly sensitive to losses of experts on the right tail of the skill distribution.

To mitigate against losses, enhancing learning in groups may be a key strategy to resisting the demographic pressure of cultural loss. Returning to the Tongan example, Helu¹⁷⁰ describes a particularly salient learning activity in the Tongan Islands:

[*Kava fakalōkua*] is a kava party of two or three farmers for fishermen that is held at the end of the day

in one of the men's houses...The topics discussed can be anything of common interest e.g. yam cultivation, a fishing method, and in general what they have been doing that day. This kava, therefore, was one that gave farmers and fishermen the opportunity to unwind, take stock of what they achieved that day, and learn from each other.

Whether a deliberate action or a consequence of the socialization around kava groups, these types of gatherings can serve as a support for knowledge that navigates complex problems.¹⁷¹

Strategies to maintain knowledge are similarly relevant at a destination where immigrants arrive. Since group membership may correlate with holders of local adaptive knowledge,¹⁵⁴ then individuals may form groups to maintain it in the face of influence from outside groups.¹⁷¹ On the other hand, intergroup contact may spur innovation,^{172,173} so we may expect locals and migrants to pay close attention to the outcomes of knowledge derived from the interaction.¹⁷⁴

Regardless of the number of individuals or the effectiveness of group learning, some domains will be lost due to the nature of migration. One key feature of the knowledge around migration is that it is provisional. When explorers stop exploring or when populations stop moving the cumulative knowledge base declines. The vast efforts to revitalize and maintain traditional knowledge, such as long-distance traditional seafaring,¹⁰⁰ faces an upward battle against social disruptions, culturally prescribed restrictions on knowledge transmission, foreign technology and incentive structures introduced by modern lifeways.¹⁰¹ Canoe building and navigation, for example, have long training periods from child play, gradual exposure, directed guidance and then mastery.^{101,175} Perhaps a population may experience out-migration again, at which point the knowledge base is either revitalized, remembered, or the process of cumulative culture begins again. This potentially wave-like pattern of cultural knowledge of migration is in contrast to more constant maintenance pressures in other knowledge domains.

5 | DISCUSSION

You see that house, that family succeeded because some of their family went overseas.

– Village elder in Tonga speaking to author, June 2006.

Two features come to the fore during this review of evidence. Across the narratives explored here a consistent appeal is made to individual-level incentives and adaptations, as well as the effect of groups and/or institutions. Optimal walking speeds for an individual may never be practiced if travel is primarily in groups of mixed size, the intrepid seafarer may feel constant pressure in a conical clan to explore and find new islands, and the modern migrant faces pressures to meet local social obligations only met by international labor migration. These multi-level pressures suggest a close accounting of individual and higher-level social forms.

TABLE 1 Examples of selective pressures or traits at the individual and group level discussed in this paper.

Level of selection	Origin	Transit	Destination
Individuals	Causal inference of resource gains; relative deprivation ²⁹ ; novelty-seeking personalities ⁸⁰	Bone morphology by terrain and activity ⁵⁰ ; search strategies ⁸⁹ ; spatial cognition ⁷⁶ ; migration brokers ⁴² ; technology ^{92,95}	Novelty-seeking personalities ⁸⁰ ; ethnic entrepreneurs ³⁹ ; cross-cultural competence ²⁰ ; conforming to majority norms
Groups	Family-level economic strategies ²⁹ ; cumulative gains; serial migration and bottlenecks of cumulative culture; knowledge maintenance, brain drain, and cooperative learning groups ¹⁷¹	Bone morphology and mobility in mixed groups ⁵⁴ ; migration brokers ³⁸ ; norms of hierarchy and knowledge titleholders ¹⁰¹	Enclave economy (Wilson and Portes, 1980); kin-biased migration ⁶⁹ ; frontier culture ¹¹¹ ; religious membership ¹³⁵

Note: Items may be repeated, with items repeated across individual and group categories represent a negotiation between the two levels of selection.

The second feature naturally follows from the first, in that responses along the timeline of migration vary widely as to their temporal dynamics. Some adaptations evolve quickly, responding to the complexities of movement, others may persist long after the migration event. Brokers or “coyotes” may constantly adjust routes to mitigate risks along the transit on a daily basis, while “frontier cultures” may persist generations after migration has stopped. The timescale differences reflect the strength and nature of selective pressures.

These two features invite a theoretical and empirical accounting of the timescale and selective pressure at each level of evolution (Table 1). Individual incentives often respond to larger decisions, norms, and policies at the origin and destination and vice versa. The mathematical formulation in Box 1 illustrates this negotiation, giving basic guidance on the calculus behind how migration may be sustained by cost-benefit forces at each level. Are socio-cultural institutions around migration shaped by individual-level incentives or are they strong enough to persist on their own and shape individual behavior?

Migration may be favored, even if individually costly, if it benefits the group such that the group grows, spreads, or persists relative to those with less migration. The more obvious examples are large-scale military campaigns with high individual costs.¹¹⁰ More subtle and variable are the decisions made at the household or kin-group level that reduces risk and increases available capital. Select kin may migrate to gain and remit resources. This strategy, dubbed “the new economics of migration,”²⁹ motivates behavior not (solely) by individual wage differentials, but family group incentives relative to others in the local/origin population. It addresses relative deprivation as locally perceived. In my own fieldwork in Tonga and in the diaspora, the “success” of a kin group is heavily tied to contributions of migrating family members, such that comments at the beginning of this section are common. The benefit to the group is the focus of this framework rather than the benefit/cost to the migrating individual.

This accounting also works the other way around with individual-benefits to migration accompanied by a group cost. The *brain drain* effect on homeland populations is difficult to stop when there are strong individual-level incentives to emigrate. When technology and knowledge is sensitive to the number of cultural practitioners and students,^{21,167} then cultural losses follow within a generation.¹⁶⁹

There are both individual and group-level incentives driving the *culture of migration* of Hyderabad, and the *society of the canoe* in the Moana Pacific, suggesting their persistence barring exogenous factors changing the cost-benefit calculation. In Hyderabad, the *brain drain* is counteracted by educational institutions built to support migration, or *brain gain*. The homeland culture also benefits from a remittance economy. Here, the individual benefits to migration are coupled with what becomes a public good.

The multi-level benefits to migration strategies, however, can become more complex with multiple evolving traits and alternative group features. Our discussion of *frontier culture* highlights a persistent cultural norm argued to be (previously) adaptive along the barely-traveled paths of society. In this case the costs and benefits to migration are intertwined with how well an individual becomes self-sufficient and independent. Alternatively, a hierarchical division of labor may also offer up advantages along the frontier, that is, the *society of the canoe*. Thus, a problem and opportunity present itself to work out how different social organizations influence individual and group-level net outcomes to migration. This opens up an inquiry into the role of diaspora enclaves that may build economies of scale, facilitate the transportation of scalable resources (e.g., crops), and other advantages.

The second fundamental feature to migration observes the timescales of adaptation. On the shortest of timelines, individual-level strategies that respond to local dynamics may be key to confronting a fast-changing environment. Here the individuals address inferential problems as cues, information, and the senses update an individual's strategy. Any knowledge that pushes is sensitive to shifts along the timeline of migration, and even after the migration event coordination may require a constant updating of how to navigate novel social groups. Further, information about a destination may be unreliable from migrants who wish to maintain an impression of success, and it remains to be investigated whether potential migrants make adjustments to potentially biased information.

In fact, the complexity of individual-level adjustments is reflected by the wide range of migrant-flow typologies developed in the migration literature. Migrant flows have been categorized as seasonal, temporary, nonseasonal, recurrent, continuous, and permanent.¹⁷⁶

Further elaboration considers settler, sojourner, yo-yo migration,^{177,178} typologies of return migration,¹⁷⁹ and the growing field of transnationalism.¹⁸⁰ In part, the driver of these typologies are migration flows and spatial proximity—the when, where, and how many—that may dictate the formation of migrant enclaves and networks.¹⁴⁰ Engaging with the potentially complex strategies migrants or groups may employ requires a continuous account of quickly evolving forces along the migration timeline.

At larger timescales the questions revolve around persistence. Do phenotypes, social norms or institutions that facilitated migration remain after the event? Under what conditions do “cultures of migration” persist indefinitely? Are the presumed physiological or genetic adaptations to migration a direct response to pressures around migration or in combination with other forces? These are key empirical and theoretical questions that motivate an accounting of the dynamics of migration flows and the pressures of the past. Doing so will uncover whether a trait is in fact a “ghost of migration past” that is presumed important for communities occupying, for example, the former frontiers of the world, such as the Moana Pacific and the western United States.

Finally, across timescales we observe questions around the occurrence of serial migration and its effects on cumulative cultural evolution. For indigenous scholars, postcolonial revitalization efforts aim to re-build lost knowledge, including knowledge around navigation and vessels of transport. Because the development of technology around migration is likely tied to the number of events it serves, any constriction of travel or abandonment of movement impacts its cumulative build-up. Thus, a reconstruction of the manner of exploration, migration, and postsettlement movement should be theoretically linked to the institutions of knowledge reproduction and innovation. For instance, as knowledge may be lost at generational timescales, then significant migration events will need to occur frequent enough during the formidable years of learning, perhaps several times in a decade. Populations that move less frequently may lose more complex aspects of migration technology.

ACKNOWLEDGMENTS

This paper benefited from conversations with Mark Stoneking, Tyler Faith, Monique Borgerhoff Mulder, Elspeth Ready, Bret Beheim, Richard McElreath, Paul Heggarty, and John Bunce. This review was written while a guest researcher at the Department of Human Behavior, Ecology and Culture at the Max Planck Institute for Evolutionary Anthropology, under sabbatical support from the University of Utah.

DATA AVAILABILITY STATEMENT

Data sharing not applicable—no new data generated.

ORCID

Adrian Viliami Bell  <http://orcid.org/0000-0002-4670-384X>

REFERENCES

1. Adhikari, K., Chacón-Duque, J. C., Mendoza-Revilla, J., Fuentes-Guajardo, M., and Ruiz-Linares, A. (2017). The genetic diversity of the Americas. *Annual Review of Genomics and Human Genetics*, 18(1), 277–296.
2. Bellwood, P. (2014). *First Migrants: Ancient Migration in Global Perspective*. John Wiley & Sons.
3. Crawford, M. H., and Campbell, B. C. (Eds.). (2012). *Causes and Consequences of Human Migration: An Evolutionary Perspective*. Cambridge: Cambridge University Press.
4. Barth, F. (1969). *Ethnic Groups and Boundaries*. Long Grove: Waveland Press, Inc.
5. Castles, S., and Miller, M. (2003). *The Age of Migration*. New York: Guilford Press.
6. Lee, E. S. (1966). A theory of migration. *Demography*, 3(1), 47–57.
7. Scheiner, S. M. (1993). Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology and Systematics*, 24(1), 35–68.
8. Sultan, S. E., and Spencer, H. G. (2002). Metapopulation structure favors plasticity over local adaptation. *The American Naturalist*, 160(2), 271–283.
9. Wells, J. C. K., and Stock, J. T. (2012). The biology of human migration: the ape that won't commit? In M. H. Crawford and B. C. Campbell (Eds.), *Causes and Consequences of Human Migration: An Evolutionary Perspective*. Cambridge: Cambridge University Press.
10. Meaney, M. J. (2010). Epigenetics and the biological definition of gene x environment interactions. *Child Development*, 81(1), 41–79.
11. Bateson, P., Barker, D., Clutton-Brock, T., Deb, D., D'Udine, B., Foley, R. A., ... Sultan, S. E. (2004). Developmental plasticity and human health. *Nature*, 430(6998), 419–421.
12. Mosher, M. J. (2012). The role of diet and epigenetics in migration: molecular mechanisms underlying the consequences of change. In M. H. Crawford and B. C. Campbell (Eds.), *Causes and Consequences of Human Migration*. Cambridge: Cambridge University Press.
13. Ruff, C. (2002). Variation in human body size and shape. *Annual Review of Anthropology*, 31(1), 211–232.
14. Richerson, P. J., and Boyd, R. (2005). *Not by Genes Alone: How Culture Transformed Human Evolution*. Chicago: University of Chicago Press.
15. Boyd, R., and Richerson, P. J. (1985). *Culture and the Evolutionary Process*. Chicago: The University of Chicago Press.
16. Henrich, J., and McElreath, R. (2003). The evolution of cultural evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, 12(3):123–135.
17. Ravenstein, E. G. (1885). The laws of migration. *Journal of the Statistical Society of London*, 48(2), 167–235.
18. Webster, T. H., and Wilson Sayres, M. A. (2016). Genomic signatures of sex-biased demography: progress and prospects. *Current Opinion in Genetics and Development*, 41, 62–71.
19. Bell, A. V. (2013). The dynamics of culture lost and conserved: demic migration as a force in new diaspora communities. *Evolution and Human Behavior*, 34(1), 23–28.
20. Bunce, J. A. (2021). Cultural diversity in unequal societies sustained through cross-cultural competence and identity valuation. *Humanities and Social Sciences Communications*, 8(1), 238.
21. Kline, M. A., and Boyd, R. (2010). Population size predicts technological complexity in Oceania. *Proceedings of the Royal Society B: Biological Sciences*, 277, 2559–2564.
22. Sober, E. (1993). *The Nature of Selection: Evolutionary Theory in Philosophical Focus*. Chicago, IL: University of Chicago Press.
23. Price, G. R. (1970). Selection and covariance. *Nature*, 227(5257), 520.
24. Smith, D. J. (2004). Burials and belonging in Nigeria: rural-urban relations and social inequality in a contemporary African ritual. *American Anthropologist*, 106(3), 569–579.
25. Ali, S. (2007). 'Go west young man': the culture of migration among Muslims in Hyderabad, India. *Journal of Ethnic and Migration Studies*, 33(1), 37–58.

26. Garip, F. (2013). The impact of migration and remittances on wealth accumulation and distribution in rural Thailand. *Demography*, 51(2), 673–698.
27. Klabunde, A., and Willekens, F. (2016). Decision-making in agent-based models of migration: state of the art and challenges. *European Journal of Population*, 32(1), 73–97.
28. Brettell, C. B. (2016). Perspective on migration theory—anthropology. In M. J. White (Ed.), *International Handbook of Migration and Population Distribution*. New York: Springer.
29. Massey, D. S., Arango, J., Hugo, G., Kouaouci, A., Pellegrino, A., and Taylor, J. E. (1993). Theories of international migration: a review and appraisal. *Population and Development Review*, 19(3), 431–466.
30. McElreath, R., Bell, A., Efferson, C., Lubell, M., Richerson, P., and Waring, T. (2008). Beyond existence and aiming outside the laboratory: estimating frequency-dependent and payoff-biased social learning strategies. *Philosophical Transactions of the Royal Society B*, 363, 3515–3528.
31. Kandel, W., and Massey, D. S. (2002). The culture of Mexican migration: a theoretical and empirical analysis. *Social Forces*, 80(3): 981–1004.
32. Horváth, I. (2008). The culture of migration of rural Romanian youth. *Journal of Ethnic and Migration Studies*, 34(5), 771–786.
33. Brown, R. P. C., and Connell, J. (2004). The migration of doctors and nurses from South Pacific Island Nations. *Social Science and Medicine*, 58(11), 2193–2210.
34. Connell, J., and Brown, R. P. C. (2004). The remittances of migrant Tongan and Samoan nurses from Australia. *Human Resources for Health*, 2(2). doi:10.1186/1478-4491-2-2
35. Stark, O., Helmenstein, C., and Prskawetz, A. (1997). A brain gain with a brain drain. *Economics Letters*, 55(2), 227–234.
36. Epstein, G. S. (2010). Chapter 2: Informational cascades and the decision to migrate. In *Frontiers of Economics and Globalization* (Vol. 8, pp. 25–44). Bingley: Emerald Group Publishing Limited.
37. Wendt, A. (1999). *Flying-Fox in a Freedom Tree: And Other Stories*. Honolulu: University of Hawaii Press.
38. Geertz, C. (1960). The Javanese Kijaji: the changing role of a cultural broker. *Comparative Studies in Society and History*, 2(2), 228–249.
39. Brettell, C. (2003). *Anthropology and Migration*. Walnut Creek: AltaMira Press.
40. Wolf, E. R. (1956). Aspects of group relations in a complex society: Mexico. *American Anthropologist*, 58(6), 1065–1078.
41. Winters, P., de Janvry, A., and Sadoulet, E. (2001). Family and community networks in Mexico—U.S. migration. *The Journal of Human Resources*, 36(1), 159–184.
42. González, Y. G. (2018). Navigating with coyotes: pathways of Central American Migrants in Mexico's Southern Borders. *The Annals of the American Academy of Political and Social Science*, 676(1), 174–193.
43. Lindquist, J. (2015). Of figures and types: brokering knowledge and migration in Indonesia and beyond. *Journal of the Royal Anthropological Institute*, 21(S1), 162–177.
44. Harestad, A. S., and Bunnell, F. L. (1979). Home range and body weight—a reevaluation. *Ecology*, 60(2), 389–402.
45. Bird, D. W., Bird, R. B., Codding, B. F., and Taylor, N. (2016). A landscape architecture of fire: cultural emergence and ecological pyrodiversity in Australia's Western desert. *Current Anthropology*, 57(S13), S65–S79.
46. Smith, B. D. (2007). The ultimate ecosystem engineers. *Science*, 315(5820), 1797–1798.
47. Marlowe, F. W. (2005). Hunter-gatherers and human evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, 14(2), 54–67.
48. Wood, B. M., Harris, J. A., Raichlen, D. A., Pontzer, H., Sayre, K., Sancilio, A.,... Jones, J. H. (2021). Gendered movement ecology and landscape use in Hadza hunter-gatherers. *Nature Human Behaviour*, 5(4), 436–446.
49. Antón, S. C., Potts, R., and Aiello, L. C. (2014). Evolution of early Homo: an integrated biological perspective. *Science*, 345(6192), 1236828.
50. Carlson, K. J. and Marchi, D. (2014). *Reconstructing Mobility: Environmental, Behavioral, and Morphological Determinants*. Springer US: Imprint: Springer, New York, NY, 1st edition.
51. Wall-Scheffler, C. M. (2012). Size and shape: morphology's impact on human speed and mobility. *Journal of Anthropology*. doi:10.1155/2012/340493
52. Holt, B., and Whittey, E. (2019). The impact of terrain on lower limb bone structure. *American Journal of Physical Anthropology*, 168(4), 729–743.
53. Ruff Christopher, B., Holt, B., Niskanen, M., Sladek, V., Berner, M., Garofalo, E.,... Whittey, E. (2015). Gradual decline in mobility with the adoption of food production in Europe. *Proceedings of the National Academy of Sciences of the United States of America*, 112(23), 7147–7152.
54. Wall-Scheffler, C. M. (2014). The balance between burden carrying, variable terrain, and thermoregulatory pressures in assessing morphological variation. In K. J. Carlson and D. Marchi (Eds.), *Reconstructing Mobility*. New York, NY: Springer.
55. Allen, J. A. (1877). The influence of physical conditions in the genesis of species. *Radical Review*, 1, 108–140.
56. Ruff, C. B. (1994). Morphological adaptation to climate in modern and fossil hominids. *American Journal of Physical Anthropology*, 37(S19), 65–107.
57. Hancock Angela, M., Witonsky David, B., Ehler, E., Alkorta-Aranburu, G., Beall, C., Gebremedhin, A.,... Di Rienzo, A. (2010). Human adaptations to diet, subsistence, and ecoregion are due to subtle shifts in allele frequency. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 8924–8930.
58. Haygood, R., Fedrigo, O., Hanson, B., Yokoyama, K.-D., and Wray, G. (2007). Promoter regions of many neural- and nutrition-related genes have experienced positive selection during human evolution. *Nature Precedings*. doi:10.1038/ng2104
59. Perry, G. H., Dominy, N. J., Claw, K. G., Lee, A. S., Fiegler, H., Redon, R.,... Stone, A. C. (2007). Diet and the evolution of human amylase gene copy number variation. *Nature Genetics*, 39(10), 1256–1260.
60. Laland, K. N., Odling-Smee, J., and Myles, S. (2010). How culture shaped the human genome: bringing genetics and the human sciences together. *Nature Reviews Genetics*, 11(2), 137–148.
61. Rees, J. S., Castellano, S., and Andrés, A. M. (2020). The genomics of human local adaptation. *Trends in Genetics*, 36(6), 415–428.
62. Neel, J. V. (1962). Diabetes mellitus: a “thrifty” genotype rendered detrimental by “progress”? *American Journal of Human Genetics*, 14(4), 353–362.
63. Minster, R. L., Hawley, N. L., Su, C.-T., Sun, G., Kershaw, E. E., Cheng, H.,... McGarvey, S. T. (2016). A thrifty variant in CREBRF strongly influences body mass index in Samoans. *Nature Genetics*, 48(9), 1049–1054.
64. Myles, S., Hradetzky, E., Engelken, J., Lao, O., Nürnberg, P., Trent, R. J.,... Stoneking, M. (2007). Identification of a candidate genetic variant for the high prevalence of type II diabetes in Polynesians. *European Journal of Human Genetics*, 15(5), 584–589.
65. Brewis, A. A., Irwin, G., and Allen, J. S. (1995). Patterns of colonisation and the “thrifty” genotype in Pacific prehistory. *Asia Pacific Journal of Clinical Nutrition*, 4(4), 361–365.
66. Gosling, A. L., Buckley, H. R., Matisoo-Smith, E., and Merriman, T. R. (2015). Pacific populations, metabolic disease and ‘just-so stories’: a critique of the ‘thrifty genotype’ hypothesis in Oceania. *Annals of Human Genetics*, 79(6), 470–480.

67. Speakman, J. R. (2008). Thrifty genes for obesity, an attractive but flawed idea, and an alternative perspective: the 'drifty gene' hypothesis. *International Journal of Obesity*, 32(11), 1611–1617.
68. Pritchard, J. K., Pickrell, J. K., and Coop, G. (2010). The genetics of human adaptation: hard sweeps, soft sweeps, and polygenic adaptation. *Current Biology*, 20(4), R208–R215.
69. Fix, A. G. (2004). Kin-structured migration: causes and consequences. *American Journal of Human Biology*, 16(4), 387–394.
70. Rogers, A. R. (1988). Three components of genetic drift in subdivided populations. *American Journal of Physical Anthropology*, 77(4), 435–449.
71. Kalmijn, M. (1998). Inter-marriage and homogamy: causes, patterns, trends. *Annual Review of Sociology*, 24(1), 395–421.
72. Casey, B. J., Getz, S., and Galvan, A. (2008). The adolescent brain. *Developmental Review*, 28(1), 62–77.
73. Kelley, A. E., Schochet, T., and Landry, C. F. (2004). Risk taking and novelty seeking in adolescence: introduction to part I. *Annals of the New York Academy of Sciences*, 1021(1), 27–32.
74. Mittal, C., Griskevicius, V., Simpson, J. A., Sung, S., and Young, E. S. (2015). Cognitive adaptations to stressful environments: When childhood adversity enhances adult executive function. *Journal of Personality and Social Psychology*, 109(4), 604–621.
75. Heyes, C. (2018). *Cognitive Gadgets*. Harvard University Press.
76. Cashdan, E. and Gaulin, S. J. C. (2016). Why go there? Evolution of mobility and spatial cognition in women and men. *Human Nature*, 27(1), 1–15.
77. Cashdan, E., Kramer, K. L., Davis, H. E., Padilla, L., and Greaves, R. D. (2016). Mobility and Navigation among the Yucatec Maya. *Human Nature*, 27(1), 35–50.
78. Vashro, L., Padilla, L., and Cashdan, E. (2016). Sex differences in mobility and spatial cognition. *Human Nature*, 27(1), 16–34.
79. Ebstein, R. P., Novick, O., Umansky, R., Priel, B., Osher, Y., Blaine, D.,... Belmaker, R. H. (1996). Dopamine d4 receptor (d4dr) exon iii polymorphism associated with the human personality trait of novelty seeking. *Nature Genetics*, 12(1), 78–80.
80. Chen, C., Burton, M., Greenberger, E., and Dmitrieva, J. (1999). Population migration and the variation of dopamine d4 receptor (drd4) allele frequencies around the globe. *Evolution and Human Behavior*, 20(5), 309–324.
81. Matthews, L. J., and Butler, P. M. (2011). Novelty-seeking drd4 polymorphisms are associated with human migration distance Out-of-Africa after controlling for neutral population gene structure. *American Journal of Physical Anthropology*, 145(3), 382–389.
82. Gören, E. (2016). The biogeographic origins of novelty-seeking traits. *Evolution and Human Behavior*, 37(6), 456–469.
83. Eisenberg, D. T. A., Campbell, B., Gray, P. B., and Sorenson, M. D. (2008). Dopamine receptor genetic polymorphisms and body composition in undernourished pastoralists: An exploration of nutrition indices among nomadic and recently settled Ariaal men of northern Kenya. *BMC Evolutionary Biology*, 8(1), 173.
84. Munafò, M. R., Yalcin, B., Willis-Owen, S. A., & Flint, J. (2008). Association of the dopamine D4 receptor (DRD4) gene and approach-related personality traits: meta-analysis and new data. *Biological Psychiatry*, 63(2), 197–206.
85. Campbell, B. C., and Barone, L. (2012). Evolutionary basis of human migration. In M. H. Crawford and B. C. Campbell (Eds.), *Causes and Consequences of Human Migration: An Evolutionary Perspective*. Cambridge: Cambridge University Press.
86. Shaw, B., Hawkins, S., Becerra-Valdivia, L., Turney, C. S. M., Cox, S., Kewibu, V., ... Brooker and Panaeati Island communities, Papua New Guinea. N. G. (2022). Frontier Lapita interaction with resident Papuan populations set the stage for initial peopling of the Pacific. *Nature Ecology and Evolution*, 6, 802–812.
87. Wilmshurst, J. M., Hunt, T. L., Lipo, C. P., and Anderson, A. J. (2011). High-precision radiocarbon dating shows recent and rapid initial human colonization of East Polynesia. *Proceedings of the National Academy of Sciences of the United States of America*, 108(5), 1815–1820.
88. Gray, R. D., and Jordan, F. M. (2000). Language trees support the express-train sequence of Austronesian expansion. *Nature*, 405, 1052–1055.
89. Irwin, G. (1992). *The Prehistoric Exploration and Colonisation of the Pacific*. Cambridge: Cambridge University Press.
90. Irwin, G. (2008). Pacific seascapes, canoe performance, and a review of Lapita voyaging with regard to theories of migration. *Asian Perspectives*, 47(1), 12–27.
91. Clarke, A. C., Cordero, M.-A., Green, R. C., Irwin, G., Klar, K. A., Quiróz, D.,... Weisler, M. I. (2011). *Polynesians in America: Pre-Columbian Contacts With the New World*. Lanham: Rowman Altamira.
92. Haddon, A. C., and Hornell, J. (1936). *Canoes of Oceania*. Honolulu: Bernice P. Bishop Museum.
93. Beheim, B. A., and Bell, A. V. (2011). Inheritance, ecology and the evolution of the canoes of east Oceania. *Proceedings of the Royal Society B: Biological Sciences*, 278, 3089–3095.
94. Rogers, D. S., and Ehrlich, P. R. (2008). Natural selection and cultural rates of change. *Proceedings of the National Academy of Sciences of the United States of America*, 105(9), 3416–3420.
95. Mitchell, P. (2015). *Horse Nations: The Worldwide Impact of the Horse on Indigenous Societies Post-1492*. New York, NY: Oxford University Press.
96. Larson, G., and Fuller, D. Q. (2014). The evolution of animal domestication. *Annual Review of Ecology, Evolution, and Systematics*, 45(1), 115–136.
97. Marshall, F., and Weissbrod, L. (2011). Domestication processes and morphological change: through the lens of the donkey and African pastoralism. *Current Anthropology*, 52(S4), S397–S413.
98. Aporta, C. (2004). Routes, trails and tracks: trail breaking among the Inuit of Igloodik. *Études/Inuit/Studies*, 28(2), 9–38.
99. Riesenberg, S. H. (1972). The organisation of navigational knowledge on Puluwat. *The Journal of the Polynesian Society*, 81(1), 19–56.
100. Finney, B. (2003). *Sailing in the Wake of the Ancestors: Reviving Polynesian Voyaging*. Honolulu: Bishop Museum Press.
101. Genz, J. (2011). Navigating the revival of voyaging in the Marshall islands: predicaments of preservation and possibilities of collaboration. *The Contemporary Pacific*, 23(1), 1–34.
102. Al Hosani, N. M. (2005). Arab wayfinding on land and at sea: an historical comparison of traditional navigation techniques. (M.A.). University of Kansas, Ann Arbor.
103. Constable, A. R., and Facey, W. (Eds.). (2013). *The Principles of Arab Navigation*. London: Arabian Publishing London.
104. Aporta, C., and Higgs, E. (2005). Satellite culture: global positioning systems, inuit wayfinding, and the need for a new account of technology. *Current Anthropology*, 46(5), 729–753.
105. Low, S. (Writer). (1983). *The Navigators: Pathfinders of the Pacific*. In S. Low (Producer). USA: Documentary Educational Resources (DER).
106. Bellwood, P. (1996). Hierarchy, founder ideology and Austronesian expansion. In J. J. Fox and C. Sather (Eds.), *Origins, Ancestry and Alliance: Explorations in Austronesian Ethnography*. Canberra: ANU Press.
107. Richerson, P., Baldini, R., Bell, A. V., Demps, K., Frost, K., Hillis, V.,... Zefferman, M. (2014). Cultural group selection plays an essential role in explaining human cooperation: a sketch of the evidence. *Behavioral and Brain Sciences*, 39, E30.
108. Kelly, R. C. (1985). *The Nuer Conquest: The Structure and Development of an Expansionist System*. Ann Arbor: University of Michigan Press.
109. Bellwood, P. (2001). Early agriculturalist population diasporas? Farming, languages, and genes. *Annual Review of Anthropology*, 30(1), 181–207.

110. Turchin, P. (2010). Warfare and the evolution of social complexity: a multilevel-selection approach. *Structure and Dynamics*, 4(3). doi:10.5070/SD943003313
111. Turner, F. J. (1920). *The frontier in American history*. New York: Henry Holt and Company.
112. Bazzi, S., Fiszbein, M., and Gebresilasse, M. (2020). Frontier culture: the roots and persistence of "rugged individualism" in the United States. *Econometrica*, 88(6), 2329–2368.
113. Portes, A. and Rumbaut, R. G. (2014). *Immigrant America: A Portrait*. Berkeley: University of California Press. 4th edition.
114. Semyonov, M., Rajjman, R., and Gorodzeisky, A. (2006). The rise of anti-foreigner sentiment in European societies, 1988–2000. *American Sociological Review*, 71(3), 426–449.
115. Cohen, E. (2012). The evolution of tag-based cooperation in humans. *Current Anthropology*, 53(5), 558–616.
116. Efferson, C., Lalive, R., and Fehr, E. (2008). The coevolution of cultural groups and ingroup favoritism. *Science*, 321(5897), 1844–1849.
117. McElreath, R., Boyd, R., and Richerson, P. J. (2003). Shared norms and the evolution of ethnic markers. *Current Anthropology*, 44(1), 122–129.
118. Rand, D. G., and Nowak, M. A. (2013). Human cooperation. *Trends in Cognitive Sciences*, 17(8), 413–425.
119. Cashdan, E., and Steele, M. (2013). Pathogen prevalence, group bias, and collectivism in the standard cross-cultural sample. *Human Nature*, 24(1), 59–75.
120. Chagnon, N. A. (1988). Life histories, blood revenge, and warfare in a tribal population. *Science*, 239(4843), 985.
121. Fincher, C. L., and Thornhill, R. (2012). Parasite-stress promotes ingroup assortative sociality: The cases of strong family ties and heightened religiosity. *Behavioral and Brain Sciences*, 35(2), 61–79.
122. Primov, G. (1974). Aymara-Quechua relations in Puno. *International Journal of Comparative Sociology*, 15(3–4), 167–181.
123. Jackson, J. E. (1983). *The Fish People: Linguistic Exogamy and Tukanoan Identity in Northwest Amazonia*. Cambridge: Cambridge University Press.
124. Tindale, N. B. (1953). Tribal and intertribal marriage among the Australian aborigines. *Human Biology*, 25, 169–190.
125. McFarland, D. D. (1970). Effects of group size on the availability of marriage partners. *Demography*, 7(4), 411–415.
126. Kramer, K. L., Ryan Schacht, and Adrian Bell (2017). Adult sex ratios and partner scarcity among hunter-gatherers: implications for dispersal patterns and the evolution of human sociality. *Philosophical Transactions of the Royal Society B*, 372, 20160316.
127. Reich, D. (2018). *Who We Are and How We Got Here: Ancient DNA and the new science of the human past*. Oxford: Oxford University Press.
128. Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., ... Schaik, C. P. V. (2008). Fission-fusion dynamics: new research frameworks. *Current Anthropology*, 49(4), 627–654.
129. Moya, C., and Boyd, R. (2016). The evolution and development of inferential reasoning about ethnic markers: comparisons between urban United States and rural Highland Peru. *Current Anthropology*, 57(S13), S131–S144.
130. Goldstein, J. R., and Stecklov, G. (2016). From Patrick to John F.: ethnic names and occupational success in the last era of mass migration. *American Sociological Review*, 81(1), 85–106.
131. Bertrand, M., and Mullainathan, S. (2004). Are Emily and Greg more employable than Lakisha and Jamal? A field experiment on labor market discrimination. *American Economic Review*, 94(4), 991–1013.
132. Dillard, J. L. (1972). *Black English: Its History and Usage in the United States*. New York: Random House.
133. Dodsworth, R. (2017). Migration and dialect contact. *Annual Review of Linguistics*, 3(1), 331–346.
134. Hagan, J., and Ebaugh, H. R. (2003). Calling upon the sacred: migrants' use of religion in the migration process. *International Migration Review*, 37(4), 1145–1162.
135. Hirschman, C. (2004). The role of religion in the origins and adaptation of immigrant groups in the United States. *International Migration Review*, 38(3), 1206–1233.
136. Wilson, K. L., and Portes, A. (1980). Immigrant enclaves: an analysis of the labor market experiences of Cubans in Miami. *American Journal of Sociology*, 86(2), 295–319.
137. Portes, A., and Manning, R. D. (2018). The immigrant enclave: theory and empirical examples. In D. B. Grusky and S. Szélenyi (Eds.), *Inequality: Classic Readings in Race, Class, and Gender*. New York: Routledge.
138. Bunce, J., and McElreath, R. (2018). Sustainability of minority culture when inter-ethnic interaction is profitable. *Nature Human Behaviour*, 2(3), 205–212.
139. Edin, P.A., Fredriksson, P., and Aslund, O. (2003). Ethnic enclaves and the economic success of immigrants—evidence from a natural experiment. *The Quarterly Journal of Economics*, 118(1), 329–357.
140. Brettell, C. B. (1981). Is the ethnic community inevitable? A comparison of the settlement patterns of Portuguese immigrants in Toronto and Paris. *The Journal of Ethnic Studies*, 9(3), 1–17.
141. Rumbaut, R. G. (2008). Reaping what you sow: immigration, youth, and reactive ethnicity. *Applied Developmental Science*, 12(2), 108–111.
142. Higgs, R. (1978). Landless by law: Japanese immigrants in California agriculture to 1941. *The Journal of Economic History*, 38(1), 205–225.
143. Wimmer, A. (2013). *Ethnic Boundary Making: Institutions, Power, Networks*. Oxford: Oxford University Press.
144. Kwong, P. (1997). Manufacturing ethnicity. *Critique of Anthropology*, 17(2), 365–387.
145. Castles, S. (2002). Migration and community formation under conditions of globalization. *International Migration Review*, 36(4), 1143–1168.
146. Kiliç, N., Williams, A. M., and Hanna, P. (2022). From 'inbetweeners' to 'transcultural mediators': Turkish-German second-generation's narratives of 'return' migration, third spaces and re-invention of the self. *Ethnic and Racial Studies*, 45(14), 1–23.
147. Lee, H. M. (2003). *Tongans Overseas: Between Two Shores*. Honolulu: University of Hawai'i Press.
148. Small, C. (1997). *Voyages: from Tongan villages to American Suburbs*. Ithaca, NY: Cornell University Press.
149. Han, W.J. (2010). Bilingualism and socioemotional well-being. *Children and Youth Services Review*, 32(5), 720–731.
150. Müller, L.-M., Howard, K., Wilson, E., Gibson, J., and Katsos, N. (2020). Bilingualism in the family and child well-being: a scoping review. *International Journal of Bilingualism*, 24(5–6), 1049–1070.
151. Portes, A., and Hao, L. (2002). The price of uniformity: language, family and personality adjustment in the immigrant second generation. *Ethnic and Racial Studies*, 25(6), 889–912.
152. Kitayama, S., Ishii, K., Imada, T., Takemura, K., and Ramaswamy, J. (2006). Voluntary settlement and the spirit of independence: evidence from Japan's "northern frontier". *Journal of Personality and Social Psychology*, 91(3), 369–384.
153. Knudsen, A. S. B. (2019). *Those Who Stayed: Individualism, Self-Selection and Cultural Change During the Age of Mass Migration* (January 24, 2019). Available at SSRN: <https://ssrn.com/abstract=3321790>; or <https://doi.org/10.2139/ssrn.3321790>
154. Boyd, R., and Richerson, P. J. (1987). The evolution of ethnic markers. *Cultural Anthropology*, 2(1), 65–79.
155. Alba, R., and Nee, V. (1997). Rethinking assimilation theory for a new era of immigration. *International Migration Review*, 31(4), 826–874.
156. Atran, S., Medin, D., Ross, N., Lynch, E., Vapnarsky, V., Ek', E. U., ... Baran, M. (2002). Folkeology, cultural epidemiology, and the spirit

- of the commons: a garden experiment in the Maya Lowlands, 1991-2001. *Current Anthropology*, 43(3), 421-450.
157. South, S. J., Crowder, K., and Chavez, E. (2005). Migration and spatial assimilation among U.S. Latinos: classical versus segmented trajectories. *Demography*, 42(3), 497-521.
 158. Berry, J. W. (1992). Acculturation and adaptation in a new society. *International Migration*, 30(s1), 69-85.
 159. Berry, J. W. (2007). Acculturation strategies and adaptation. In J. E. Lansford, K. Deater-Deckard, & M. H. Bornstein (Eds.), *Immigrant Families in Contemporary Society* (pp. 69-82). New York: The Guilford Press.
 160. Laland, K. N., Odling-Smee, J., and Feldman, M. W. (2001). Cultural niche construction and human evolution. *Journal of Evolutionary Biology*, 14(1), 22-33.
 161. Anderson, E. (1952). *Plants, Man and Life*. Boston: Little, Brown.
 162. Kirch, P. V. (1982). The impact of the prehistoric Polynesians on the Hawaiian ecosystem. *Pacific Science*, 36(1), 1-14.
 163. Kirch, P. V. (1982). Transported landscapes. *Natural History*, 91(12), 32-35.
 164. Kirch, P. V. (2000). *On the Road of the Winds: An Archeological History of the Pacific Islands Before European Contact*. Berkeley, CA: University of California Press.
 165. Ejarque, A., Anderson, R. S., Simms, A. R., and Gentry, B. J. (2015). Prehistoric fires and the shaping of colonial transported landscapes in southern California: a paleoenvironmental study at Dune Pond, Santa Barbara County. *Quaternary Science Reviews*, 112, 181-196.
 166. Berman, M. J., and Pearsall, D. M. (2020). Crop dispersal and Lucayan tool use: investigating the creation of transported landscapes in the Central Bahamas through Starch Grain, Phytolith, Macrobotanical, and artifact studies. *Journal of Field Archaeology*, 45(5), 355-371.
 167. Henrich, J. (2004). Demography and cultural evolution: how adaptive cultural processes can produce maladaptive losses—the Tasmanian case. *American Antiquity*, 69(2), 197-214.
 168. Derex, M., Beugin, M.P., Godelle, B., and Raymond, M. (2013). Experimental evidence for the influence of group size on cultural complexity. *Nature*, 503(7476), 389-391.
 169. Bell, A. V. (2015). Linking observed learning patterns to the evolution of cultural complexity. *Current Anthropology*, 56(2), 277-281.
 170. Helu, F. (1993). Identity and change in Tongan society since European contact. *Journal de la Société des Océanistes*, 97, 184-194.
 171. Bell, A. V., and Hernandez, D. (2017). Cooperative learning groups and the evolution of human adaptability. *Human Nature*, 28(1), 1-15.
 172. Ozgen, C., Nijkamp, P., and Poot, J. (2012). Immigration and innovation in European regions. In P. Nijkamp, J. Poot, & M. Sahin (Eds.), *Migration Impact Assessment* (pp. 261-298), Gloucestershire: Edward Elgar Publishing.
 173. Powell, A., Shennan, S., and Thomas, M. G. (2009). Late Pleistocene demography and the appearance of modern human behavior. *Science*, 324(5932), 1298-1301.
 174. Derex, M., and Boyd, R. (2016). Partial connectivity increases cultural accumulation within groups. *Proceedings of the National Academy of Sciences of the United States of America*, 113(11), 2982-2987.
 175. Feinberg, R. (1988). *Polynesian Seafaring and Navigation: Ocean Travel in Anutan Culture and Society*. Kent, OH: Kent State University Press.
 176. Gonzalez, N. (1961). Family organization in five types of migratory wage labor. *American Anthropologist*, 63, 1264-1280.
 177. Chavez, L. (1988). Settlers and Sojourners: the case of Mexicans in the United States. *Human Organization*, 47(2), 95-108.
 178. Margolis, M. L. (1995). Transnationalism and popular culture: the case of Brazilian immigrants in the United States. *The Journal of Popular Culture*, 29(1), 29-41.
 179. Gmelch, G. (1980). Return migration. *Annual Review of Anthropology*, 9, 135-159.
 180. Lee, H. M., and Francis, S. T. (Eds.). (2009). *Migration and Transnationalism: Pacific Perspectives*. Canberra: ANU E Press.

AUTHOR BIOGRAPHY

Adrian Viliami Bell is an associate professor of anthropology who works on the dynamics of identity, ethnic marking, migration, and culture. He conducts fieldwork in the Kingdom of Tonga and among the Tongan diaspora of Utah.

How to cite this article: Bell, A. V. (2023). Selection and adaptation in human migration. *Evolutionary Anthropology*, 1-17. doi:10.1002/evan.22003