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SPECIAL ISSUE

Biotic homogenization: a new research agenda for conservation biogeography

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ABSTRACT

Aim Biotic homogenization describes the process by which species invasions and extinctions increase the genetic, taxonomic or functional similarity of two or more biotas over a specified time interval. The study of biotic homogenization is a young and rapidly emerging research area in the budding field of conservation biogeography, and this paper aims to synthesize our current knowledge of this process and advocate a more systematic approach to its investigation.

Methods Based on a comprehensive examination of the primary literature this paper reviews the process of biotic homogenization, including its definition, quantification, underlying ecological mechanisms, environmental drivers, the empirical evidence for different taxonomic groups, and the potential ecological and evolutionary implications. Important gaps in our knowledge are then identified, and areas of new research that show the greatest promise for advancing our current thinking on biotic homogenization are highlighted.

Results Current knowledge of the patterns, mechanisms and implications of biotic homogenization is highly variable across taxonomic groups, but in general is incomplete. Quantitative estimates are almost exclusively limited to freshwater fishes and plants in the United States, and the principal mechanisms and drivers of homogenization remain elusive. To date research has focused on taxonomic homogenization, and genetic and functional homogenization has received inadequate attention. Trends over the past decade, however, suggest that biotic homogenization is emerging as a topic of greater research interest.

Main conclusions My investigation revealed a number of important knowledge gaps and priority research needs in the science of biotic homogenization. Future studies should examine the homogenization process for different community properties (species occurrence and abundance) at multiple spatial and temporal scales, with careful attention paid to the various biological mechanisms (invasions vs. extinctions) and environmental drivers (environmental alteration vs. biotic interactions) involved. Perhaps most importantly, this research should recognize that there are multiple possible outcomes resulting from the accumulation of species invasions and extinctions, including biotic differentiation whereby genetic, taxonomic or functional similarity of biotas decreases over time.

Keywords

Biotic differentiation, biodiversity, complementarity, conservation biogeography, conservation planning, faunal homogenization, floral homogenization, spatial scale, species extinction, species invasion.

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> 'In considering the distribution of organic beings over the face of the globe, the first great fact which strikes us is, that neither the similarity nor the dissimilarity of the inhabitants of various regions can be accounted for by their climatal and other physical conditions … A second great fact which strikes us in our general review is, that barriers of any kind, or obstacles to free migration, are related in a close and important manner to differences between the productions of various regions.' Charles Darwin (1859).

INTRODUCTION

The regional distinctiveness of biotas across the globe reflects the influence of physical isolation, ecological interactions, and evolutionary diversification on the historical biogeography of species (Darwin, 1859). The palaeontological record demonstrates that large-scale biotic mixing can occur when physical barriers to movement are removed, such as those seen during the Great American Interchange between the land biotas of North and South America, and the transpolar interchange between the cold-water marine biotas of the North Pacific and Arctic-Atlantic basins (Vermeij, 1991). For example, the formation of the Panamanian land bridge during the Great American Interchange permitted the mixing of species between North and South America that formerly had no mammal families in common (Crisci *et al.*, 2003).

In contrast to these episodic events, recent times have witnessed the breaching of natural biogeographical barriers from human activities at rates far exceeding those observed during the history of the Earth (Elton, 1958). Construction of the Suez Canal and the opening of the St Lawrence Seaway are two striking examples of where humans have facilitated the movement of hundreds of marine species (Galil, 2000; Ricciardi & MacIsaac, 2000). In short, human activities have greatly increased the rate and the spatial extent of species introductions across the globe by means of a number of vectors including ballast-water discharge from international shipping, bait-bucket releases associated with recreational fishing, the exotic pet trade, intentional translocations of wildlife for recreation purposes, biological control, and inadvertent releases from aquaculture and horticulture activities (e.g. Courtenay & Stauffer, 1990; Carlton & Geller, 1993; Ludwig & Leitch, 1996; Ruiz *et al.*, 2000; Naylor *et al.*, 2001; Reichard & White, 2001; Drake & Lodge, 2004).

In response to the massive influx of non-indigenous species across the globe, evidence suggests that biological diversity is changing in fundamentally different ways at different spatial scales. Although human activities have led to decreased global species diversity as a result of species extinctions, at regional and local scales the introduction of non-indigenous species has often outweighed the loss of natives such that species richness has increased over time (Sax & Gaines, 2003). A less recognized aspect of these trends, however, is that, although local or α-diversity has increased, this is typically at the expense of decreased β-diversity or increased community similarity among regions (Harrison, 1993; Hobbs & Mooney, 1998). The process by which regionally distinct, native communities are gradually replaced by range-expanding, cosmopolitan, non-native communities (i.e. decreasing β-diversity over time) has been termed biotic homogenization (McKinney & Lockwood, 1999). In many respects, biotic homogenization is the logical consequence of human activities that have recreated in a very short time-span the biological equivalent of reuniting the continents into one large landmass, only seen over 260 Ma by the coalescence of continents into Pangaea. This has led some to argue that we are entering a period characterized by widespread faunal and floral homogenization, fittingly dubbed the 'Homogecene', in a place appropriately called the 'New Pangaea'. Sadly, we could view biotic homogenization as the by-product of a global anthropogenic blender (Fig. 1).

In the wake of continued human enhancement of species invasions and extinctions, biotic homogenization is a young and rapidly emerging topic of interest in ecology and evolution (Fig. 2). The study of biotic homogenization is a unique research challenge because it is a multi-faceted process that subsumes many facets of the modern biodiversity crisis, including species invasions, extirpations and environmental alteration, and it requires the explicit consideration of how the identities of communities (not species richness) change over both time and space (Olden *et al.*, 2004). For this reason, I view biotic homogenization as representing an important research agenda in the budding field of conservation biogeography (*sensu* Whittaker *et al.*, 2005), in that it draws heavily

Figure 1 The 'Anthropogenic Blender' that is homogenizing the world's faunas and floras. Pictured from west to east are a number of prominent invasive species located in their native area of origin: red swamp crayfish (*Procambarus clarkii*), largemouth bass (*Micropterus salmoides*), nutria (*Myocastor coypus*), red fire ant (*Solenopsis invicta*), Asian gypsy moth (*Lymantria dispar*), house sparrow (*Passer domesticus*), purple loosestrife (*Lythrum salicaria*), zebra mussel (*Dreissena polymorpha*), Polynesian rat (*Rattus exulans*), kudzu (*Pueraria montana*), Asian longhorned beetle (*Anoplophora glabripennis*) and brown tree snake (*Boiga irregularis*).

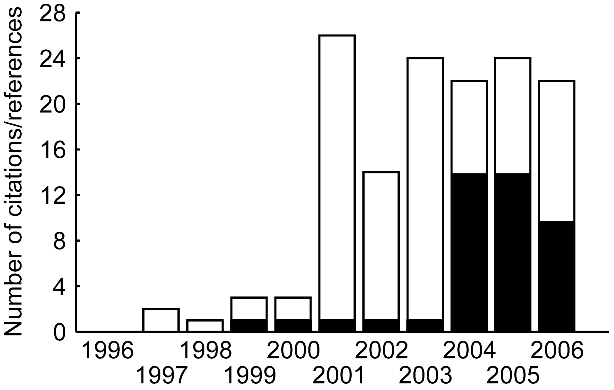

Figure 2 The numbers of citations and references to biotic homogenization in the literature over the past 10 years. Citation frequency includes the number of 'hits' for the search term 'biotic homogenization' using the Web of Science as of February 2006 (black bars) and the Google Scholar search engine (white bars). The spike in 2001 corresponds to the publication of the edited book *Biotic Homogenization* by Lockwood & McKinney (2001).

upon the principles, theories and analyses from the disciplines of historical biogeography, invasion biology, landscape ecology, community ecology and evolutionary biology.

In light of past efforts, I argue that the time is ripe for synthesizing our current knowledge of biotic homogenization and for advocating a more systematic approach to its investigation. The primary goal of this paper is to provide a foundation for such an approach by setting a research agenda for the science of biotic homogenization. While I do not contend that this agenda is necessarily a correct one, nor that I am the most appropriate person to provide it, my hope is that, by reviewing our current state of knowledge, information gaps and priority research needs will be revealed that serve to advance the study of biotic homogenization. This paper has two objectives. First, I provide a comprehensive review of biotic homogenization that explores the ecological mechanisms of the process, the current evidence for faunal and floral homogenization, and the potential ecological and evolutionary consequences. Second, I identify important gaps in our knowledge and highlight promising areas of research for advancing our current thinking on biotic homogenization. In addressing these topics, I will argue that biotic homogenization should be investigated at multiple spatial and temporal scales, with careful attention paid to the various biological mechanisms (invasions vs. extinctions), various environmental drivers (environmental alteration vs. biotic interactions) and various community properties (species occurrence vs. abundance) involved. My discussion also recognizes that there are multiple possible outcomes resulting from the accumulation of invasions and extinctions, including biotic differentiation whereby β-diversity increases over time. This paper deliberately asks more questions than it answers with the singular hope that it will initiate greater, and more directed, research on the topic of biotic homogenization.

A REVIEW OF THE PROCESS OF BIOTIC HOMOGENIZATION

Definition of biotic homogenization

It has long been recognized that species invasions and extinctions (the latter used synonymously with species extirpation) can influence the biological distinctiveness of regions. For example, Charles Elton (1958) envisioned that global commerce would lead to the breakdown of Wallace's faunal realms describing distinct biological regions of the world. Only recently, however, has interest in this area of research been rekindled. McKinney & Lockwood (1999) define biotic homogenization as 'the replacement of local biotas with non-indigenous species', a process that 'often replaces unique endemic species with already widespread species'. More generally, biotic homogenization refers to an increase in the taxonomic similarity of biotas over a specified time interval, or, in other words, a decrease in β-diversity over time (Olden & Poff, 2003). Both these definitions correctly depict biotic homogenization as the process by which species similarity across space increases over time as a result of species invasions and extinctions, as opposed to the pattern resulting from this process. An equally likely outcome of the combined effects of invasions and extinctions is a decrease in taxonomic similarity over time (i.e. increased β-diversity). This is referred to as biotic differentiation (Olden & Poff, 2003).

Quantifying biotic homogenization

Biotic homogenization is quantified simply as the change in the pairwise community similarity between two time periods, and is typically based on records of species presence or absence. Previous efforts to measure biotic homogenization have used species–area curves, a variety of similarity indices and measures of spatial turnover, and multivariate ordination and clustering approaches (see the review by Olden & Rooney, 2006). Data selection is an important step in the quantification of biotic homogenization. The most straightforward approach is to survey the species pool across multiple sites at two points in time (e.g. Radomski & Goeman, 1995; Rooney *et al.*, 2004). In the absence of such data, species pools can be 'reconstructed' from published lists of native and non-native species by comparing native faunas before known introductions, extirpations or extinctions associated with humans (i.e. pre-European fauna) with present-day faunas representing native and non-native species that include species extirpations (e.g. Rahel, 2000; Taylor, 2004; Marchetti *et al.*, 2006). The degree of homogenization is typically presented as the average change in pairwise community similarity (based on an index of similarity) between historical and extant time periods, although a number of approaches can be used.

Genetic, taxonomic and functional homogenization

Biotic homogenization is considered an overarching ecological process that encompasses either the loss of genetic, taxonomic or functional distinctiveness (Olden *et al.*, 2004). *Genetic homogenization* is defined as an increase in the genetic similarity of gene pools over time owing to intra- and inter-specific hybridization primarily with non-indigenous species. Genetic homogenization can be defined in terms of the allelic composition of a particular locus or set of loci (i.e. identity of genotypes) or their frequencies (i.e. relative abundance of genotypes). *Taxonomic homogenization* refers to an increase in the phylogenetic similarity of biota over time owing to the establishment of cosmopolitan species and extirpation of endemic species (see definition above). Taxonomic homogenization has been the primary focus of previous research and is used interchangeably with the term biotic homogenization throughout the literature (and herein). *Functional homogenization* is defined as an increase in the functional similarity of biotas over time because of the establishment of species with similar 'roles' in the ecosystem (i.e. species with several functional equivalents) and the loss of species possessing unique functional 'roles' (i.e. species with no or little functional redundancy). One approach to assessing functional similarity is based on the presence or absence of species traits or the frequency distribution of traits in the community (i.e. similarity in species' ecological niches). Functional homogenization has similarities to the idea of ecological homogenization described by McKinney & Lockwood (1999).

Ecological mechanisms of biotic homogenization

In the simplest sense, human activities that increase rates of species invasions and extinctions are the ultimate cause of biotic homogenization (Rahel, 2002). However, biotic homogenization is not synonymous with species invasions and extinctions, but in fact can arise when only species invasions occur without commensurate loss of species, or conversely when only species extinctions occur. In other words, species additions or replacements need not occur for communities to become homogenized or even differentiated over time (Olden & Poff, 2003). It is the subtlety by which the homogenization process operates that causes confusion in the literature (see the recent exchange between Wilkinson, 2004 and Olden & Poff, 2004a). This illustrates the importance of understanding the various ecological mechanisms underlying the homogenization process. Recently, Olden & Poff (2003) proposed a conceptual model describing a number of distinct mechanisms operating in both aquatic and terrestrial systems by which biotic homogenization or differentiation may occur in response to the specific sequence of invasions and extinctions. In a simple graphical example, Fig. 3 shows how the invasion of a group of similar species and the extinction of unique species can result in varying levels of biotic homogenization (also see Rahel, 2002). This illustration emphasizes that the introduction of cosmopolitan species will, by itself, increase homogenization, but this effect is magnified if endemic species that contribute to the uniqueness of the system are lost. This example also shows that biotic homogenization or differentiation can occur with or without changes in species richness: a topic that will be re-visited later.

Empirical evidence for biotic homogenization

The term biotic homogenization is used throughout the literature, for example with respect to birds (Blair, 2001, 2004; Crooks *et al.*, 2004), fishes (Radomski & Goeman, 1995; Rahel, 2000; Marchetti *et al.*, 2001, 2006; Walters *et al.*, 2003; Taylor, 2004), plants (McKinney, 2004a; Rooney *et al.*, 2004; Kühn &

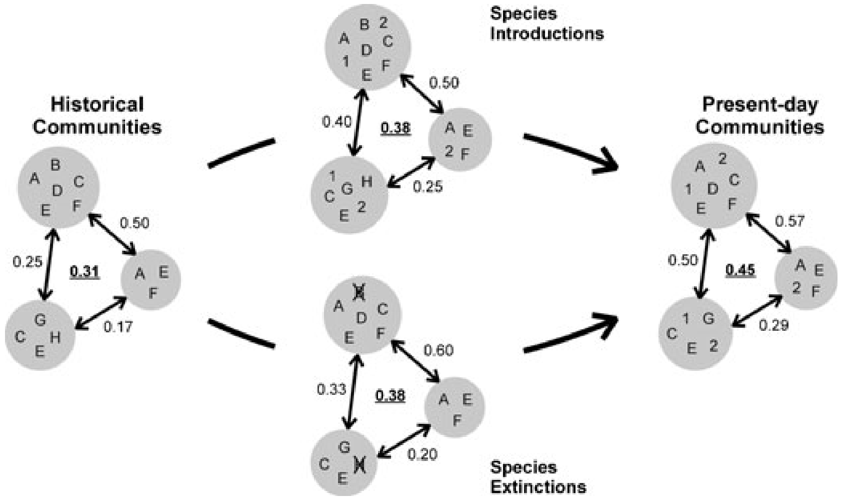

Figure 3 Schematic depicting how species invasions and extinctions lead to biotic homogenization. Grey circles represent the species pool of a site (letters: native species; numbers: non-native species), and values represent the taxonomic similarity between sites and averaged across sites (underlined values) according to Jaccard's similarity coefficient. The top scenario illustrates only species introductions (spp. 1 and 2) and the bottom scenario illustrates only species extirpations (spp. B and H), both of which result in taxonomic similarity increasing from 0.31 to 0.38 (i.e. 8% homogenization). Together, the introduction of cosmopolitan species and the extirpation of endemic species increase taxonomic similarity from 0.31 to 0.45 (i.e. 14% homogenization). Notably, biotic homogenization is accompanied by increases in local and regional species richness.

Klotz, 2006; Schwartz *et al.*, 2006), amphibians and reptiles (Duncan & Lockwood, 2001; Smith, 2006), snails (Cowie, 2001), and ants (Holway & Suarez, 2006), yet it has been measured only in a limited number of studies. A review of the literature shows that estimates are sparse and highly variable within and between taxonomic groups (Table 1). Below I review a number of these studies.

For freshwater fish faunas, Rahel (2000) and Taylor (2004) compared species similarity before European settlement with the present-day similarity to assess the degree of fish homogenization for US states and Canadian provinces, respectively. Both studies found evidence for homogenization that was primarily the result of cosmopolitan species invasions associated with fish stocking for recreational purposes or aquaculture (e.g. common carp, *Cyprinus carpio* and brown trout, *Salmo trutta*), and to a smaller degree the extirpation of endemic species (e.g. harelip sucker, *Lagochila lacera*). Marchetti *et al.* (2001, 2006) performed the same comparison for freshwater fishes in California and observed homogenization among zoogeographic provinces but differentiation among watersheds. This contrasting pattern is, in part, a result of the different spatial scales of analysis and different sources of species introductions (more on this later in the paper). It also emphasizes that biotic differentiation is a valid and expected outcome of species invasions and extinctions. Using data from the studies discussed above, Olden & Poff (2004b) explored the specific ecological drivers of fish fauna homogenization/differentiation at three spatial scales in the United States – the entire continent, zoogeographic provinces in California, and watersheds within these provinces. This study found strong empirical support for the importance of widespread introductions of cosmopolitan species and either no or differential spatial patterns of native species extirpations for driving homogenization across multiple spatial scales. At a smaller spatial scale, Radomski & Goeman (1995) used fisheries survey data for 62 lakes in Minnesota, USA, to show

Table 1 Review of the published studies that report estimates of community similarity change between two time periods in the context of biotic homogenization. Mean Δ similarity refers to the mean pairwise difference between historical and extant community similarity across all sites. Positive values indicate homogenization and negative values indicate differentiation

Taxonomic group	Mean Δ similarity (%)	Reference
Fish		
Canada – Species lists for 13 provinces/territories	1.3	Taylor (2004)*
United States – Species lists for 48 contiguous states	7.2	Rahel (2000)*
California, USA – Species lists for 6 zoogeographic provinces	20.3	Marchetti *et al.* (2001)*
British Columbia, Canada – Species lists for 8 aquatic ecoregions	−3.5	Taylor (2004)*
California, USA – Species lists for 43 watersheds	−10.7	Marchetti *et al.* (2001)*
South Dakota, USA – Species lists for 16 watersheds	2.4	C.W. Hoagstrom (unpublished data)*
Minnesota, USA – Community composition for 62 lakes surveyed in 1940–55 and 1985–92	9.0	Radomski & Goeman (1995)*
Plants		
United States – Species list for 20 parks and local areas	0.8	McKinney (2004a)*
North America – Species list for selected states/provinces	−0.6	Rejmánek (2000)*
Wisconsin, USA – Community composition for 62 mixed-deciduous coniferous forest stands surveyed in 1950 and 2000	2.6	Rooney *et al.* (2004)†
Wisconsin, USA – Community composition for 21 tallgrass prairie sites surveyed in 1950 and 2000	1.4	T.P Rooney (unpublished data)†
California, USA – Species list for 12 counties	2.0	Schwartz *et al.* (2006)‡
Amphibian and Reptiles		
Florida, USA – Amphibian and reptile species lists for 12 counties	−0.01	Smith (2006)*

Taxonomic similarity based on: *Jaccard's similarity index, †Bray–Curtis similarity index, ‡Sörensen's similarity index.

that fish assemblages have been homogenized over a 43-year time period (1940–55 to 1985–92), primarily from the stocking of a common set of sportfish species across the landscape, and to a smaller degree from the loss of native species.

For plant floras, Rooney *et al.* (2004) re-surveyed 62 upland forest stands in northern Wisconsin, USA, to assess the degree of floral homogenization between 1950 and 2000. Incorporating changes in species occurrence and relative abundance, the authors found that two-thirds of the sites became more similar in their composition as a result of declines in rare species and increases in regionally abundant species. Schwartz *et al.* (2006) found that the county floras of California, USA, have shown slight homogenization. The introduction of noxious weeds played a central role in shaping patterns of homogenization, but the authors suggest that the greatest potential for future homogenization is from extirpations of extant populations within counties. At a broader scale, McKinney (2004a) found that exotic plant species contributed significantly to floral homogenization of 20 parks/local areas across the United States, although the magnitude of homogenization was relatively low and in some cases negative (indicating differentiation). Cosmopolitan plant species most responsible for the observed homogenization included curly dock (*Rumex crispus*), dandelion (*Taraxacum officinale*) and bluegrass (*Poa annua*). For amphibian and reptiles in counties of Florida, USA, Smith (2006) found little evidence for an overall change in herpetofaunal similarity, although > 40% of the county pairs did exhibit increased taxonomic similarity.

Based on a review of the literature it is apparent that we have little evidence for biotic homogenization, despite the fact that the literature portrays homogenization to be the default outcome of species invasions and extinctions. Olden *et al.* (2006) recently used estimates of native and non-native species richness and the conceptual model of Olden & Poff (2003) to provide the first estimates of homogenization for five major taxonomic groups – land birds, freshwater fishes, terrestrial mammals, plants, and freshwater reptiles and amphibians – at the continental scale of North America. Predictions from this study suggest the following levels of biotic homogenization across North America: plants, 22%; fishes, 14%; reptiles/amphibians, 12%; mammals, 9%; and birds, 8%, although at the state/provincial level there was substantial variation in predictions of community similarity. Importantly, these represent estimates of biotic homogenization because they are not based on species identities, but are derived from species richness data and the perceived importance of particular ecological mechanisms. However, given the paucity of quantitative estimates of biotic homogenization, especially at broad spatial scales, the values above provide a good first-cut comparison of homogenization among different taxonomic groups.

Environmental determinants of biotic homogenization

Environmental degradation is considered one of the primary threats to biodiversity (Sala *et al.*, 2000), but the manner in which these impacts shape patterns of biotic homogenization remains relatively unexplored. By virtue of the relationship between human activities and species invasions and extinctions, however, we might expect that biotic homogenization would exhibit a smilar association. Recently, urbanization of the landscape has been forwarded as a primary homogenizing force (McKinney, 2006). While quantitative evidence for this statement has been slow to accumulate, urban–rural gradient studies have provided some of the first insights.

Blair (2004) found that temporal changes in bird community composition varied in a similar fashion along an urban–rural gradient in the oak-woodlands of northern California and in the eastern broadleaf forests of Ohio, USA. The degree of taxonomic overlap in the bird communities increased from *c.* 5% in the least developed sites to *c.* 20% in the most urbanized sites – an outcome of the replacement of local endemic species (often urban-sensitive species) by ubiquitous non-native species (urban-adapted species). Similarly, Crooks *et al.* (2004) found that avian assemblages in southern California were progressively more similar to those in northern California and Ohio as sites became more urban. In contrast, Jokimäki & Kaisanlahti-Jokimäki (2003) and Clergeau *et al.* (2006) found that avifaunal similarity of town centres in Europe was actually lower than in less urbanized habitats. These two studies caution that urbanization should not be viewed as a process that monotonically increases the similarity of bird communities, and that similarities/differences in local habitat conditions must be accounted for when comparing community similarity across urbanization gradients.

In aquatic ecosystems, Scott & Helfman (2001) and Walters *et al.* (2003) reported that cosmopolitan species richness increased and endemic species richness decreased along a human-impact gradient. Scott & Helfman (2001) used a watershed-scale measure of land-use intensity describing the degree of deforestation and density of buildings and roads, and suggested that land-use change associated with urbanization has essentially led to abiotic homogenization of streambed substrate conditions. In support of this idea, Walters *et al.* (2003) found that local-scale siltation reduces habitat complexity, which favours introduced species that are silt-tolerant while negatively affecting endemic species. Although these two studies did not quantify homogenization *per se*, they are suggestive of the relationship between changes in land use and fish fauna homogenization. At a larger spatial scale, Marchetti *et al.* (2001) observed that measures of human occupancy and aquatic habitat alteration, including the density of dams and aqueducts in the watershed, were associated with increased fish community similarity of zoogeographic provinces in California. However, at a smaller scale, Marchetti *et al.* (2006) found a negative relationship between change in community similarity and the proportion of the watershed in development (including commercial, industrial, urban and suburban), or in other words, more developed watersheds showed greater biotic differentiation.

Two recent studies have compared patterns of floral homogenization in urban and rural areas. Schwartz *et al.*

(2006) reported floristic homogenization of urbanized counties in southern California, whereas they found no change in more rural areas of northern California. The study by Kühn & Klotz (2006), on the other hand, found no overall relationship between patterns of homogenization and urbanization across Germany. In a revealing study, Rooney *et al.* (2004) found that flora homogenization of forest understory communities in northern Wisconsin, USA, predominantly occurred in areas without deer hunting. This finding supported the idea that overabundant deer populations were a key driver of community change, with the likely mechanism being selective grazing of species with showy flowers.

Holway & Suarez (2006) examined native ant communities in scrub and riparian habitats of mediterranean California to test the hypothesis that the invasion of the Argentine ant (*Linepithema humile*) has caused biotic homogenization. By comparing invaded and uninvaded sites in similar habitats, the authors showed that sites invaded by Argentine ants have lower β-diversity than do uninvaded sites. Because Argentine ant abundance in the seasonally dry mediterranean environments is positively correlated with soil moisture, the authors hypothesized that the homogenizing effects of Argentine ant are facilitated by inputs of urban and agricultural runoff that act to create mesic soil conditions. This supports the notion that anthropogenic modifications to the environment indirectly cause biotic homogenization by creating opportunities for the invasion of the Argentine ant, as opposed to threatening the persistence of native ants directly.

Ecological and evolutionary consequences of biotic homogenization

While it is generally acknowledged that a loss of species diversity brings ecological, evolutionary and social costs (Ehrlich & Ehrlich, 1992; Kinzig *et al.*, 2002; Moritz, 2002), an understanding of the consequences of biotic homogenization may require a broader spatial and temporal perspective (Olden *et al.*, 2004). Here I discuss a few examples out of the likely numerous consequences related to changing patterns of biological similarity in time and space. Genetic homogenization arising from inter-specific hybridization between genetically distinct species may enhance the probability that 'hybrid swarms' will genetically extirpate native taxa (Rhymer & Simberloff, 1996). Intra-specific hybridization resulting from the extensive translocation of species across the landscape can compromise the unique genetic make-up of geographically distinct populations (Stockwell *et al.*, 1996), as is seen from the wide-spread stocking of cutthroat trout (*Oncorhynchus clarki*) and the loss of a genetically distinct subspecies of trout (Perry *et al.*, 2002). Homogenization of gene pools may also increase community vulnerability to invasion by promoting the success of hybrid competitors (Lee, 2002) and may reduce ecosystem resilience to environmental change (Hughes & Stachowicz, 2004). For example, the invasion success of the Argentine ant results in large part from the genetic homogenization of the founding populations, which reduced genetically controlled intra-specific aggression among colonies and led to the creation of competitively superior supercolonies (Tsutsui *et al.*, 2000).

Taxonomic and functional homogenization is also expected to have a number of important implications for community and ecosystem properties. Functional homogenization of inter-connected local communities within a region (or metacommunities) may 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. Taxonomic homogenization may lead to a simplified food-web structure with the possibility of positive feedback among multiple trophic levels. For example, Beisner *et al.* (2003) found that the invasion of rainbow smelt (*Osmerus mordax*) into two northern temperate lakes resulted in fish community homogenization through the spread of invaders, as well as the homogenization of the zooplankton community structure by means of the direct predation effects of smelt and indirect effects acting through competitive interactions among zooplankton. Simplification by means of homogenization might also play a significant role in influencing the rate of species spread and community resistance to future invasions. García-Ramos & Rodríguez (2002) 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.

We expect that biotic homogenization will also be accompanied by significant evolutionary consequences. Much like how the future of speciation is tightly linked with the future of species diversity (Rosenzweig, 2001), biotic homogenization may compromise the potential for future speciation because of limited spatial variability in species diversity and composition. Local adaptation and drift contribute to the genetic variability among isolated populations, which is expected to be significant in how species respond evolutionarily to environmental change. Consequently, genetic homogenization may jeopardize the future resilience of biological communities by decreasing the capacity for adaptation to environmental change (Olden *et al.*, 2004). Ultimately, this may compromise the potential for evolutionary diversification (Day & Young, 2004). Finally, taxonomic homogenization may alter evolutionary trajectories by limiting the number and breadth of novel species interactions, thereby weakening the selection pressures in the homogenized communities (Mooney & Cleland, 2001; Rosenzweig, 2001).

CHALLENGES AND PRESSING RESEARCH NEEDS

What is the magnitude and spatial extent of biotic homogenization?

Limited empirical quantification of biotic homogenization continues to impede our ability to make defendable statements regarding its magnitude and spatial extent for different taxonomic groups (Table 1). In fact, our knowledge is almost completely restricted to the freshwater fish faunas and plant floras of the United States, and even for these groups we have only a minimal understanding. Therefore, perhaps the most fundamental research need is to quantify temporal changes in β-diversity for faunal and floral groups in different geographic regions. Such studies will also provide the opportunity to conduct cross-taxonomic comparisons of biotic homogenization, for example between different taxonomic groups or the same group in different environmental settings. We might expect varying degrees of biotic homogenization in different systems and for different taxa because of differences in regional rates of species invasions and extinctions (e.g. Case, 1996; Lonsdale, 1999). Moreover, different mechanisms are likely to be driving these patterns. If, for example, marine species are less prone to extinction than terrestrial species (Carlton, 1996) and rates of spread of invasive species are generally lower in marine systems than in terrestrial systems (Grosholz, 1996), greater rates of homogenization in terrestrial ecosystems are likely. However, because this prediction is independent of taxonomic patterns in species invasions, and given the relatively higher number of cosmopolitan species in marine ecosystems, one might predict that marine systems have exhibited greater homogenization (Rapoport, 1994). Once data are collected and temporal changes in β-diversity are quantified for a larger number of taxonomic groups, it will be possible to test such hypotheses. Until this occurs, however, we will continue to have only limited insight into the taxonomic and geographic extent of biotic homogenization.

In contrast with the case for taxonomic homogenization, the processes of genetic and functional homogenization have received much less attention in the literature. Because species invasions and extinctions are not random, but are related in large part to intrinsic life-history characteristics of species that exhibit higher-order phylogenetic affinities (reviewed by McKinney, 1997; Kolar & Lodge, 2001), taxonomic homogenization is likely to be accompanied by both functional and genetic homogenization. Do empirical data support this hypothesis? Only qualitatively. Duncan & Lockwood (2001) discussed how the transition from flowing-river (lotic) to standing-water (lentic) habitats associated with dam construction was mirrored by changes from lotic-adapted to lentic-adapted fish species and the 'wholesale replacement of functional groups' in the south-eastern US. Rooney *et al.* (2004) found that floral homogenization was associated with declines in the relative abundance of animal-pollinated and animal-dispersed species, suggesting that guild structure has changed over time. Blair (2004) found that avifaunal homogenization in response to urbanization was the result of the replacement of specialist, urban-sensitive species by generalist, non-native species more adapted to urban environments. Similar evidence was provided by Clergeau *et al.* (2006), who found that avifaunal homogenization has been associated with declines in the number of ground-nesting bird species and bird species preferring bush-shrub habitats that have been reduced by urbanization. Finally, Holway & Suarez (2006) found that the homogenization of ant communities was accompanied by a transition to smaller-bodied workers with lower thermal tolerance and a reduced diversity of behaviours (i.e. nesting habits, dispersal strategies, and foraging behaviours).

While these studies have provided casual descriptions of how the functional attributes of communities have changed over time, we do not yet have a formal understanding or quantification of functional homogenization (in addition to genetic homogenization). What evidence is there for genetic/functional homogenization or differentiation? What are appropriate measures of genetic and functional homogenization? Is there a relationship between taxonomic, genetic and functional homogenization? Research addressing these questions is critically needed.

How is biotic homogenization different from species diversity loss?

Important and illuminating as past efforts have been to understanding patterns of biotic homogenization, upon reviewing the literature it becomes overwhelmingly evident that the term 'biotic homogenization' is often erroneously used as a synonym for species diversity loss. Future efforts should focus on clearly defining this process and explicitly examining its similarities to and differences from other components of biodiversity (Olden & Rooney, 2006). For instance, recent studies have explored the relationship between the various components of biodiversity (Loreau, 2000) and between the various measures of β-diversity (Koleff *et al.*, 2003), but we still have much to learn about the relationship between changes in species richness and community similarity over time. Gaining this knowledge is essential not only for improving our understanding of biotic homogenization, but also for communicating the importance of this process to the lay public and policy makers. A preliminary look at the relationship between percentage change in species richness and the degree of biotic homogenization for fish and plant communities in the United States and Canada reveals a strong positive and logarithmic relationship (Fig. 4). This suggests that taxonomic homogenization may increase rapidly in response to small changes in species richness, after which the level of homogenization plateaus. Additional support for this relationship comes from Marchetti *et al.* (2001), who found that zoogeographic provinces showed both homogenization and a net increase in fish species richness, and from Rooney *et al.* (2004), who reported the same positive relationship for forest understory communities. The preliminary results presented here highlight the need for future research into how biotic homogenization covaries with other components of biodiversity.

What are the relative roles of species invasions vs. species extinctions for biotic homogenization?

Species invasions and extinctions both play an important role in shaping patterns of biotic homogenization (see the section

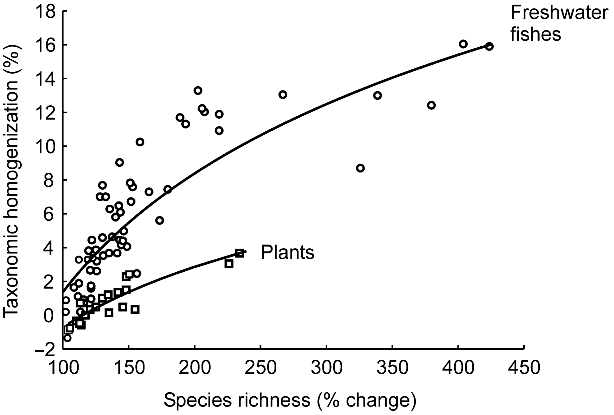

Figure 4 Degree of biotic homogenization and percentage change in fish species richness for US states and Canadian provinces/territories ($n = 63$) and plant species richness for parks and local areas in the US ($n = 20$). Comparisons were made between pre-European settlement (present-day native species including extirpated species) and present-day (native and non-native species) biotas. Fish homogenization showed a significant logarithmic relationship with percentage change in species richness ($R^2 = 0.77$, $F_{1,59} = 194.7$, $P < 0.0001$), as did plant homogenization ($R^2 = 0.79$, $F_{1,18} = 69.4$, $P < 0.0001$). Data sources are Rahel (2000), McKinney (2004a) and Taylor (2004).

entitled Empirical evidence for biotic homogenization). However, less clear are the relative roles of invasions and extinctions in the homogenization process and how they may vary in different taxonomic groups, ecological systems and across spatial scales. Another interesting question is whether the homogenizing effects of non-native species introductions from within a country exceed the effects of alien species introductions from other countries. Recently, McKinney (2005) found that species introduced from within the United States have a greater homogenizing effect on fish and plant community composition than species from more distant sources. In summary, future research is needed to explore the relative roles of species extinctions and species invasions from different sources for biotic homogenization.

What are the environmental determinants of biotic homogenization?

To date, we have made little progress in elucidating the key environmental drivers of biotic homogenization. Previous efforts have focused solely on the relationship between patterns of community change and static, present-day descriptors of the environment, predominantly measures of urbanization. We can advance this area of research in at least three ways. First, because the process of biotic homogenization encompasses both spatial and temporal dimensions, future research efforts should focus on developing innovative environmental descriptors that quantify changes in the environment over the same spatial and temporal scales. We might expect that these variables will be more predictive compared to the static variables that describe the environment at a single point in time and space (typically present-day conditions). Second, while urbanization is no doubt a driver of biotic homogenization at some level (McKinney, 2006; Olden *et al.*, 2006), this is not always the case (see Kühn & Klotz, 2006; Marchetti *et al.*, 2006). Future research should focus on quantifying the specific natural and anthropogenic processes (including those related to human urbanization) that shape patterns of biotic homogenization. Third, to advance our understanding of biotic homogenization we must investigate how habitat modification directly threatens the persistence of native species, and indirectly facilitates the establishment and potential impact of non-indigenous species (Olden & Poff, 2003). In short, by identifying the dynamic drivers of biotic homogenization (both direct and indirect) we will broaden our mechanistic understanding of this process, which will ultimately assist in the development of predictive models that forecast levels and rates of homogenization across the landscape.

What are the potential repercussions of biotic homogenization?

Beyond initial speculation regarding the ecological and evolutionary consequences of biotic homogenization (McKinney & Lockwood, 1999; Rahel, 2002; Olden *et al.*, 2004), we have yet to focus our attention on distilling the broader implications of this process. The growing realization that species composition, not richness, defines the role that biodiversity plays in maintaining ecosystem function (Kinzig *et al.*, 2002) should play an important role in this regard by helping to focus future experiments and observational research. Importantly, we should study these topics through an objective lens and ask whether we expect biotic homogenization always to be associated with negative impacts. Distinguishing between the processes of biotic homogenization and biotic impoverishment (which are often used interchangeably) is a critical first step in this investigation. In doing so we will be able to identify the context in which the ecological and evolutionary impacts of biotic homogenization are likely to be manifested.

What are the temporal dynamics of biotic homogenization?

Biotic homogenization is a continuous process, yet our current understanding is limited to comparisons of community similarity between just two points in time. The time course of biotic homogenization will reflect the magnitude and pattern of species gains and losses over time, and therefore is likely to differ among taxonomic groups and in different geographic settings. Generally, we might expect the following temporal sequence of biotic homogenization. After the initial human settlement of an area, biotic differentiation may occur at first because accidental and intentional introduction of non-indigenous species will occur sporadically across the landscape (supported by McKinney, 2004b). This will be offset, to some degree, by the rapid extinction of highly vulnerable, native species that were unique elements of the historical biota. Because colonization is a much faster process than extinction, it is likely that species introductions will play a greater role in shaping initial patterns of differentiation. A transition towards gradual biotic homogenization will occur in subsequent years as non-indigenous species spread (and are introduced) to more areas across the landscape. Homogenization is likely to continue as cosmopolitan species spread progressively through natural and human-assisted dispersal, but eventually will decrease as non-indigenous species saturate the landscape. During this period, biotic homogenization will probably be magnified, to a small degree, by the gradual extirpation of endemic, native species, but may also be dampened by the continual introduction of new non-indigenous species. The temporal dynamics of biotic homogenization is an interesting area of research that deserves more attention.

If, in fact, rates of biotic homogenization are not constant but vary through time, it naturally follows that perceived patterns of change in community similarity will be influenced by the choice of time period and length of investigation. For example, fish community similarity increased by 9% in Minnesota lakes between 1940 and 1992 (Radomski & Goeman, 1995) and by 20% in California zoogeographic provinces between pre-1850 and 2000 (Marchetti *et al.*, 2001). It is extremely difficult to disentangle methodological from biological differences when comparing these findings. California may exhibit a greater degree of homogenization simply because of a longer data record and because the Minnesota lakes were examined over the past 60 years and after an initial phase of high homogenization. This raises a number of interesting questions with respect to how observed patterns of biotic homogenization may be sensitive to different temporal scales of investigation. Careful simulations and empirical studies might assist in addressing such questions.

How does spatial scale influence the study of biotic homogenization?

Spatial scale, referring to the sampling unit (e.g. plot), grain (level of resolution), focus (level of analysis) and extent (total geographic area), is an important consideration when studying biotic homogenization. Currently, we have only a limited understanding of how spatial grain and extent influence estimates of biotic homogenization. We can, however, make a number of simple predictions. For example, larger spatial grains should result in greater probabilities of recording the introduction of a given species and lower likelihoods of observing the extirpation of a native species by virtue of a greater total area and diversity of habitats. By contrast, at smaller grains we expect higher probabilities of observing the introduction of rare, non-native species. Based on these assumptions, we would expect greater levels of homogenization at coarser spatial grains of investigation – an expectation supported by a few studies. Fish fauna homogenization was greater for zoogeographic provinces of California than for watersheds within these provinces (Marchetti *et al.*, 2001, 2006), and homogenization among Canadian provinces was greater than for ecoregions within a single province (Taylor, 2004). In summary, without an understanding of the spatial dependence of biotic homogenization the interpretation and comparison of previous findings will be greatly complicated, if not rendered impossible. Until we do this it will be difficult to draw generalizations regarding patterns of biotic homogenization within and across taxonomic groups.

Closely associated to the importance of spatial scale is the appropriate choice of observation unit. Previous studies have, for the most part, quantified biotic homogenization based on species lists for political units (i.e. states, provinces, counties) because data are typically available in this format. Analyses based on political units, however, are likely to underestimate biotic homogenization because historical similarity will be higher because natural, biogeographical barriers (e.g. mountain ranges, watershed divides) that define the historical distinctiveness of a region are not respected. Related to this is the fact that historical similarity decreases with increasing distance between regions because of greater environmental differences and limited dispersal potential (Nekola & White, 1999). In fact, a number of studies have found that biotic homogenization decreases as the distance between samples increases (e.g. McKinney, 2004a; Clergeau *et al.*, 2006). This raises a number of questions. What are the implications of using artificial rather than natural biogeographical regions when quantifying biotic homogenization? Is the calculation of a mean pairwise change in community similarity a valid measure of overall biotic homogenization?

What community properties are facing biotic homogenization?

Although biotic homogenization is typically quantified on the basis of species' presence or absence data, our understanding of this process would benefit from an examination of changes in species' abundances over time. For example, we might expect increased non-native species dominance or decreased species evenness to be indicative of biotic homogenization and its potential ecological consequences (e.g. Rooney *et al.*, 2004). McKinney & Lockwood (2005) recently suggested that the homogenization of community similarity based on species' presence/absence may be positively related to the homogenization of species abundances. Quantifying biotic homogenization in terms of community properties that incorporate species' abundance requires further investigation.

CONCLUSION

We do not have biotic homogeneity and perhaps never will, but the future is certain to bring considerable ecological re-shuffling as people influence ecosystems in various ways. A general case for biological heterogeneity was eloquently made by Michael Huston (1994), who simply stated, 'Diversity would not be interesting if the level of diversity were the same everywhere'.

Indeed, greater biological homogeneity will influence not only how we view the world, but also our motivation to experience it (Olden *et al.*, 2005). To the uninitiated, recent evidence showing increases in local species diversity owing to species invasions could well undermine efforts to battle invasive species and sustain native biological diversity. Consequently, it is critical that conservation biologists facilitate greater awareness of the various components of biodiversity, including the process of biotic homogenization and its unique role in the modern biodiversity crisis. By placing biotic homogenization in an ecological and social context we will gain the ear of policy makers and the lay public with regard to the considerable consequences of this process. Throughout this paper I have cited a number of pressing research needs in the study of biotic homogenization with the hope that it will challenge researchers and promote future efforts. I hope that the provision of a framework emphasizing a more comparative and systematic rather than an anecdotal and piecemeal approach to the study of biotic homogenization will help to prioritize research needs and advance this newly emerging area of research within the field of conservation biogeography.

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BIOSKETCH

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