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Opinion

The Tangled Evolutionary Legacies of Range Expansion and Hybridization

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Spatial sorting of dispersal-enhancing traits has been implicated in substantial directional changes in the phenotypic and genotypic makeup of populations undergoing range expansion. We explore here the evolutionary consequences of such changes when two divergent lineages come into secondary contact. We combine instances from the study of contemporary range expansions and historical hybridizations, and highlight links between dispersal, sexual, and physiological traits during the non-equilibrium conditions imposed by range expansions. We argue that a stronger research focus on processes of spatial sorting of multiple traits will improve our understanding of subsequent hybridization dynamics and their evolutionary outcomes, including genomic introgression and speciation.

Historical Hybridizations and Contemporary Range Expansions

Hybridization (see Glossary) between divergent lineages can have fundamental evolutionary consequences, shaping reproductive isolation, **introgression**, hybrid speciation, and even adaptive radiations [1]. However, a full appraisal of the many processes contributing to this diversity of outcomes, and of their relative roles, has long been hampered by the inherent difficulties of observing these processes directly (but see e.g., [2]). In a natural world increasingly altered by humans, where many animal populations are forced to adapt *in situ*, move, or face extinction, opportunities to study evolutionary processes in action are now increasing [3–5], further augmented by technological and analytical advances (e.g., [6,7]).

Much of our knowledge about the role of hybridization in evolution comes from the study of **hybrid zones** formed from **range expansions** and secondary contacts during Quaternary environmental change [8]. The complexity of evolutionary processes triggered by the formation of hybrid zones has been explained primarily through various combinations of drift, natural selection, and sexual selection, before and after the range expansion phase [1]. Moreover, most evolutionary models applied to study these processes assume that range expansions were initiated and propagated by individuals carrying random samples of the genotypic and phenotypic diversity of source populations – in other words, that **dispersal** is an essentially stochastic process (e.g., [9–11]). However, recent advances in the study of contemporary range expansions and other spatial processes (e.g., metapopulations, gene flow, source–sink dynamics) do not support this assumption [12–14]. Instead, it is becoming clear that dispersers often carry suites of traits enhancing dispersal propensity and ability, and that the spatial sorting of these traits during range expansions can cause deterministic changes in the phenotypic and genotypic makeup of expanding populations [15–17].

Trends

Mounting data show that substantial, rapid, and deterministic changes in the phenotypic and genotypic makeup of populations can occur during range expansions by spatial sorting of dispersal-related traits.

Traits associated with dispersal also influence other fundamental biological processes, such as reproduction, physiology, and behavior.

Dispersal, sexual, physiological, and behavioral traits are of crucial importance for hybridization dynamics between divergent lineages upon secondary contact.

A stronger focus on multiple trait associations and spatial sorting during range expansion could improve our understanding of subsequent hybridization events and their evolutionary outcomes.

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We explore here how non-random, trait-based dispersal during range expansions affects subsequent hybridization dynamics and their major evolutionary outcomes. There is growing evidence that traits associated with dispersal also influence other fundamental biological processes of crucial importance for hybridization dynamics (e.g., reproduction, physiology, and behavior [18]). We characterize these trait associations and their population-level implications during the non-equilibrium conditions imposed by range expansions, and highlight how their non-random spatial sorting might affect hybridization dynamics upon secondary contact. We aim at stimulating broader empirical investigations and theoretical analyses of the evolutionary legacy of non-random dispersal during range expansion and secondary contact. A closer inspection and integration of the diverse processes which promote (and prevent) hybridization will help in addressing several unresolved issues concerning its role in evolution.

## Trait Sorting and Hitchhiking During Range Expansion

Range expansion is inherently a non-equilibrium process because it requires colonization of habitat previously unoccupied by the focal species, although the duration of this initial, non-equilibrium stage will vary depending on intrinsic and extrinsic factors (e.g., reproductive potential of the focal species, interactions with resident species). During this non-equilibrium phase, inter-individual variation in traits affecting dispersal becomes spatially assorted because, at each generation, the best dispersers aggregate at the expanding front, seeding new populations. Notably, inter-individual variation is an inherent property of all natural populations, with profound implications for non-equilibrium processes such as range expansion and hybridization that have long been neglected, most often for the sake of simplicity [19]. As the expansion wave advances, the process of spatial sorting can promote rapid directional evolution of traits favoring dispersal, thus further accelerating the establishment of populations in newly colonized areas [15–17]. The traits increasing dispersal ability might be discrete, but might also occur in **dispersal syndromes**. Interestingly, these traits – whether discrete or as components of dispersal syndromes – have also been implicated in other major organismal functions, as vividly exemplified by **animal personality** (Figure 1A–C).

Animal personality has become an area of active research in recent years [20], following evidence that it is implicated in central ecological and evolutionary processes across the animal kingdom [21,22]. Personality can influence the evolution of virtually all the features of an organism, including morphology, physiology, and genetics [22–25]. Personality is also a crucial contributor of the dispersal syndromes of a wide range of animal species (Figure 1A). Specifically, personality traits have been shown to influence the propensity to depart and explore novel habitats, dispersal distance, and the response to unfavorable conditions and new biotic interactions during both transience and settlement (see Table 1 in [26]). Moreover, new variants at other traits affecting dispersal (e.g., morphological, physiological) have been proposed to spread within and among populations by **hitchhiking** on personality traits [24]. Several personality traits show a variable degree of plasticity in response to environmental factors both during ontogeny and adulthood [27], which adds another level of complexity but also an additional layer of variation that is immediately available for coping with the challenges encountered during range expansion.

Many of the same personality traits that influence dispersal also affect and are affected by intrasexual competition, mate choice, and sexual selection [28] (Figure 1B). For example, personality traits such as boldness, exploration, activity, and aggression have been linked to major components of sexual selection, including reproductive success of the chosen sex and perceived quality of potential mates by the choosing sex [28]. Equally interconnected are animal personality and energy metabolism (Figure 1C). Personality traits affect food intake and rates of energy consumption [29–31], and significant associations have been found between metabolic rates and all personality traits [30,32]. Mitochondrial genes and mito-nuclear interactions also play a central role in energy metabolism, and patterns of mitochondrial DNA variation have long

Glossary

Animal personality: behavioral differences between conspecific individuals that are consistent across time and contexts.

Assortative mating: pattern of non-random mating. It can be positive, when individuals tend to mate with others having similar phenotype or genotype, or negative (also known as disassortative mating), when individuals preferentially mate with those of dissimilar phenotype or genotype.

Dispersal: permanent movement from the birth or breeding site, occurring in three steps: departure, transience, and settlement in the novel habitat.

Dispersal syndrome: covariation of multiple traits, such as behavioral, life-history, physiological, and morphological traits, associated with dispersal.

Hitchhiking effect: change in the state or frequency of a character (e.g., morphological, genetic, behavioral) which is not driven by processes acting directly on this character (e.g., natural selection) but on another trait to which it is tightly linked.

Hybrid zone: a geographic region where individuals belonging to genetically distinct populations come into contact, mate, and produce offspring of mixed ancestry.

Hybridization: mating between individuals from genetically distinct populations that produces offspring.

Introgression: incorporation of alleles from a species or population into the gene pool of a second, divergent population through hybridization and backcrossing of the hybrids with individuals from one of the parent populations.

Pre-mating isolation barriers: reproductive isolation mechanisms that prevent copulation between members of different populations through ecological, temporal, morphological, or behavioral isolation.

Reinforcement: the enhancement of pre-mating isolation barriers between sympatric taxa, driven by natural selection against maladaptive hybridization events.

Range expansion: colonization of a previously unoccupied area by a species or population that can occur by a series of small-scale dispersal events through contiguous habitats, or by long-distance movements, as in the case of island colonization.

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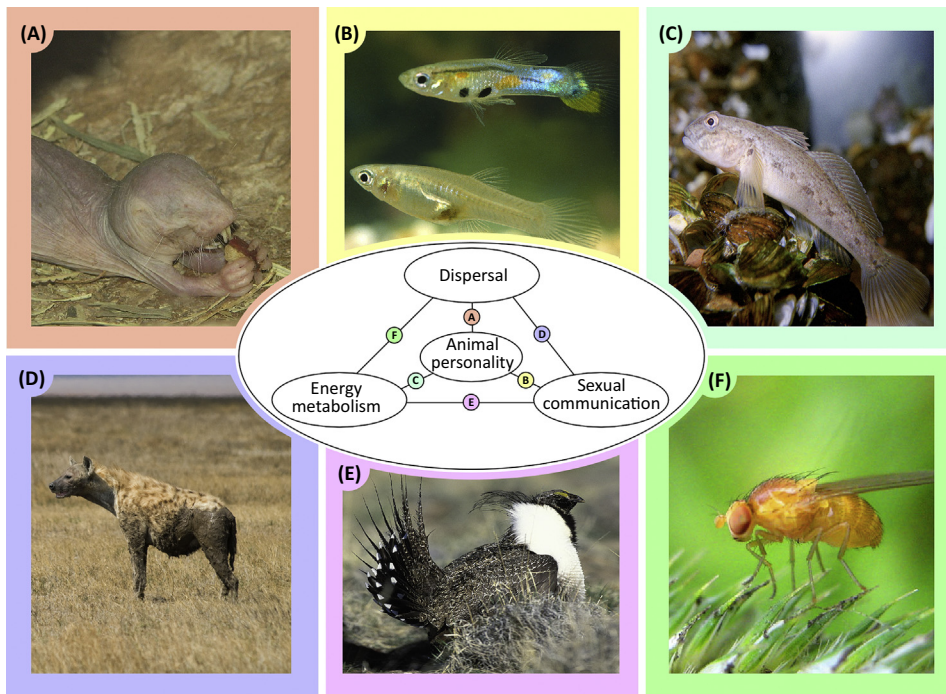
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Figure 1. Associations Among Dispersal, Sexual Communication, and Energy Metabolism Traits, and Their Mutual Links With Animal Personality. (A) Personality traits in all behavioral categories described in animals could contribute to the various steps of a dispersal process (departure, transience, settlement) [26]. In the naked mole (*Heterocephalus glaber*), a dispersal phenotype has been identified; dispersers are more active in foraging and movements, less social, and also larger and fatter than the average individual in the natal colony [69]. (B) Personality traits can influence survival and reproductive success [70]. In the Trinidadian guppies (*Poecilia reticulata*), bolder, more-active, and exploratory individuals cope better with predation risk, are usually more colorful, and are preferred by females over less-conspicuously colored males [71,72]. An elegant mate-choice experiment uncoupling color patterns from behavioral traits showed that female preferred bolder males, irrespective of their color, when they were given the opportunity to observe the behavior of the males [71]. (C) Being bolder, more exploratory, and more active could provide diverse benefits, but all are likely to involve changes in energy metabolism [29–31]. In the round goby (*Neogobius melanostomus*), bolder males showed not only higher dispersal tendency but also higher resting metabolic rates [73]. (D) Inbreeding avoidance and intrasexual competition have been implicated as primary causes of dispersal patterns, including the widespread pattern of sex-biased dispersal [74,75]. In the spotted hyena (*Crocuta crocuta*) dispersal is male-biased, as in many mammals, and this pattern appears to be promoted by female mate-choice to reduce the risk of incest [76]. (E) Honest signaling of male quality to females, and male–male competition, entail energy costs [43,77]. Consequently, during breeding activities, increased metabolic rates and significant weight loss have been documented in several animal species, including male sage grouse (*Centrocercus urophasianus*) [78]. (F) Resources available to an individual are finite, and dispersal is an extremely demanding activity [18]. In the fruit fly (*Drosophila melanogaster*), early experimental data documented substantial energy costs of dispersal, with implications for reproductive success [79]. Later studies [80] showed that allelic variation at a single gene with pleiotropic effects influences larval foraging behavior as well as adult dispersal propensity and probability of long-distance dispersal. Photo credits (Wikimedia Commons): (A), T. Shears; (B), A.E. Deacon, H. Shimadzu, M. Dornelas, I.W. Ramnarine, and A.E. Magurran; (C), E. Engbretson; (D), S. Nygaard; (E), G. Kramer; (F) Botaurus.

been used to infer historical range dynamics across a variety of environmental, spatial, and temporal scales [33]. Interestingly, recent experimental data from humans and non-human animals show that mitochondrial DNA variation is a driver of behavioral variation in traits such as boldness and activity [34–37].

Dispersal, sexual, and metabolic traits are tightly linked to one another, are heritable to varying degrees, and entail fitness consequences – independently of their association with personality [12,29,38] (Figure 1D–F). For example, dispersal and sexual activities are widely viewed as costly in terms of predation risk, competition, exposure to diseases and parasites, time and, notably,

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energy allocation [18,39]. Consequently, an extensive literature has analyzed and debated how trade-offs, selection, and constraints acting on one set of traits might influence evolutionary pathways in the others [18,32,40]. Furthermore, we know that these associations among dispersal, sex, and energy metabolism (as well as personality) can be driven by genes with pleiotropic effects [41] or by supergenes [42]. These links appear to be so intimate that authors have even hypothesized that each category of traits may be responsible for the genesis and maintenance of variation of traits in the other categories [28–30,43,44].

Growing evidence indicates that contemporary and past range expansions have been promoted and sustained by non-random – and non-average – phenotypes of the source populations [26], that the ecological and social contexts of source populations might dictate which phenotypes contribute to the expansion [45], and that context-dependent maternal effects could also be implicated [46–48]. Furthermore, the tight links among traits outlined above suggest that spatial sorting of dispersal-associated phenotypes sets the stage for the rapid evolution of traits affecting personality, sexual selection, and metabolic activity, through a hitchhiking effect. The strength and outcome of these sorting-related evolutionary processes are likely mediated by local factors at the expanding range front, particularly intraspecific density gradients and novel (often stressful) environmental conditions [49–52]. More broadly, the proximate drivers and long-term legacy of range expansion can be viewed as an interaction of these two sets of processes – sorting of dispersal-associated phenotypes and local ecological conditions. This interaction will play out along the expansion front to shape non-random patterns of spatial variation in a wider range of traits than those directly implicated with the evolution of dispersal. Interestingly, there is a growing body of evidence for changes in state or altered level of expression of the traits outlined above along expansion fronts, including extreme trait values (Box 1).

In the context of sexual selection, traits are intimately linked to choice. Changes in traits of the chosen sex should, to some extent, match the mating preference by the choosing sex to spread within a population (but see [53]). Likewise, traits might change in response to altered preferences. Interestingly, several lines of evidence suggest that mating patterns might change during range expansions. Females could become more choosy during range expansions, given the higher fitness differential between high- and low-quality mates under altered environmental conditions and lower demographic density [52,54]. Moreover, within equilibrium populations, individuals carrying extreme trait values (e.g., boldness) have been often found especially prone to **assortative mating** (e.g., by personality) [55,56]. Because these individuals are also those likely to contribute most to range expansions (see above), the tendency to mate assortatively could increase at the expansion front. In addition the over-representation of individuals with dispersal-enhancing traits (i.e., spatial sorting) will increase the frequency of mates with similar phenotypes at the expansion front [16], potentially increasing *de facto* rates of assortative mating even at very low population density, when females might become more flexible in their choosiness owing to a shortage of potential mates.

It is clear that we must move beyond the assumptions that range expansions are driven by random samples of the source population, and that the genotypic and phenotypic make-up of expanding lineages are shaped by drift and adaptation to novel environments alone. In the following we explore how this realization might help to improve our understanding of some hybridization patterns in secondary contact zones, and of the evolutionary implications of these patterns (Figure 2, Key Figure).

Range Expansion and Pre-Mating Barriers Against Hybridization
By promoting changes in multiple characters, including (but not limited to) behavioral, morphological, physiological, and sexually relevant characters, range expansions could influence the

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Box 1. Rapid Evolution of Multiple Traits During Range Expansions

Range expansions expose individuals to novel demographic and environmental conditions and, consequently, to novel evolutionary pressures. Density-dependent and condition-dependent processes (e.g., dispersal, growth, reproduction) are particularly affected by these novel conditions and, consequently, the traits sustaining these processes are likely to evolve rapidly, as exemplified by the following case studies.

Invasive Cane Toads in Australia

Introduced to Queensland from Hawaii in 1935, the cane toad (*Rhinella marina*) spread across tropical Australia for some 80 years at an accelerating pace (Figure IA). During this expansion, toad populations underwent substantial changes in traits promoting dispersal at the invasion front, such as longer legs, straighter dispersal paths, longer time spent in dispersal. In addition, toads at the invasion front have different immunology and reduced parasite load, lower rates of reproduction (not necessarily implying lower individual fitness), as well as significant upregulation of enzymes involved in energy metabolism and the response to oxidative stress, including nucleus-encoded mitochondrial enzymes (see [81–83]).

Fruit Fly Invasion in Eastern Australia

Some 100 years ago, *Drosophila melanogaster* fruit flies were introduced into northern Australia. Researchers observed substantial changes in several characters by comparing populations along the eastern coast of Australia, from the introduction site southward (Figure IA). Clines were documented in morphological traits (including wing size), life-history traits, stress tolerance, and metabolic enzymes (reviewed in [84]). Several of these clines have been associated with adaptation to novel environmental conditions at the invasion front, whereas the causes of other clines remain unknown. Notably, clinal variation was observed in cuticular hydrocarbons, which are involved in species- and mate-recognition mechanisms, as well as in wing size and shape, which affect dispersal ability, species-specific courtship song, and male mating success [85–87].

Recent Expansions of Juncos

Birds often show remarkable color variation within and among closely related species, as in the case of North American juncos (Figure IB). A phylogeographic investigation [88] revealed that a single continent-wide range expansion within the past 10 000 years promoted rapid diversification of plumage color patterns, often with a prominent increase in melanins (see also [41]). In the dark-eyed junco (*Junco hyemalis*), plumage coloration reflects dominance status and mating success, together with behavioral traits [89,90]. Furthermore, with the colonization of a novel anthropogenic habitat – a college campus – in the 1980s, dark-eyed juncos showed changes in suites of hormonal, behavioral, and life-history traits [91–93]. Colonists were bolder, more explorative, and less responsive to stressors, but also less aggressive and dark, likely as a consequence of adaptation to the open environment and a novel predatory context.
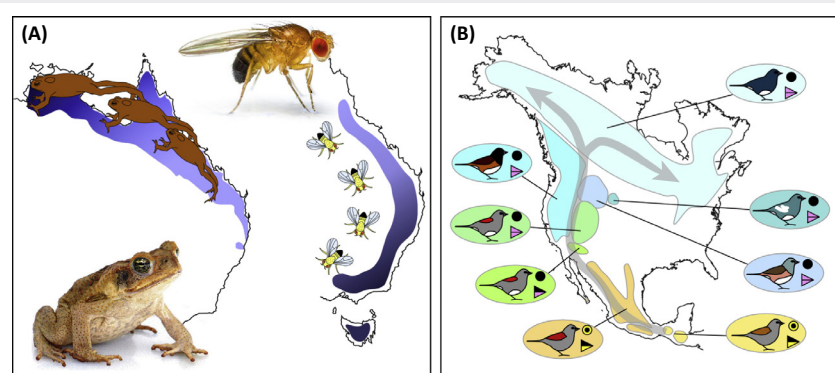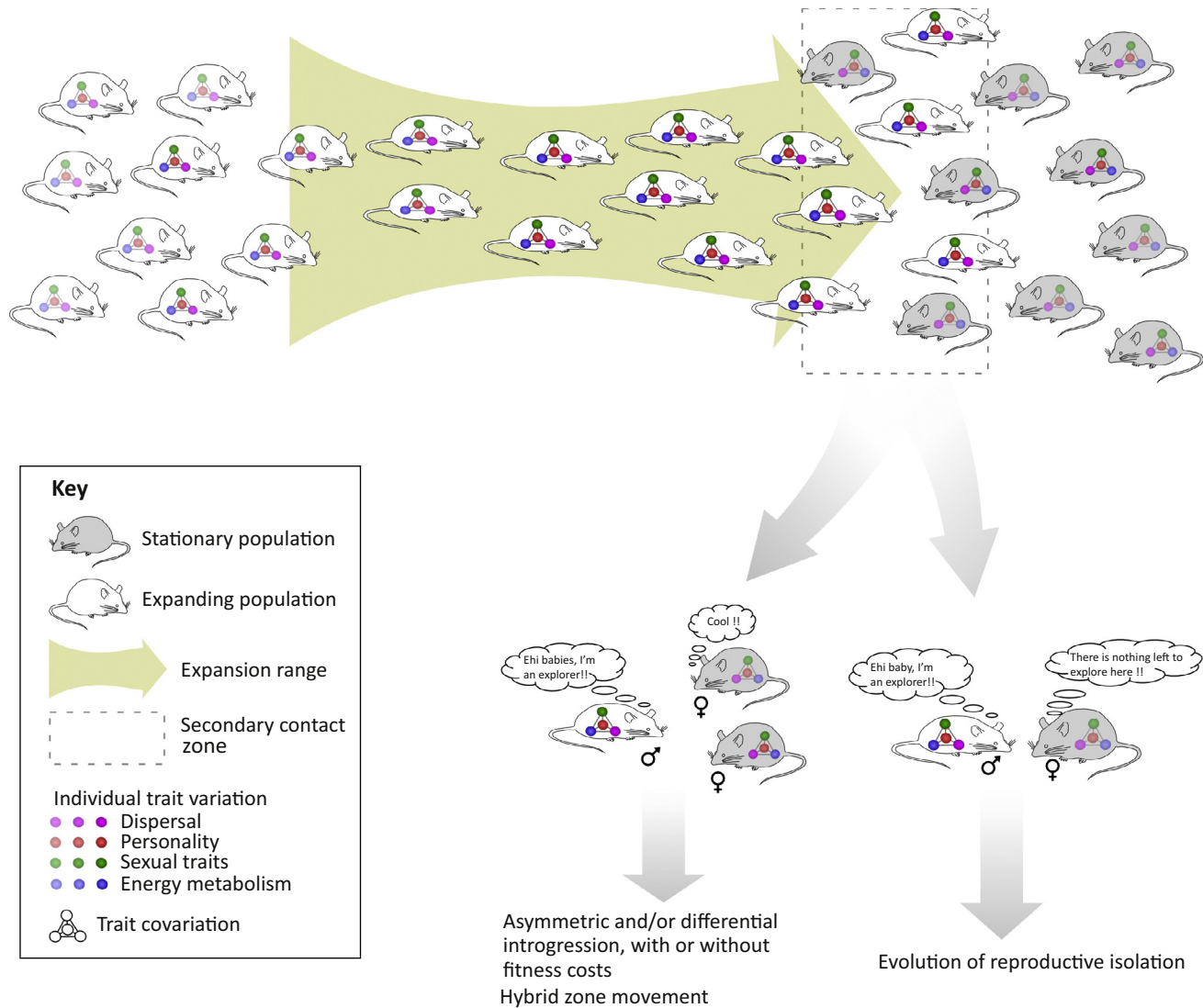

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Figure I. Phenotypic Changes During Recent Range Expansions. (A) During a biological invasion lasting about 80 years, cane toads underwent important phenotypic changes, including larger body size and longer legs, and the rate of spread of the expansion front across tropical Australia increased from about 10 km/year (light blue) to over 50 km/year (dark blue) [94]. In addition, while colonizing eastern Australia, but moving southward, fruit flies underwent substantial phenotypic changes, including changes in wing morphology, which is implicated in both flight abilities and sexual interactions [84–87]. Photo credits: S. Fraser-Smith (Wikimedia Commons); Roblan (Shutterstock). (B) Climate change since the last glacial maximum primed major reshuffling of the distributions of species across a wide range of animal and plant taxa worldwide. The remarkable variation of plumage color shown by Juncos across Central and North America originated during continent-wide range expansion which took place within the last 10 000 years [88]. Modified from [88].

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Key Figure

Spatial Sorting of Multiple Traits During Range Expansion Can Influence Hybridization Dynamics and Their Outcomes

Figure 2. Interindividual variation in traits affecting dispersal is documented in a wide range of species and populations. During range expansion, such variation becomes spatially assorted because, at each generation, the best dispersers will contribute most to the colonization of novel areas. However, traits affecting dispersal ability (e.g., personality and/or morphological traits) are often linked to other individual functions, such as sexual interactions and energy metabolism. As a consequence of such trait associations, covariation of individual traits can occur with range expansion, and populations at the expansion front will soon diverge from source populations in several traits. Upon secondary contact with a closely related and stationary lineage, the phenotypic and genotypic changes promoted by this process of spatial sorting will either increase or decrease the likelihood of heterotypic mating (i.e., hybridization), depending on several intrinsic and extrinsic factors (e.g., degree of incompatibility achieved between lineages, environmental context, extent and direction of trait changes). This influence of spatial sorting on hybridization dynamics will extend to their major evolutionary outcomes, including patterns of genomic introgression and speciation.

rate, cost, and outcome of hybridization at the onset of a secondary contact between divergent lineages.

Mate choice plays a central role in determining the likelihood of hybridization with secondary contact. Although hybridization can entail fitness costs, heterospecific mates can be favored in some circumstances, particularly during early phases of secondary contact. Following the northward range expansion of the Carolina chickadee (*Poecile carolinensis*), its hybrid zone with the black-capped chickadee (*P. atricapillus*) is moving to the north too [57]. In mate-choice tests [58], females of both species chose dominant males (usually *P. carolinensis*), irrespective of whether they were homo- or heterospecific, which have higher survival and gain better territories. Similar patterns have been reported in a wide range of taxonomic groups and between both intra- and interspecific lineages (e.g., [59,60]), and have been invoked to explain hybridization rate in the wild, hybrid zone movement, and asymmetric introgression (see next section). Remarkably, traits hypothesized to regulate mate recognition and the cost–benefit balance for heterotypic versus homotypic mates, including boldness, aggressiveness, body size, and metabolic rate, are now recognized as integral components of the 'dispersal phenotype', and have been shown to change in state and frequency along the expanding front. Therefore, range expansions could affect the direction, rate, and spatial extent of hybridization, as well as hybrid zone movement, in cases where a 'dispersal phenotype' gains advantages in terms of mate choice, dominance, or male–male competition.

Range expansions are also likely to affect the honesty of sexual signaling during early phases of hybridization. Boldness, for example, has been identified both as a component of the dispersal syndrome and a target for sexual selection. Nevertheless, other components of dispersal syndromes (e.g., faster exploration, higher metabolic rates) to which boldness is often bound during range expansions can be disadvantageous as population densities increase following the expansion phase [61]. Accordingly, traits signaling potentially high-quality mates under equilibrium conditions might 'dishonestly' favor low-quality hybrid mates during early phases of a secondary contact. Notably, traits favoring hybrid mates might *per se* turn into a dishonest signaling in the presence of even modest genomic incompatibility between the hybridizing lineages.

Conversely, range expansions could also reduce hybridization rates during the early phases of secondary contact. Specifically, phenotypic changes during the expansion phase could strengthen species recognition systems by fuelling divergence in sexually selected traits, and by promoting assortative mating within the expanding lineage (e.g., [52]). In these cases, spatial sorting of phenotypes during range expansion would contribute to building **pre-mating isolation barriers** against hybridization or could provide the raw material for subsequent **reinforcement**. An interesting implication of this scenario is that geographic clines in reproductive isolation outside the areas of range overlap (e.g., [62,63]) could be generated during the preceding range expansion rather than by gene flow from the sympatric to allopatric areas, as usually thought. Accordingly, pre-mating barriers might evolve during range expansions in the absence of post-mating isolation (i.e., without hybridization costs).

Greater consideration of the role of range expansion in molding pre-mating barriers against hybridization might help to explain some counterintuitive patterns observed in nature, where pre-mating isolation barriers are found to be stronger between allopatric than sympatric populations of the interacting lineages [64]. These patterns are very difficult to explain under a scenario of reinforcement of pre-mating barriers against hybridization, but they could be explained by the evolution of traits involved in pre-mating barriers during range expansions. Indeed, evidence for

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spatial sorting of multiple traits and for links between trait suites suggest that changes are likely to occur during range expansion. However, these factors do not dictate the direction of changes in mating barriers because they are driven primarily by spatial sorting of traits determining dispersal ability, not those involved in interspecific recognition. As a consequence, individual components of pre-mating barriers can emerge, be enhanced, or be suppressed during range expansion, and this can produce positive or negative clines in underlying traits along transects from allopatric to sympatric areas. Intriguing insights in this respect come from comparisons of song patterns in hand-raised versus wild-type nestlings of several songbirds (reviewed in [65]). Songs of birds raised untutored can differ substantially from those of their natal population. In several comparisons, songs of hand-raised individuals resembled wild-type songs of closely related species or subspecies. Furthermore, when housed together (i.e., not as isolates) hand-raised individuals usually sing similar songs. These findings suggest that small populations at the expanding range margin might diverge in song patterns from source populations and converge with other marginal populations in both song and recognition, possibly toward heterospecific patterns [65].

Range Expansion and Patterns of Introgressive Hybridization

Spatial sorting of multiple traits during range expansions could affect the direction and extent of gene exchange between the interacting lineages and, consequently, contribute to the shaping of several commonly observed patterns of introgressive hybridization between closely related species and intraspecific lineages. Specifically, these patterns include differential introgression between loci and asymmetric introgression between lineages.

Traits and genotypes that are adaptive under the non-equilibrium selective and demographic regimes at a range expansion front can become disadvantageous once the expansion phase ends. In the great tit (*Parus major*), experimental tests showed that fast explorers were selectively favored at low demographic densities, whereas slow explorers were favored at increasing densities [61]. Upon secondary contact with a resident interbreeding lineage, and in the absence of strong genetic incompatibilities, an expanding lineage could benefit from introgression of genetic variants from the resident, providing variation in behavioral, physiological, and other traits that are favored under equilibrium conditions (e.g., higher demographic density). More broadly, this process might contribute to the adaptive landscape favoring the asymmetric introgression often observed from residents toward expanding lineages [26].

Differential introgression patterns might also arise from disparities between lineages in sexual traits and preferences that are established during range expansion. As discussed above, sexual traits and preferences can evolve not only during the allopatric and secondary sympatric phases but also during range expansions (or through various combinations of processes active during either phase). In the common wall lizard (*Podarcis muralis*), an elegant experimental design analyzing both natural and human-driven secondary contact zones showed that asymmetric introgression patterns have arisen from differences in male competitive ability and mating success between two intraspecific lineages, promoted by significant behavioral and morphological trait divergences [59]. In addition, in the spotted salamander (*Ambystoma maculatum*) a preference by females of one lineage for larger males of a second lineage has been recently hypothesized to explain the geography of mito-nuclear discordances across a hybrid zone in central USA [60].

Finally, spatial sorting of dispersal traits during range expansions could help to explain the rapid spread of introgressive hybridization even in cases of reduced Darwinian fitness of hybrids, as illustrated by studies of hybridization dynamics between native and introduced lineages (Box 2).

Box 2. Range Expansion and Hybridization in Real Time

Species introductions and the alteration of natural environments have led to hybridization between previously geo-graphically isolated species [95–97]. In some cases these conditions lead to introgressive hybridization, where genes from a non-native species spread through populations of a native species by hybridization and fertility of the hybrid progeny. While hardly desirable, these cases of introgressive hybridization enable direct observation of the complex evolutionary processes that occur when range expansion and hybridization coincide.

The spread of introgressive hybridization appears to be regulated by both the fitness and dispersal propensity of hybrids. When hybrids have increased Darwinian fitness relative to the native parental species (i.e., survival and reproductive success), introgressive hybridization is likely to advance across the native range. In these cases, the rate of advance is determined by the fitness differential (e.g., the selective advantage of hybrid genotypes within invaded populations, and the number of hybrid offspring available to colonize uninvaded populations), as well as the dispersal propensity of hybrids. However, introgressive hybridization can also spread rapidly when hybrids have reduced Darwinian fitness [98], suggesting that dispersal rates of hybrids can play a primary role in the advance of introgressive hybridization [99].

High dispersal rates can introduce low-fitness hybrids to native populations, but shouldn't selection against hybrids within invaded populations halt further advances? We see here the influence of the genomic ratchet during range expansion, where all of the progeny of a hybrid are hybrids, irrespective of the identity of the other parent (e.g., hybrid, non-native, native). Consequently, even a few hybrids in the breeding population are enough to ensure the retention and proliferation of non-native genes [100,101]. Genomic data from contemporary cases of introgressive hybridization show the strength of the genomic ratchet, as well as the ineffectiveness of natural selection at removing introgressed genes from populations [102–106].

Introgressive hybridization between introduced rainbow trout (*Oncorhynchus mykiss*) and native westslope cutthroat trout (*O. clarkii lewisi*) has spread rapidly over the past 30 years [102], even though the native trout is favored by natural selection [98]. This spread occurs because hybrid fish are much more likely to disperse to other streams than are native trout [106]. Admixture with the non-native barred tiger salamander (*Ambystoma tigrinum mavortium*) has spread across ~20% of the range of the native California tiger salamander (*A. californiense*) [103]. Field and experimental data show native-genotype fitness advantages in the ephemeral ponds that dominate undisturbed native grasslands, but hybrid fitness advantages in perennial ponds [107,108]. It appears, therefore, that both hybrid dispersal and wetland mod-ification promoted introgressive hybridization in this system. Finally, hybridization is thought to promote rapid invasive-ness in plants [109–111], and invasive plants often have traits in the new range that promote greater dispersal than in the home range [112,113].

Concluding Remarks and Future Directions

Dispersal and range expansion dynamics play a central role in the formation of geographic patterns of biological diversity, variation over time in these patterns, the spread of individuals and novel traits out of their place of origin, species response to environmental changes when *in situ* adaptation is not an option, and the formation of hybrid zones between previously allopatric populations. Accordingly, range expansions have gained considerable attention in ecology, evolution, and the subdisciplines of biogeography, population genetics, climate change biology, and invasion biology. In many respects, however, research on ecological and evolutionary implications of range expansions suffers from 'the tyranny of the golden mean' [66], a drawback still shared by most areas of the life sciences. Specifically, interindividual diversity, albeit ubiquitous within natural populations, is commonly summarized and analyzed with descriptive statistics, thus sacrificing insight on the biological meaning of such diversity. Increasing appre-ciation of the crucial importance of such diversity is opening exciting new avenues in several research fields (e.g., [19,20,29,67]).

Taking interindividual diversity in correlated traits into account, and considering the role of non-average individuals, leads to the view that non-equilibrium conditions during range expansion can be 'creative', rather than merely transient, with lasting evolutionary and ecological legacies. As we have attempted to illustrate here, this changing view has far-reaching implications, opening urgent questions (see Outstanding Questions) and providing fresh insight on many research fields dealing with both historical and contemporary processes molding biodiversity patterns (e.g., [68]). How could one not agree with Grant and Grant [2]? – these are exciting times to be an evolutionary biologist.

Outstanding Questions

What are the mechanistic bases of trait associations affecting and affected by range expansions and hybridizations? Pleiotropy, epistatic interactions, as well as structural and functional link-ages, have been identified between traits and genes implicated in a wide range of organismal functions, includ-ing personality, energy metabolism, immune function, sexual interactions, and dispersal ability. However, data are mostly available for a few model organisms studied under controlled and/or equilibrium conditions. More data on a wider range of species, envi-ronmental contexts, and trait suites will be necessary.

To what extent does environmental, demographic, social context, and tem-poral variation in these contexts (e.g., under stressful conditions) influence patterns of association among traits within source, expanding, and hybrid-izing populations? In addition, what is the role of heritable epigenetic changes and plastic responses in this regard?

How widespread are non-random spa-tial patterns of (co)variation of multiple traits and preferences across the range of recently expanded populations? Spatial patterns of variation have been documented for a wide range of traits and study organisms. However, spatial covariation in multiple traits is seldom investigated, and even more rare are studies setting spatial patterns of trait covariation in the context of range expansions.

To what extent do changes in sexual traits, mating patterns, and mating preferences during range expansions contribute to geographic patterns of pre-mating isolation? Knowledge of the evolutionary history of populations of the focal species, including sympat-ric and allopatric populations in the expansion zone, will be crucial to answer this question.

Do trait changes during range expan-sions trigger phenotypic innovations (e.g., in behavioral and cognitive traits)? Further, what part do these innovations play in shaping hybridization dynamics?

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