



Ecological and evolutionary consequences of biotic homogenization

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Biotic homogenization, the gradual replacement of native biotas by locally expanding non-natives, is a global process that diminishes floral and faunal distinctions among regions. Although patterns of homogenization have been well studied, their specific ecological and evolutionary consequences remain unexplored. We argue that our current perspective on biotic homogenization should be expanded beyond a simple recognition of species diversity loss, towards a synthesis of higher order effects. Here, we explore three distinct forms of homogenization (genetic, taxonomic and functional), and discuss their immediate and future impacts on ecological and evolutionary processes. Our goal is to initiate future research that investigates the broader conservation implications of homogenization and to promote a proactive style of adaptive management that engages the human component of the anthropogenic blender that is currently mixing the biota on Earth.

Anthropogenic environmental alterations and human-assisted dispersal of exotic species have sparked widespread changes in the global distribution of biota. The resulting modifications have predominantly been in two directions: (i) range expansions of cosmopolitan, non-native species; and (ii) range contractions of regional and endemic native species. This replacement of specific native forms by generalist non-natives in space and time has mixed the taxonomic composition of once disparate biotas, an occurrence termed 'biotic homogenization' [1].

Biotic homogenization is not a new phenomenon in the history of Earth. Episodic mixing of historically isolated taxa has occurred throughout the paleontological record [2]. More recently, humans have accelerated this process by facilitating biotic exchange among regions, as was first noted by Elton [3], who observed a breakdown of Wallace's Faunal Realms (i.e. geographic regions containing distinct biota) owing to global commerce. But, only in the past decade has interest and concern regarding biotic homogenization been rekindled. Recent studies have either discussed or documented increased similarity in the composition of

communities across an array of taxonomic groups (plants [4], birds [5], reptiles and mammals [6], insects [7], fish [8], mussels and amphibians [9], marine algae [10] and snails [11]). In fact, this global erosion of regional distinctiveness has ushered in a new era, aptly dubbed 'The Homocene', which is creating, in turn, 'The New Pangaea' [12].

Lockwood and McKinney [13] recently emphasized the importance of identifying and understanding present-day patterns of biotic homogenization for establishing proactive conservation goals aimed at reducing its future ecological effects. Although many investigations have provided considerable insight into empirical patterns of homogenization [4–11], the specific ecological and evolutionary consequences of this process still remain unexplored. Obviously, a loss of species diversity carries ecological [14], evolutionary [15] and economic [16] costs, yet, to deepen our understanding of biotic homogenization, a distillation of broader and more globally significant perspectives is required. Why has this been slow to emerge? Higher order implications might be much more subtle and difficult to grasp than, say, those associated with a simple gain or loss of species [17]. This is particularly so given the broad spatial and temporal milieu within which biotic homogenization operates. It is clearly a more distinct and complex phenomenon than was previously thought, and one whose consequences warrant explicit and extensive investigation.

Here, we identify three forms of homogenization (genetic, taxonomic and functional) and explore the immediate and future impacts of each on ecological and evolutionary processes. Our goal is to elucidate conservation implications of biotic homogenization, particularly as they relate to human dimensions, with the hope that directed research and an emerging synthesis will define not only the manner in which this process threatens global biotas, but also the proactive management scenarios required to suppress it.

Causes and consequences of genetic homogenization for species and populations

Genetic homogenization reduces the spatial component of genetic variability within a species or among populations of a species (Box 1). It can occur through a variety of

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mechanisms: (i) intentional translocation of populations from one part of the range to another; (ii) intentional introductions of species outside of their normal ranges; and (iii) extirpation of local or regional faunas. Genetic homogenization is a serious but often less recognized threat to the integrity of endemic gene pools, and can have several important implications.

Translocation of population(s) would enhance the potential for intraspecific hybridization, with the end result being the assimilation of previously differentiated gene pools [18,19]. Introductions of species outside of their original range(s) could result in a founder effect and yield reduced levels of genetic variability, as well as setting the stage for interspecific hybridization [20]. And finally, if extirpations were a cause for faunal homogenization, then one consequence might be bottleneck(s) in local populations of the impacted species, along with lowered

effective population size(s) [21]. This would occur directly via removal of individuals from source populations, or indirectly by habitat modifications. Here, we explain these considerations in greater detail.

Intraspecific hybridization

Intraspecific hybridization can homogenize the unique characteristics of geographically distinct populations [22], as well as compromise the fitness of individuals by disrupting local adaptations [19]. Intentional intraspecific introductions (either to replace or to supplement declining or extirpated populations) often result in an overt loss of genetic variability [18], resulting from founder effects, bottlenecks and the resulting low genetic variability that they engender (e.g. [23]). For example, global stocking of cutthroat trout *Oncorhynchus clarki* from a single source region has yielded substantial genetic homogenization and, in at least one instance, has played a primary role in the loss of a genetically distinct subspecies [24]. As above, widespread aquaculture practices are often the catalyst for such homogenization in many fish species, yet ramifications are only now being unraveled [25].

Genetic homogenization of populations can also influence the capacity of a species to expand its distribution. Mixing of locally adapted populations (e.g. peripheral with central) can impede species expansion, because phenotypes favored in central areas might be maladapted for conditions encountered at the distributional periphery [26,27]. Similarly, intraspecific hybridization and subsequent breakdown of regional distinctiveness can also increase vulnerability to invasion and, conversely, might enhance the success of hybrid competitors [21]. It might even promote the expansion and ultimate success of the invading species. An interesting example of the latter involves the Argentine ant *Linepithema humile*. Here, spatial segregation of nests is determined genetically by innate aggression against non-nestmates [28]. However, recently invading populations in California experienced a genetic bottleneck owing to founder effects that resulted in widespread genetic similarity among populations. This, in turn, reduced intraspecific aggression and promoted the formation of aggressive supercolonies that significantly impacted community- and ecosystem-level processes [29]. Development of single, large colonies might be unstable over the long term [30], yet a more immediate solution was sought to enhance the recovery of invaded ecosystems. One solution was to introduce new alleles into the invasive populations so as to reduce genetic homogeneity and eliminate widespread development of supercolonies [28]. Clearly, genetic consequences of homogenization, particularly with regard to invader and resident, are only now beginning to be understood. This is as much a function of technological developments (such as application of single nucleotide polymorphisms to population-level problems [31]) as it is of theoretical development.

Interspecific hybridization

Hybridization between genetically distinct species can create new adaptive systems and, thus, new ecological niches [32]. This is particularly evident in aquatic ecosystems, where human-mediated dispersal has

Box 1. Measuring genetic, taxonomic and functional homogenization

Biotic homogenization, whether referring to genetic, taxonomic or functional homogenization, is defined as an increase in the spatial similarity of a particular biological variable over time, and is usually evaluated by comparing the average pairwise similarity of the variable calculated at two discrete times.

Genetic homogenization can be quantified using a variety of genetic characteristics, such as the allelic composition of a particular locus or set of loci (i.e. identity of genotypes), their frequencies (i.e. relative abundance of genotypes), or by one of many metrics derived from the above parameters, such as percent polymorphic loci, mean number of alleles per locus and mean heterozygosity. In addition, levels of population divergence can also be assessed by indices of genetic similarity such as F_{st} or using a variety of cluster analyses (e.g. Bayesian inference). These measures of genetic diversity are usually assessed in a comparative spatial framework (i.e. introduced versus source population, or disturbed versus non disturbed populations), but they are rarely examined in a temporal framework (i.e. pre- and post disturbance), simply because no genetic baseline data were collected before the homogenization event. It is in this temporal context where research is needed to elucidate genetic consequences of homogenization. Furthermore, the choice of genetic markers (i.e. level of resolution) is crucial to detect the potential subtle genetic differences inherent to homogenization.

Taxonomic homogenization is calculated using species presence or absence data to examine the degree of similarity in community composition, and can be quantified using any one of a suite of similarity indices, diversity indices, cluster analyses or ordination approaches. Of the many similarity indices used in ecology for quantifying community similarity, Jaccard's coefficient (based on species occurrence data) is employed almost exclusively in homogenization studies. Other approaches include using β diversity to quantify spatial turnover of species, comparison of species similarity based on cluster membership of communities, and the examination of position and distance between communities in reduced, species-ordination space.

Functional homogenization can be calculated in a similar fashion by first calculating the site-by-trait matrix (in the simplest case, calculated as the product of the species-by-site matrix and the trait-by-species matrix) and then examining community similarity using one of the same approaches for taxonomic homogenization. Community similarity in functional characteristics could be assessed based on the presence or absence of species traits or the frequency distribution of traits in the community. Whether the species traits are discrete (binary or multi-state) or continuous will dictate the choice of similarity coefficient or multivariate statistical approach.

promoted numerous and dramatic hybridization events [33]. Fish provide the best examples, owing simply to their external mode of fertilization coupled with weakly developed reproductive isolating mechanisms [34]. The situation becomes exacerbated when the introduced fish has evolved allopatrically, yet is closely related to the indigenous one. The poster child for this phenomenon are indigenous salmonid fishes of North America [24].

We posit that mechanisms driving genetic homogenization are actually synergistic and that human interventions (as above) simply amplify the potential for hybridization within a given system. Human-mediated, long-distance dispersal and colonization events, for example, elevate the probability that pairwise interactions between species will yield hybrids, whilst human-provoked environmental disturbances will likewise provide habitats that are suitable for hybrid progeny [35]. This human dimensions aspect enhances the probability that ‘hybrid swarms’ will genetically extirpate native taxa [20]. Although such events are thought to occur over many years, even decades (as with trout), examples do exist where genetic swamping has occurred within abbreviated time frames. For example, within a four-year period following its introduction, the exotic pupfish *Cyprinodon variegatus* was involved in a large-scale introgressive hybridization event with the endemic *C. pecosensis* across 430 km of the Pecos River in New Mexico [36]. Genetic swamping can occur relatively rapidly and over extended distances, and the seriousness of this phenomenon cannot be underestimated simply because its effects are deemed slower than, say, overt predation.

In summary, in spite of a limited number of studies, it is apparent that much uncertainty remains regarding the ecological consequences of genetic homogenization. This topic clearly deserves further investigation. Indeed, genetic homogenization might gain greater attention in the future given the emergence of the field of landscape genetics [37] and the importance of population diversity for ecosystem services [38].

Causes and consequences of taxonomic and functional homogenization for communities and ecosystems

To date, scientific research on homogenization has been pursued largely from a phylogenetic perspective [13,39], where the term ‘taxonomic homogenization’ is used to describe an increase in the compositional similarity among communities owing to the successful invasion of ‘winning’ species and the extirpation of ‘losing’ species [1] (Box 1). Accounting for taxonomic change in communities is important and achieved relatively easily [40]; however, ecologically profound functional changes might occur in homogenized communities that are largely independent of taxonomic identity. Thus, a more subtle ecological examination of homogenization is required.

Species contribute individually and collectively to the functional stability of communities and ecosystems. Winners and losers in the homogenization lottery are not randomly distributed taxonomically; rather, invasion success and extirpation vulnerability are primarily defined by the interaction between intrinsic species traits and extrinsic environmental characteristics [1]. Ecological

implications of biotic homogenization might be more profitably examined by considering ‘functional diversity’ (i.e. the composition of and variation in community traits, and its spatial distribution across landscapes) (Box 1). Modifying the functional diversity of a community might result in functional homogenization involving the replacement of ecological specialists by the same widespread generalists. Although functional diversity is recognized as a determinant of ecosystem processes [41], the importance of functional homogenization has received inadequate attention.

We present a conceptual model to assess the manner in which species introductions and/or extirpations can lead to functional homogenization with subsequent changes in overall community function and a reduction in ecosystem resilience (Box 2). Modifications to within- and between-community trait compositions will probably impinge upon community and ecosystem function, and resistance to environmental change. A decrease in functional diversity might reduce overall community and ecosystem functioning [42], stability [43] and resistance to environmental change by simply narrowing the available range of species-specific responses [44]. Consider a severe drought (the disturbance oval; Box 2, Figure 1b) that strongly affects a subset of species in a community that has (or lacks) a particular suite of functional traits. Historical communities, with much greater breadth in functional space, should exhibit higher resistance or resilience when compared with homogenized communities.

The functional homogenization of all local communities within a region (i.e. metacommunities) can increase vulnerability to large-scale environmental events by synchronizing local biological responses across individual communities. This, in turn, would reduce variability among communities in their response to disturbance and would compromise the potential for landscape- and regional-level buffering. Because community composition defines the range of functional traits that influence ecosystem functions (such as nutrient retention or energy flow; e.g. [45]), biotic homogenization might jeopardize ecosystem function by limiting the pool of species that can compensate for local extinctions (i.e. reduce spatial patterns in functional redundancy). Homogenized communities might therefore exhibit a decreased resilience to environmental disturbance, because elevated similarities among communities might dampen or eliminate potential recolonizations by species with locally extirpated trait(s). Susceptibility of homogenized communities to environmental alteration might be particularly high in areas, such as urban ecosystems, that experience more frequent and severe disturbance events [46].

Although our model for functional homogenization (Box 2) is hypothetical, it offers a methodological framework for future studies. Knowledge of the functional characteristics of spatially distinct biological communities could be used with observational and experimental data to explore the functional implications of community changes in trait types and frequencies that result from homogenization. An exploration of community similarities in multidimensional functional space should advance our understanding of biotic homogenization and its long-term

Box 2. A conceptual, trait-based framework for assessing the potential ecological consequences of functional homogenization

The occurrence and relative abundance of functional traits contributed by constituent species determines the functional diversity of a biological community. Figure 1 presents a conceptual framework where each functional trait is represented by a single axis, and the collection of functional traits contributed by all species of the community defines the n -dimensional hypervolume in functional space occupied by the community (analogous to the species-specific functional niche of Rosenfeld [56] extended to the entire community). For each single functional trait, species occupy some tolerance range along the environmental axis defined relative to that trait. The cumulative distribution of the trait states of all species represents the aggregate environmental tolerance for the community; therefore, an alteration of species composition (e.g. by invasion or extinction) can modify the overall community tolerance to the environmental condition. Figure 1a illustrates the effects of homogenization on a distribution of a single functional trait (i.e. one-dimensional trait space) for three hypothetical communities. The replacement of species with unique trait states (e.g. via the extirpation of rare species) by species with similar trait states (e.g. via the introduction of generalist species) during the homogenization process will truncate the tails of the trait distribution and compress the overall trait range for the community. Consequently, historical differences in the trait distribution among the three communities might be lost, causing them to become homogenized in functional space (i.e. current trait distributions converge toward some common central tendency).

In Figure 1b, this conceptual framework is extended to a suite of species traits represented in multi-dimensional functional space for the same three hypothetical communities. It shows how the replacement of native species with unique trait states by introduced species with common trait states results in reduced breadth (i.e. trait variation) of the current or homogenized communities in functional space compared to the historical communities. Furthermore, the locations of the communities in functional space are shifted toward a common central tendency, as indicated by greater overlap in the three community trait polygons (Figure 1b), an indication of functional homogenization. Note that, because the 'winners' in biotic homogenization are often generalist species [1], the introduction of non-native species will result in reduced within-community functional diversity. However, if specialist non-native species are introduced (i.e. species with trait combinations that do not exist in the recipient communities), the within-community functional diversity is expected to increase; however, greater between-community trait similarity is still expected to occur because the same species (and therefore traits) are introduced to the communities.

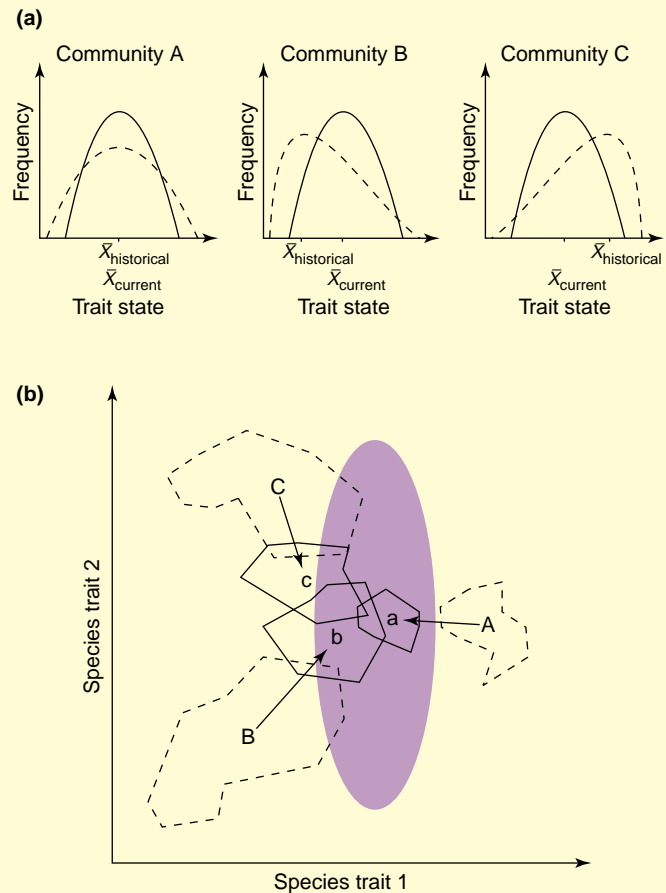


Figure 1. A conceptual model of functional homogenization. **(a)** The effects of homogenization on a distribution of a single functional trait (i.e. one-dimensional trait space) for three hypothetical communities (A–C), where 'Trait state' can refer to the value of a continuous trait or the category of a discrete trait, and 'Frequency' can refer to the frequency of species or individuals in the community that have particular trait values or categories. $\bar{X}_{\text{historical}}$ and \bar{X}_{current} represent the mean trait states for the historical (dashed line) and current or homogenized (solid line) communities, respectively. **(b)** The effects of homogenization on a set of species traits that are represented in multi-dimensional functional space (shown in two-dimensions for simplicity but can be readily extended to n -dimensions) for communities (A–C). Upper-case letters and dashed trait polygons represent historical communities, and lower-case letters and solid trait polygons represent current or homogenized communities. The shaded area represents a hypothetical environmental disturbance that affects a limited set of species in a community that has (or lack) a particular suite of functional traits (indicated by the degree of overlap between the community polygons and the disturbance oval in functional space), and shows the relative resilience of the homogenized communities to future disturbances.

ecological consequences, including the potential effects of homogenization on food-web structure and community susceptibility to species invasions (Box 3).

Evolutionary consequences of biotic homogenization

An evolutionary dimension to the current biotic crisis was perhaps best expressed by Soulé [47] who stated: 'death is one thing, an end to birth is something else'. We believe the potential evolutionary impacts associated with species invasions [48] and endemic extirpations [15] are a useful framework within which the evolutionary implications of biotic homogenization can be addressed.

Speciation is a result of numerous ecological and evolutionary processes, which arguably act on the same biological template: the species. Rosenzweig [49] recently suggested that the future of speciation is intricately linked with the future of species diversity. Although we agree, we further expect biotic homogenization to provide a critical context within which speciation can occur, because future spatial variability in species diversity and composition is likely to be reduced greatly. A common component of most proposed mechanisms of speciation is that geographical isolation of sister populations (co-adapted gene complexes) is required for allopatric speciation, the putative source of

Box 3. Effects of homogenization on food-web structure and future species invasions

Simplification of food-web structure

Given that species invasions and extirpations are acting in concert at all trophic levels, biotic homogenization could affect any of the many processes in communities that vary in space and time, such as spatial subsidies and food-web dynamics, and thereby have cascading effects elsewhere on the landscape. For example, increased spatial similarity in the species identity of predators and competitors could have direct and indirect effects on species at lower and higher trophic levels by increasing extirpation rates via intensified species-specific interactions (i.e. functionally similar species might utilize the same resources).

In a recent study, Beisner *et al.* [57] showed that the invasion of rainbow smelt *Osmerus mordax* into two north temperate lakes resulted in fish community homogenization through the spread of invaders, as well as the homogenization of zooplankton community structure via direct predation effects of smelt and indirect effects acting through competitive interactions among zooplankton. Therefore, positive feedback mechanisms of homogenization might exist where the simplification of one trophic level leads to increased simplification of other interconnected trophic levels (*cf.* [58]).

Investigations of biotic homogenization across multiple trophic levels will therefore become increasingly important for understanding the relationship between biotic mixing and food-web structure and dynamics. We believe that research examining how food-web dynamics are influenced by invasive species introductions (e.g. [59]), invasive species removal (e.g. [60]), keystone native species (e.g. [61]) and rare species (e.g. [62]), and how changes in food-web structure influence ecosystem processes (e.g. [63]) could provide important insight into our understanding of the food-web consequences of biotic homogenization.

Increased susceptibility of communities to species invasions

Simplification via homogenization might also play a significant role in influencing the rate of species spread and community resistance to future invasions. García-Ramos and Rodríguez [26] found that the speed of species invasion increased with environmental homogenization, which points to the importance of spatial heterogeneity in reducing population expansion of invasive species. Furthermore, fluctuating resource theory [64] describes how species deletions are accompanied by resource release, which might make a community susceptible to further invasions. The loss of rare species from systems (a pattern commonly associated with homogenization; e.g. [39]) might substantially facilitate future species invasions and their associated ecological impacts (e.g. [62]). In addition to individual rare species, the simplification of the taxonomic and functional composition of entire communities could have important implications for future invasions and their ecological impacts. For example, grassland communities with low functional diversity exhibit decreased resistance to species invasions [65]. Communities with low functional diversity are also more likely to exhibit similarities in temporal patterns of resource use, which ultimately translate into synchronized dynamics in species abundances. Temporal synchrony in population dynamics and the lack of complementary use of resources in time could increase the probability that resources are available to facilitate species invasions (e.g. [44]).

most new species. Human facilitation of population dispersal across natural biogeographical barriers has diminished geographical isolates that are necessary for eventual allopatric speciation, thereby limiting future potential species diversity. Furthermore, the source of future biodiversity might also be restricted through the fusion of incipient evolutionary lineages via hybridization and introgression [33].

Alternatively, there is some possibility that biotic homogenization will promote the origin and diversification

of new species, as invasive species evolve in new environments, or as greater hybridization opportunities create new species [21,50]. Species diversification might indeed be likely, given the many examples of contemporary evolution (i.e. evolutionary changes observable over less than a few hundred years) involving invasive species [51]. The question of whether homogenization will actually promote diversification via novel genetic convergences in new environments requires additional studies, perhaps using 'home and away' comparisons of invasive species with respect to energetics and life-cycle dynamics (e.g. [52]), behaviour and population genetics (e.g. [28]) and habitat and resource use (e.g. [53]).

The widespread use of captive and genetically modified stocks to supplement dwindling wild populations will continue to cause mixing of formerly isolated populations. Immediate consequences of these events would be a compromise in disease or parasite resistance for the hybrid population, and a disruption of its capacity for local adaptation. Local adaptation and drift contribute to the genetic variability of isolated populations that helps ensure that species respond evolutionarily to environmental change. Long-term consequences thus depend on the capacity for adaptation to environmental change [54], which is a function of genetic background. Accordingly, homogenized genetic and/or functional variation might jeopardize the future resilience of biological communities by increasing the chances of species extirpations via reduced adaptive capacity. Indeed, paleontological evidence suggests that mass extinctions have never entirely reset the evolutionary clock because enough taxa (and therefore, functional diversity) survived to seed the recovery process without the origin of new phyla [55]. However, the extent to which extensive homogenization might constrain genetic or functional diversity and limit recovery in the face of future extinction events is uncertain.

In addition, the introduction of new species into new regions will result in multiple founder effects and could lead to novel selection pressures that have not previously been observed [48]. This has the potential to alter evolutionary trajectories, irrespective of the extirpation of native species. Interestingly, although homogenization might facilitate novel species interactions, the number and breadth of these interactions are likely to be limited, owing to the taxonomic and functional simplification of the communities via common species invasions and extirpations. These simplifications in biotic interactions could lead to weaker selection pressures in the homogenized communities, and biotic mixing could therefore even endanger the long-term success of species that are seemingly the 'winners' in the homogenization process.

Conclusion

Homogenization is now considered one of the most prominent forms of biotic impoverishment worldwide. To date, we have begun to understand patterns in biotic homogenization in both aquatic and terrestrial ecosystems; however, we still cannot predict the consequences of these events, particularly for the provisioning of environmental goods and services. We believe that elucidating the

future ecological and evolutionary threats of biotic mixing requires expanding our focus beyond isolated cases of species invasions and extinctions to the accumulation of multiple events that collectively occur across the entire landscape over time. Because the biotic homogenization process operates at larger spatial and temporal scales, we must incorporate this broader context into our thinking if we want to quantify and understand the risks of genetic, taxonomic and functional homogenization to various levels of biological organization. Moreover, there is an increasing need to expand the dimensions of biotic homogenization, to include the abiotic context of global environmental homogenization, which promotes biotic simplification. It is in these areas that research will most effectively contribute new knowledge about the ecological and evolutionary implications of biotic homogenization. This will be a challenge given that continued growth and expansion of the human population will result in large-scale environmental upheaval and subsequent pressures on regional biotas. However, we must place a premium on this research, and on the adaptive management scenarios that it will produce, to ensure that the ecosystems on Earth retain their resilience and sustainability in the face of this anthropogenic blender.

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