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Opinion
Bolder Takes All? The Behavioral Dimension of Biogeography

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Animal personality can be seen as behavioral polymorphism that could play a direct and active role in driving evolutionary pathways. We argue here that consistent individual differences in key personality traits affecting dispersal and other density-dependent processes have provided substantial contributions to molding biogeographic patterns. Building upon opportunities recently opened by genomics and other novel approaches, we explore the hypothesis that Pleistocene range expansions, island colonizations, and other historical biogeographic processes could have been promoted by non-random samples of behavioral types of the founder populations. We provide context and testable hypotheses, based on case studies, that could bring new implications to our understanding of the processes shaping spatial and temporal patterns of variation in animal biodiversity.

Animal Personality as a Pacemaker of Evolutionary Processes

The role that behavior plays in actively promoting evolutionary change has long been recognized [1–3]. More recently, the realization that animals possess individual **personalities** (see Glossary) with a heritable, physiological, and epigenetically regulated basis has deeply impacted on several areas of ecology and evolution [4], and has strengthened this view up to the hypothesis that behavioral variation can 'act as a 'pacemaker' of evolution for non-behavioral traits' through various mechanisms and at different ecological levels [5–7].

Behavioral polymorphisms involving the five most common personality categories of traits described in animals (i.e., boldness–shyness, exploration, activity, aggressiveness, and sociability [8]) have been associated with **dispersal** propensity and population structure in several empirical studies and theoretical models. These studies provide fundamental contributions to numerous of research fields including population ecology, contemporary evolution, invasion biology, and climate change biology [9–16]. Surprisingly, how behavioral polymorphisms might have contributed to key past processes structuring biogeographic patterns is a substantially unexplored area of research.

We propose here a context in which to study how behavioral polymorphisms within-species could have contributed to molding current geographic patterns of species distribution and genetic diversity. Our aim is to bridge (historical) biogeography with behavioral biology because we are certain that this 'getting closer' will shed new light on the diversity of processes that have shaped temporal and spatial patterns of variation in animal biodiversity.

Why Should Biogeographers Care About Animal Personality?

Biogeography is, by definition, the study of the present and past distribution of biological diversity and their causal processes. Many new perspectives and technical advances have

Trends

Animal personality can influence dispersal processes. Evidence is emerging that personality traits can affect departure, distance covered, transience/settlement success, as well as density-dependent processes related to both natal and novel habitats.

Non-random spatial distributions of the behavioral types that affect dispersal suggest in several instances that dispersers (i.e., colonizers, founders) could be a non-random sample of behavioral types from the source population.

Recent advances in studying the heritability of animal personality indicate that the contribution of additive genetic variance to personality variation is substantial.

The potential contribution of behavioral polymorphism to key historical biogeographic processes is a substantially unexplored research area.

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deeply reshuffled historical biogeography in the past decades to become 'prototypic of integrative science' [17–22]. Accordingly, research around long-recognized key processes in biogeography, such as dispersal, has also changed its 'physiognomy'.

Dispersal (including departure, transience, and settlement) is a central process in the entire range of disciplines dealing with ecology, evolution, and conservation of biodiversity [23]. Since its inception, historical biogeographic investigation has been mostly concerned with extrinsic factors (geology, climate, or ecological), which influence the likelihood of dispersal between habitats (e.g., barriers and corridors) in relation to the organism's dispersal abilities (i.e., dispersal modes and distance covered) [24]. However, dispersal is a strongly conditional process [25,26] which directly relates to lineage range-variation over time [27]. Although biogeography research has largely integrated instances where dispersal is context-dependent (e.g., relative to changing environmental conditions and demographic parameters [28,29]) and non-random (depending on individual variables such as sex, e.g., [30]), the emphasis here is on personality-dependent dispersal [31–33].

In Table 1 we list a set of predictions of behavioral polymorphism in key personality traits leading to non-random dispersal, based on empirical studies. Notably, in many cases dispersal propensity is not best predicted by behavioral polymorphisms alone, but by their interaction with socio-ecological factors related to the natal and novel habitat [32]. These factors can include foraging, competition, risk of predation, risk of inbreeding, and partner availability – most of which have been associated with behavioral polymorphisms, are relevant in both natal and novel habitats, and are **density-dependent**. Thus, behavioral polymorphism could have influenced all the steps (departure, transience, and settlement) of past dispersal events, ultimately affecting several historical processes that are iconic research grounds for historical biogeography, including range variations in response to Quaternary environmental changes and island colonizations.

Toward an Integration of Animal Personality and Biogeographic Research

From a historical biogeographic perspective, dispersal events of special interest are diffusion and long-distance dispersal, given their immediate link to contiguous range expansions and colonizations [22,24]. Recent technological progress has allowed extensive documentation of genetic and biogeochemical imprints of these long-controversial events [19,22,34], and deep reappraisal of their role in the shaping of biogeographic patterns. In fact, diffusion and long-distance dispersal were once considered to be rare, somewhat incidental (particularly long-distance dispersal), and the outcome of interactions between the unconditional dispersal capabilities of an organism and rare historical events (e.g., geological, climatic, ecological). Instead, owing to recent advances, they are now best depicted as the (rare, successful) outcome of the complex, conditional, continuous, and ubiquitous dispersal process [31,33]. Since Dobzhansky and Wright's [35] landmark research on *Drosophila* flies, there is now compelling evidence that individuals dispersing 'extremely' long distances are widespread in animal populations, albeit often at very low frequency [9]. Therefore, long-distance and non-random dispersal appear to be integral rather than incidental in animal populations. Further, their underlying mechanisms need to be fully disclosed for a thorough understanding of the processes ultimately leading to the geographic patterns of biological diversity and their changes over time.

Evidence of behavioral polymorphism-dependent dispersal, its interactions with density-dependent and -independent processes, and its contribution to the dynamic spatial structure of populations clearly invites an integration of the behavioral polymorphism into the historical biogeographic research agenda. Nevertheless, merging inputs from two such apparently disparate fields is undoubtedly challenging. However, we believe that efforts in this direction

Glossary

Behavioral polymorphism: the occurrence of more than one behavioral phenotype within a population.

Bio-logging: the use of miniaturized electronic tags attached to free-ranging animals, and which record or remotely relay data about an animal's behavior, physiology, and environment.

Density-dependent processes: a heterogeneous set of processes that are regulated by the demographic density of a population. They include, but are not limited to, allele effects, competition, predation, and, in behavioral ecology, foraging and sociosexual behaviors. Personality traits influencing exploratory behavior and dispersal have been frequently observed to be at least partly density-dependent.

Dispersal: the permanent movement of individuals from a natal to a novel habitat, including three steps: departure, transience, and settlement. Dispersal and migration are distinct movement patterns, the latter indicating directional and often cyclical movements between two locations (e.g., a foraging and a breeding area). The two terms, however, are often used interchangeably in evolutionary literature under the meaning of dispersal (e.g., migration out-of-Africa).

Genomics: the study of content, structure, function, and evolution of genomes by using molecular biology technologies and bioinformatics analytical tools.

Heritability: the amount of phenotypic variation explained by additive genetic variance (so-called 'narrow-sense' heritability).

Novelty-seeking: the tendency of an individual to explore unfamiliar stimuli and environments.

Personality in animals: consistent behavioral differences between conspecific individuals across time and context. Statistically, animal personality is the repeatable, non-zero between-individual variance of behavior.

Phenotypic gambit: the idea that the phenotypic structure of personality reflects its genetic structure, and that details of this genetic structure do not influence the evolution of behavior substantially.

Table 1. Behavioral Categories Subject to Polymorphisms and their Predicted Effects on the Dispersal Process[a,b]

Behavioral Categories	Predicted Effect		Refs
	Departure	Transience–Settlement	
Exploration Propensity to explore novel, unfamiliar environments. Assessed by latency to explore, time duration, and activity level in a novel area.	High explorers have a higher propensity to depart.	High explorers have higher transience success and disperse farther. Propensity to explore influences transience/settlement decision. If exploration is positively coupled with aggressiveness, this can help to outcompete competitors in the initial settlement phase.	[9,10,32, 56,61]
Activity An individual's level of activity in a familiar environment. Assessed by measuring time spent in locomotion (e.g., walking, hopping, swimming).	More-active individuals have a higher propensity to depart.	More-active individuals tend to disperse farther.	[62,63]
Boldness An individual's response towards a risky situation. Assessed for example by measuring latency to exit a shelter in a risky situation (e.g., by simulating predation risk).	Bolder individuals are more likely to depart. This can depend on the degree of perceived risk (e.g., by predation).	Bolder individuals tend to disperse farther.	[9,64]
Aggressiveness The propensity for aggression towards another individual. Assessed by latency to attack, attack frequency, and time spent in agonistic interactions.	Aggressiveness influences a departure decision, but the relation is poorly predictable owing to contrasting evidence. Usually aggressiveness is positively related to exploration. More-aggressive individuals are more likely to depart. (but also) Less-aggressive (e.g., subordinate) individuals are forced to disperse.	High aggressiveness helps to cope with competitors in transient and novel areas, but can become costly as intraspecific density increases.	[8,16,56, 65,66]
Sociability An individual's non-aggressive response to conspecifics. Assessed by measuring active search/avoidance of conspecifics (or their cues) and social exploration.	More-social individuals tend to depart when at low densities. Less-social individuals tend to depart at high densities.	Less-social individuals tend to disperse at greater distances. Less-social individuals cope better with initial low population density. More-social individuals cope better at increasing population density.	[63,67–69]

[a]See Figure 2 in [8] for a flow diagram representing possible links between behavioral categories. Syndromes (suites of correlated behaviors) could enhance the overall dispersal success across multiple steps (see main text).
[b]Social systems of populations (e.g., eusociality, cooperative breeding) might modify the predicted effects, although the study of personality in relation to social systems is still in its infancy.

should focus on: (i) exploiting the whole range of opportunities opened by **genomics** to explore behavioral polymorphisms in space and time, and (ii) investigating and integrating empirical evidence of personality-dependent dispersal, both across multiple spatial and temporal scales. Although still scant, research contributions are now emerging along these avenues.

Several excellent reviews and perspectives have been published that address the potential opportunities genomic approaches provide to the study of both biogeography and the genetic architecture of complex traits, including animal personality [36–42]. We emphasize here that these approaches can promote the integration of animal personality research into the study of the mechanisms underlying organism distribution. Indeed, using genomic approaches, three fundamental and previously barely-accessible steps toward this integration can be addressed: (i) unveiling the genetic architecture of animal personality; (ii) studying the geographic variation of genetic diversity in genes that are associated with behavioral polymorphism, and the contribution of various types of selection to this variation; and (iii) investigating how biotic and abiotic environmental features modulate their expression patterns. The diversity and flexibility of genomic techniques (e.g., in terms of the number of individuals and genes analyzed) allow scaling each experimental phase based on features of the study organism, the specific research questions, and (to some extent) the analytical resources of each laboratory. Noteworthy, in addition to continuous improvements of genomics technologies, bioinformatics tools for population genomics, phylogenomics, and (comparative) phylogeographic analysis methods are also improving [41–46], allowing researchers to go deeper into the study of non-neutral genetic variation and its role in driving spatial and temporal patterns of diversity.

Our emphasis here on genomic approaches is mostly based on the huge opportunities offered by this rapidly developing research area at increasingly accessible costs. Nonetheless, it is worth mentioning that other potentially useful approaches, assuming the **phenotypic gambit**, have received support by major achievements in the study of the **heritability** of personality traits [36,37,47]. Heritability is a key issue when studying the evolutionary dynamics of personality, and recent studies show that a substantive portion of personality variation is heritable [36,37,47]. These findings give general support for the phenotypic gambit [37], and indicate that 'first-line' insights concerning evolutionary dynamics can also be drawn from phenotypic estimates (but see [39]).

In Box 1 we present two case studies showing the implication of the behavioral polymorphism in shaping biogeographic patterns through behavioral polymorphism-dependent dispersal. In these examples, either by analyzing geographic patterns of genetic variation or by (implicitly) assuming the phenotypic gambit, the authors showed that **novelty-seeking** behavioral traits (including boldness, exploration, risk-taking, and reactivity to novel stressors) were implicated in a recent island colonization by the common frog *Rana temporaria*, and in the range expansion of our own species out-of-Africa.

A crucial point in these dynamics is that not all individuals within a population successfully pass through the stages of an expansion/colonization process. Because only a subset of individuals manage to overcome any stage successfully, these processes could constitute a 'selective filter' on behavioral polymorphisms [14]. Therefore, not only could historical demographic processes have been affected by behavioral polymorphism, but the genetic and phenotypic individual composition of the populations could also have been affected. Support for this scenario also comes from the non-random spatial distribution of personality traits across the range of expanding populations. For example, among house sparrow populations in Kenya, a greater propensity toward exploration and neophilia was found at the expanding range edge [48,49]. Moreover, theoretical models, including spatial selection, spatial sorting, and analyzing the dynamics of both equilibrium and non-equilibrium populations of an expanding lineage, predict

Box 1. Animal Personality and Historical Biogeographic Patterns

Evidence is emerging (albeit still in short supply) that animal personality could influence several biogeographic patterns through effects on the dispersal process (Table 1), including island colonizations and Pleistocene range expansions.

Island Colonizations. Although there are many potential benefits to successfully colonizing new habitats, dispersal also carries a variety of costs and a high risk of failure for individuals [70]. Accordingly, dispersal propensity (and distance covered) has often been linked to personality traits favoring 'risk taking', such as boldness and more-exploratory behavior [9]. In a recent study [71] these personality traits have been compared between island and neighboring mainland populations of the common frog *Rana temporaria* in Sweden. Tadpoles and froglets (i.e., the more-dispersing life-stages) from insular populations were consistently bolder and more exploratory (Figure IA). The authors considered alternative explanations for this pattern, such as effect of other potential factors (e.g., different predator environments), and they concluded that colonizers were not a random sample of the founder population but were a subset of the founder population that was bolder and more exploratory than the average random frog.

Pleistocene Range Expansions. Once we understand the genetic underpinnings of personality traits, the study of geographic variation at the underlying genes can provide insights into the implication of these traits during the formation of biogeographic patterns. In the human population there is a well-established correlation between polymorphisms in the dopamine receptor D4 (*DRD4*) gene, levels of neuronal reactivity, and personality traits related to novelty-seeking (NS), which include boldness and exploratory behavior. Notably, this correlation is also emerging from studies in other species (e.g., [72,73]). Studies [74,75] have demonstrated a substantial correlation between the frequency of alleles linked to high NS and the dispersal distance 'out-of-Africa' in humans (Figure IB) by analyzing the pattern of geographic variation in the *DRD4* gene. This event was the major range expansion of our species, which occurred since the Late Pleistocene (~100 000 years ago onward). Importantly, these studies show that the correlation could not be accounted for by neutral genetic processes alone (i.e., genetic drift and admixture), which implies natural selection for high NS during the expansion of populations toward new habitats. As with the above-mentioned study on the common frog, these analyses revealed that migrant individuals were not a random sample of the founder population.
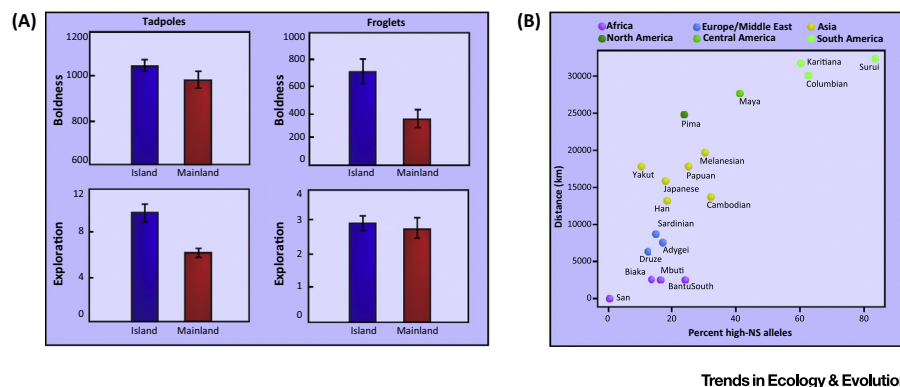

Figure I. Boldness, Exploration, Novelty-Seeking, and Dispersal. (A) Mean personality trait values in tadpoles and froglets of the common frog from island populations in Sweden compared to source populations from the mainland (modified from [71]). Boldness was measured as the difference between maximum time(s) taken to exit from a refuge and the latency time; exploration tendency was measured as the amount of area explored in a given time after exiting the refuge. Error bars denote standard errors. (B) Relationship between the summed frequency of high-NS alleles at the *DRD4* exon3 in human populations, and migration distance out-of-Africa, after controlling for population structure (modified from [75]).

non-random spatial distributions of traits favoring dispersal abilities (including personality traits), and suggest that their (genetic) imprints might persist long after the completion of a range-expansion process [50–52]. Interestingly, growing evidence from the study of successful invaders supports these predictions, as nicely exemplified by the case of the cane toad *Rhinella marina* in Australia ([53,54] and references therein).

From this picture, the hypothesis of a 'dispersal-prone personality' might be generated, with more-active explorers, bold, and less-social individuals appearing as those with a higher propensity to disperse, to disperse longer, and therefore with a higher probability to contribute to range expansions (or other forms of long-distance movement [55]) (Table 1) and to the

personality make-up of newly established populations. Noteworthy, if 'founders' represent this type of non-random behavioral sample of the source population, then behavioral polymorphisms would have played a role even in some putatively neutral and density-dependent processes that generate and sustain uneven patterns of geographic distribution of genetic diversity within species – such as progressive founder events at the leading front of post-glacial range expansions, (sequential) island colonizations, and high-density blocking [29].

However, in several situations the influences of the behavioral polymorphism on the spatial population structure and dynamics that ultimately primed large-scale range changes might have been significantly more complex than predicted by this scenario. For example, some personality traits can be advantageous during some but not all of the phases of an expansion process. This point is vividly exemplified by long-term studies of the western bluebird [27,56]. In this species, high aggression is coupled with a high dispersal tendency that promotes waves of colonization of new habitats and displacements of its native competitor, the mountain bluebird. However, colonization waves need to introduce a range of behavioral traits to allow actual population increase in new areas over time. The occurrence of successive dispersal waves of individuals with different personality types has also been suggested by studies of invasive species [11]. In addition, to explain the success of many invasions (departure and transience are often assisted phases, which potentially relax their link to individual phenotypes; but see [14,57]), it has been proposed that successful invaders have high levels of behavioral polymorphism within the invasion pool, which allow both the establishment and reinforcement of new populations in subsequent phases [13].

Box 2. Range Expansions, Mitonuclear Biogeographic Discordances, and Behavioral Polymorphisms

We hypothesize here that behavioral polymorphism is a factor in the massive introgression of the mitochondrial genome (hereafter mtDNA) from a resident into an expanding species or intraspecific lineage, leading to a commonly observed and extensively discussed pattern of nuclear–mitochondrial biogeographic discordance [76].

Geographic Pattern and its Putative Causes

Range expansions can occur toward areas that are either empty of – or are already occupied by – a related species or lineage. In the latter case, hybridization and introgression can follow secondary contact. In this situation, mtDNA introgression has often been observed as being strongly asymmetric, both in quantitative terms (i.e., massive) and in its geographic extent. Moreover, reviews of evidence and spatially-explicit simulations indicate that introgression most frequently proceeds from the resident towards the expanding lineage [77].
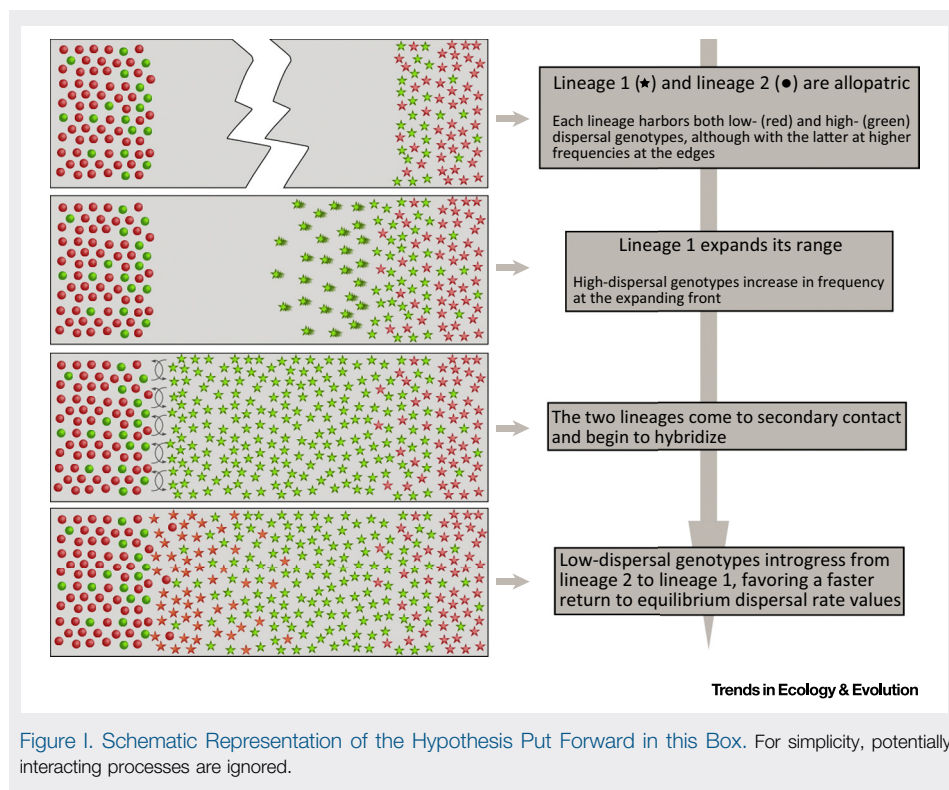
Several explanations of this pattern have been proposed [76] that encompass sex-biased asymmetries in mating likelihood or offspring production, *Wolbachia* infection in insects, hybrid zone movements, and, most frequently, adaptive introgression and demographic disparities between the interacting lineages.

mtDNA and Animal Personality

Recent evidence indicates that mtDNA (especially via mitonuclear epistatic interactions) can affect personality traits such as activity, boldness, and exploration behavior, which in turn have been linked to dispersal propensity. This has been shown experimentally, either by manipulating mitonuclear introgression lines in seed beetles [78], or by analyzing the personality and physiological differences between pure and introgressed wild-caught individuals of the bank vole from Finland [79].

Potential Contribution of Personality Differences Between Colonizers and Residents

As discussed in the main text, personality (and other) traits favoring dispersal often increase in frequency during a range expansion. When the range expansion stops, and secondary contact occurs, low dispersal genotypes are recruited mostly through (slow) gene flow from the rear [52]. On the other hand, the resident lineage (i.e., not expanding), might harbor both low- and high-dispersal genotypes. Introgression of low-dispersal genotypes (or of genotypes promoting low-dispersal phenotypes when in the new nuclear background) from the residents could favor a faster return to equilibrium dispersal rate values among colonizers. Because mtDNA can contribute to personality variation in traits which affect dispersal propensity, we hypothesize that it might contribute to the adaptive landscapes that promote asymmetric introgression patterns between residents and colonizers. The process hypothesized here could interact with other processes (e.g., [77]; i.e., it is not posed as an alternative hypothesis), and it could affect other genomic regions linked to personality trait variation. Interestingly, it could be experimentally tested by using, for example, designs already adopted in studies linking mtDNA and personality variation [78,79] (Figure I).

Figure I. Schematic Representation of the Hypothesis Put Forward in this Box. For simplicity, potentially interacting processes are ignored.

Bridging the perspectives, methods, and results of two traditionally disparate research fields of biogeography and behavioral biology will be challenging in many respects, but we anticipate that new insights and testable hypotheses will emerge. In Box 2 we attempt to exemplify this by looking at the mitochondrial genome (which is iconic to phylogeographic investigation) through both biogeographic and behavioral points of view, and by exploring a potential implication of such a 'contamination'.

Concluding Remarks

Trait-based approaches allowing a direct link between ecological and evolutionary processes with biogeographic patterns have proven powerful to 'opening the black-box of biogeographic processes' [58]. However, previous research has focused predominantly on morphological characters. We have considered here how behavioral traits (which might also influence morphological trait changes [6]) are involved in the processes that promote range variation over time, because these processes have direct and outstanding importance for historical biogeographic research. Previous reviews (e.g., [5,59]) suggested several different ecological and evolutionary implications of behavioral polymorphism, affecting life history, disease dynamics, social evolution, evolvability, speciation, species interactions, community structure, and ecosystem processes, each potentially affecting biogeographic patterns. Importantly, robust hypothesis-testing, hampered until recently by the lack of suitable methods, is becoming increasingly accessible.

While we rooted our arguments on the opportunities opened by genomic approaches in the study of heritability, the genetic architecture of animal personality, and their spatial and temporal variation, it is worth noting that advances in several other fields will likely prove essential in building and testing hypotheses. **Bio-logging** technologies, for example, are revolutionizing the

Outstanding Questions

What are the genetic and non-genetic underpinnings of personality variation within and among wildlife populations? Despite insightful research with model organisms, there are few data on wild populations. Future research in this area will allow robust applications of comparative and candidate gene approaches for an increasing number of species, further boosting our comprehensive knowledge.

How widespread are non-random distribution patterns of behavioral polymorphism and their genetic underpinnings across taxa and geographical contexts? What is the relative contribution of selection, spatial sorting, and stochasticity in driving their formation?

To what extent do personality-dependent dispersal processes contribute to shaping (meta)population genetic structure? To what extent do they scale-up from local to range-wide patterns of non-random variation?

Does the range distribution of boldness, exploration, and other personality traits co-vary with morphological and physiological traits affecting the range?

How temporally persistent are the genetic signatures of personality-dependent dispersal processes in structured and non-structured populations?

How does behavioral polymorphism affect the colonization–competition tradeoff?

How do personality traits of colonizers influence the assembly and structure of biological communities in novel habitats?

study of ecology, physiology, and behavior of wild animal populations (including cryptic and wide-ranging species), and these will allow researchers to develop and test entirely new theories in these fields [60]. Careful integration of personality research methods, bio-logging technologies, and genomic approaches could plausibly provide the utmost power of resolution across a wide range of spatial and temporal scales along the ecological–evolutionary continuum. These integrations will prove essential to move forward (see Outstanding Questions) toward the effective bridging of the behavioral and biogeographic sciences that we aimed to promote here.

Acknowledgments

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