Biotic Homogenization

Julian D Olden, *University of Washington, Seattle, Washington, USA*

Biotic homogenization is the process by which species invasions and extinctions increase the genetic, taxonomic or functional similarity of two or more locations over a specified time interval. Biotic homogenization is now considered a distinct facet of the broader biodiversity crisis having significant ecological, evolutionary and social consequences.

Keynote article

Article Contents

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Introduction

Humanity's migrations across, and subsequent modification of, the landscape have had innumerable effects on the many organisms in which we share this world. Mounting evidence suggests that the dual processes of human-mediated extirpation of native species and the introduction of nonnative species have resulted in significant changes in biological diversity at different spatial scales. Global species diversity has decreased over time as a result of native species extinctions, but at regional and local scales species diversity has typically increased because the establishment of nonnative species has outpaced the loss of native species. Furthermore, species gains are frequently the result of the widespread invasion of ubiquitous nonnative species into areas containing rare, and often unique, native species. As a result, increases in local or alpha-diversity typically occur at the expense of decreased beta-diversity or increased community similarity among regions. The process by which species invasions and extinctions increase the genetic, taxonomic or functional similarity of two or more locations over a specified time interval (i.e. beta-diversity decreases over time) is called biotic homogenization (McKinney and Lockwood, 1999). Another outcome of the combined effects of invasions and extinctions is a decrease in biological similarity over time (i.e. increased beta-diversity), referred to as biotic differentiation (Olden and Poff, 2003). **See also**: Biodiversity – Threats; Conservation of Biodiversity; Conservation Biology and Biodiversity; Species Richness: Small Scale

Biotic homogenization is now considered a distinct facet of the broader biodiversity crisis having significant ecological, evolutionary and social consequences (Olden *et al.*, 2004). Some critics, however, argue that biotic homogenization is not a new phenomenon in the earth's history. Indeed, the palaeontological record is replete with examples of episodic mixing of biotas causing homogenization when physical barriers to movement are removed. For example, the opening of the transpolar corridor between the Pacific and Atlantic oceans and the formation of the Panamanian land bridge between North and South America during the Great American Interchange permitted the massive flux of species between formerly isolated regions. However, in sharp contrast to these episodic events, recent times have witnessed the breaching of natural biogeographical barriers from human activities at rates and distances far exceeding those observed during the history of the earth. Charles Elton (1958) was perhaps the first to recognize this phenomenon when he discussed the breakdown of Wallace's Faunal Realms by global commerce during European settlement. In more recent decades, human activities have greatly hastened the mixing process by increasing the frequency and the spatial extent of species introductions across the globe through ballast-water discharge from international shipping, bait-bucket releases associated with recreational fishing, the global pet trade, intentional translocations of wildlife for recreation purposes, biological control and inadvertent releases from aquaculture and horticulture activities. **See also**: Dispersal: Biogeography; Macroecology

The Process of Biotic Homogenization

The study of biotic homogenization represents a unique challenge to scientists because it is a multifaceted process encompassing both species invasions and extirpations, and it requires the explicit consideration of how the identities of species (not species richness) change over both space and time. The number and manner in which species introductions and extirpations occur may lead to very different levels of homogenization or differentiation (Olden and Poff, 2003). In the absence of any extirpation, the introduction of the same nonnative species at two separate localities will lead to increases in the similarity of the invaded communities. Conversely, the introduction of a different nonnative species at each locality will decrease community similarity (**Figure 1**). Although this example is useful to illustrate the simplest examples by which biotic homogenization can

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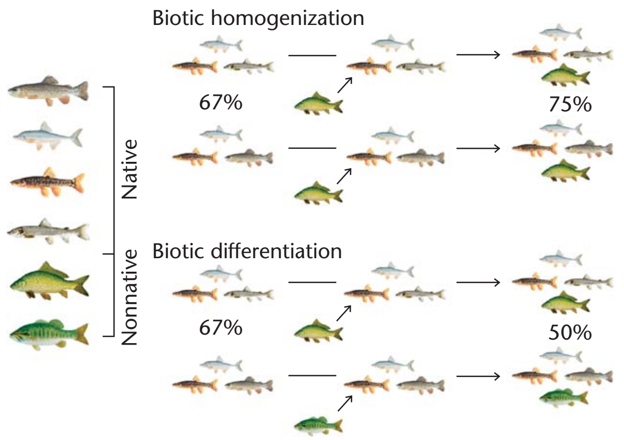

Figure 1 Illustration of how species invasions and extinctions can cause either biotic homogenization or differentiation, depending on the identity of the species involved. A pair of communities for each scenario is illustrated where introduction events are represented by the arrow and appearance of a species icon. For simplicity, no species go extinct. Both scenarios share the same species pool (four native fish species, two nonnative fish species) and species richness. Community similarity is presented as a percentage.

occur, both empirical data and theoretical modelling suggests that this process is both complex and particular to the spatial and temporal scale of investigation (Olden and Poff, 2003). Differential patterns of invasions and extirpations of the same or different species can lead to both increases (homogenization) and decreases (differentiation) in community similarity.

Biotic homogenization is considered as an overarching ecological process that encompasses either the loss of genetic, taxonomic or functional distinctiveness over time (Olden *et al.*, 2004). Taxonomic similarity has been the primary focus of previous research and continues to be referred to as biotic homogenization throughout the literature (as it is throughout this article). However, imposing a narrow phylogenetically based definition of biotic homogenization does not reflect accurately the truly multidimensional nature of this process. Consequently, biotic homogenization should be defined pluralistically to describe the broader ecological process by which formerly disparate biotas lose biological distinctiveness at any level of organization, including in their genetic and functional characteristics. According to this view, two additional forms of biotic homogenization can be recognized.

At the molecular level, intra- and inter-specific hybridization can lead to an increase in the genetic similarity of gene pools over time (Olden *et al.*, 2004). Genetic homogenization could be observed in the allelic composition or frequencies of a particular locus or set of loci (i.e. identity and relative abundance of genotypes) among populations. At a higher level of organization, functional homogenization may occur because species invasions and extinction are not random, but are related to intrinsic life-history traits of species that exhibit higher-order phylogenetic affinities. This process would result in an increase in the functional convergence of biotas over time associated with the establishment of species with similar 'roles' in the ecosystem (e.g. high redundancy of functional forms or traits) and the loss of species possessing unique functional 'roles' (McKinney and Lockwood, 1999; Olden *et al.*, 2004). For example, increased prevalence of nonnative species that are functionally redundant with respect to certain traits favoured by humans and present-day environments would be expected to decrease spatial variability in the functional composition of regional biotas. To date, the majority of scientific research has focused on quantifying patterns of taxonomic homogenization, whereas the processes of genetic and functional homogenization have received considerably less attention.

Patterns and Drivers of Biotic Homogenization

Recent years have witnessed enhanced interest and research effort in the study of biotic homogenization across taxonomic groups and geographic regions. Below I highlight a number of studies that have examined the homogenization of freshwater fishes, plants and birds, and refer the reader to Olden (2006) and the Further Reading list for additional examples.

Fishes

To date, the homogenization of freshwater fish faunas has received the greatest attention by scientists. Rahel (2000) compared the species similarity of present-day versus pre-European settlement in the United States and found that pairs of states averaged 15.4 more species in common now than they did in the past. On average, fish faunas became more similar by 7.2%, with the highest levels observed in western and northeast United States. The high degree of biotic homogenization is best illustrated by the fact that the 89 pairs of states that historically had zero similarity (no species in common) now have an average similarity of 12.2% and an average of 25.2 species in common. Patterns of fish homogenization were primarily the result of species introductions associated with fish stocking for recreational purposes (brown trout, *Salmo trutta*; rainbow trout, *Oncorhynchus mykiss*; and smallmouth bass, *Micropterus dolomieu*) or aquaculture (common carp, *Cyprinus carpio*), and to a smaller degree the extirpation of endemic species (harelip sucker, *Lagochila lacera*).

Olden *et al.* (2008) found strong evidence for the homogenization of Australian fish faunas in response to human-mediated species introductions. Fish compositional similarity among major drainages increased 3.0% from a historical similarity of 17.1% to a present-day similarity of 20.1%. In some cases, the degree of faunal similarity between drainages doubled or even tripled with time. Fish faunal homogenization was the result of the widespread introduction and subsequent escape/spread of fishes for recreation (rainbow trout), aquaculture (common carp) and mosquito control (mosquitofish, *Gambusia affinis*), and from the ornamental/aquarium trade (goldfish, *Carassius auratus*; guppy, *Poecilia reticulata*). Geographical patterns of homogenization were highly concordant with levels of disturbance associated with human settlement, infrastructure and land use. These results suggest that human settlement may directly increase the likelihood of intentional or accidental introductions, and disturbance associated with physical infrastructure and land-use change may promote the establishment of nonnative species by disrupting environmental conditions. This finding agrees with recent, but still limited, evidence suggesting that urbanization is a primary driver of freshwater fish homogenization.

Clavero and García-Berthou (2006) used distributional data for freshwater fish in four time periods to assess the temporal dynamics of biotic homogenization among river basins in the Iberian Peninsula. The authors found strong evidence for biotic homogenization, with faunal similarity among river basins increasing 17.1% from historical times to present-day. Changes in faunal similarity were highly dynamic in time. The establishment of nonnative species in 1995 resulted in a small decrease in average basin similarity of fish faunas (i.e. biotic differentiation), and by 2001 the expansion of previously introduced species caused biotic homogenization in some regions and the continuing addition of new introduced species led to biotic differentiation in others.

The research highlighted above, in addition to a number of other studies in the literature, has provided compelling evidence linking human-induced environmental change to fish faunal homogenization. Collectively, this research has shown that urbanized regions are often characterized by greater increases in taxonomic similarity, suggesting that humans are playing a central role in promoting the homogenization process by introducing new species and favouring the persistence of nonnative species over native species. Although empirical evidence is mounting, this association is still far from universal. For example, research in California has found a negative relationship between change in fish community similarity and the proportion of the watershed in development (including commercial, industrial, urban and suburban). In other words, more developed watersheds showed greater biotic differentiation (Marchetti *et al.*, 2006). Clearly, there is still much to learn with regard to the major factors influencing patterns of biotic homogenization in freshwater environments, in particular across different spatial scales.

Plants

In recent years, scientific research has shifted toward the examination of biotic homogenization of plant communities. Smart *et al.* (2006) used botanical data for higher plants in Great Britain to test the hypothesis that plant communities have become taxonomically and functionally more similar over the past 20 years in human-dominated landscapes. Although little evidence was found for the taxonomic homogenization of plant communities, this study revealed that plant traits related to dispersal ability and canopy height increased in their occurrence across the communities over time. The authors suggest that environmental change has caused different plant communities to converge on a narrower range of winning trait syndromes (i.e. functional homogenization), whereas species identities remain relatively constant. At a smaller spatial scale, Rooney *et al.* (2004) re-surveyed 62 upland forest stands in northern Wisconsin, USA, to assess the degree of floral homogenization of understory communities between 1950 and 2000. By incorporating changes in both species occurrence and relative abundance, the authors found that two-thirds of the sites had become more similar in their composition as a result of declines in rare species and increases in regionally abundant species. Interestingly, levels of homogenization were greatest in areas without deer hunting, suggesting that selective grazing by overabundant deer populations were a key driver of flora homogenization.

Birds

Avifauna homogenization has been another area of recent focus. Cassey *et al.* (2007) explored patterns of invasion and extirpation and their influence on the similarity of global oceanic bird assemblages from the Atlantic, Caribbean, Indian and Pacific Oceans. The authors found that patterns of homogenization differed significantly between and among archipelagos, but in general, avian assemblages tended to be more similar to other islands within their archipelago than to islands outside their archipelago. Islands in the Indian Ocean exhibited the greatest homogenization, whereas biotic differentiation occurred for most islands in the Atlantic Ocean. However, although avifauna homogenization was apparently the rule rather than the exception for islands in the Indian Ocean, the authors found that relationship of this change to initial similarity was scale dependent. At smaller spatial scales (islands within archipelagos), the expected pattern of low initial similarity leading to greater homogenization was observed, whereas this relationship reversed at the larger spatial scale of islands between archipelagos.

In summary, this study illustrated that the spatial extent of investigation and evolutionary history can influence patterns of taxonomic homogenization and differentiation within and across what appear to be equivalent spatial units (i.e. ocean basins).

Ecological, Evolutionary and Social Consequences of Biotic Homogenization

Although it is generally acknowledged that a loss of species diversity brings ecological, evolutionary and social costs, an understanding of the consequences of biotic homogenization is still lacking. In the absence of research demonstrating these consequences, Olden *et al*. (2004) made a number of broad predictions, which are briefly summarized below.

In situations where genetic homogenization arises from inter-specific hybridization between genetically distinct species, we might expect elevated probabilities that 'hybrid swarms' will form and threaten native taxa. Similarly, intra-specific hybridization resulting from the extensive translocation of species across the landscape may compromise the unique genetic make-up of geographically distinct populations. For example, the widespread stocking of cutthroat trout (*Oncorhynchus clarki*) in the western United States currently threatens the genetic distinctiveness of endemic subspecies of native trout. Taxonomic and functional homogenization is also expected to have a number of important ecological implications. More simplified local communities may increase the susceptibility of a region 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 resilience and recovery.

Biotic homogenization may also be accompanied by significant evolutionary consequences. Much like how the future of speciation is tightly linked with the future of species diversity, 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 critical 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. Moreover, biotic mixing may alter evolutionary trajectories by limiting the number and breadth of novel species interactions, thereby weakening the selection pressures in the homogenized communities. **See also**: Speciation: Genetics

Biotic homogenization is also likely to be associated with a number of social consequences. From a purely ethical perspective, one could argue that biotic homogenization will degrade the quality of human life by bestowing biological communities with an aesthetically unappealing uniformity. Biological diversity and its endemic features contribute to a person's attachment to a particular place, become part of a person's identity and therefore support an individual's psychological wellbeing and a community's identity and image of itself. This so-called sense of place, which links issues of individual and community identity, or who we are, to issues of place, or where we are, may be directly threatened by biotic homogenization as endemic elements of the landscape that typify geographic regions and cultures are slowly replaced by ubiquitous forms. Biotic homogenization may influence not only how we view the world but also affect our motivation to experience it. Thus one might expect biotic homogenization to compromise the public's incentive to travel far distances to visit areas similar to those in closer proximity (Olden *et al*., 2005).

Conclusion

Biotic homogenization is now considered one of the most prominent forms of biotic impoverishment worldwide, and it will likely continue to increase in response to anthropogenic forces associated with growing human populations. To date, we have begun to better understand patterns of biotic homogenization in both aquatic and terrestrial ecosystems (McKinney and Lockwood, 1999; Olden and Poff, 2003; Olden, 2006); however, we still know very little about the mechanisms and consequences of biotic homogenization at different spatial and temporal scales. How rates and patterns of biotic homogenization will respond to future environmental change and pathways of species introductions is almost unclear. Increasing globalization and changing geographic routes of international trade will likely enhance the opportunity for long-distance introductions of nonnative species. Similarly, climate change may promote the secondary spread of invasive species and threaten the continued existence of endemic native species. Both processes will surely influence changes in species composition and may hasten the rate of biotic homogenization.

References

Cassey P, Lockwood JL, Blackburn TM and Olden JD (2007) Spatial scale and evolutionary history determine the degree of taxonomic homogenization across island bird assemblages. *Diversity and Distributions* **13**: 458–466.

Clavero M and García-Berthou E (2006) Homogenization dynamics and introduction routes of invasive freshwater fish in the Iberian Peninsula. *Ecological Applications* **16**: 2313–2324.

Elton CS (1958) *The Ecology of Invasions by Animals and Plants*. London, UK: Methuen.

Marchetti M, Lockwood JL and Light T (2006) Urbanization promotes invasion and extinction but not homogenization among California freshwater fishes. *Biological Conservation* **127**: 310–318.

McKinney ML and Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution* **14**: 450–453.

Olden JD (2006) Biotic homogenization: a new research agenda for conservation biogeography. *Journal of Biogeography* **33**: 2027–2039.

Olden JD, Douglas ME and Douglas MR (2005) The human dimensions of biotic homogenization. *Conservation Biology* **19**: 2036–2038.

Olden JD, Kennard MJ and Pusey BJ (2008) Species invasions and the changing biogeography of Australian freshwater fishes. *Global Ecology and Biogeography* **17**: 25–37.

Olden JD and Poff NL (2003) Toward a mechanistic understanding and prediction of biotic homogenization. *American Naturalist* **162**: 442–460.

Olden JD, Poff NL, Douglas MR, Douglas ME and Fausch KD (2004) Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution* **19**: 18–24.

Rahel FJ (2000) Homogenization of fish faunas across the United States. *Science* **288**: 854–856.

Rooney TP, Wiegmann SM, Rogers DA and Waller DM (2004) Biotic impoverishment and homogenization in unfragmented forest understory communities. *Conservation Biology* **18**: 787–798.

Smart SM, Thompson K, Marrs RH *et al*. (2006) Biotic homogenization and changes in species diversity across human-modified ecosystems. *Proceedings of the Royal Society of London, Series B* **273**: 2659–2665.

Further Reading

Castro SA, Muñoz M and Jaksic FM (2007) Transit towards floristic homogenization on oceanic islands in the south-eastern Pacific: comparing pre-European and current floras. *Journal of Biogeography* **34**: 213–222.

Devictor V, Julliard R, Couvet D, Lee A and Jiguet F (2007) Functional homogenization of urbanization on bird communities. *Conservation Biology* **21**: 741–751.

LaSorte FA, McKinney ML and Pyšek P (2007) Compositional similarity among urban floras within and across continents: biographical consequences of human-mediated biotic interchange. *Global Change Biology* **13**: 913–921.

Leprieur F, Beauchard O, Huguency B, Grenouillet G and Brosse S (2008) Null model of biotic homogenization: a test with the European freshwater fish fauna. *Diversity and Distributions* **14**: 291–300.

Olden JD and Rooney TP (2006) On defining and quantifying biotic homogenization. *Global Ecology and Biogeography* **15**: 113–120.

Poff NL, Olden JD, Merritt DM and Pepin DM (2007) Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences of the USA* **104**: 5732–5737.

Qian H and Ricklefs RE (2006) The role of exotic species in homogenizing the North American flora. *Ecology Letters* **9**: 1293–1298.

Rahel FJ (2002) Homogenization of freshwater faunas. *Annual Review of Ecology and Systematics* **33**: 291–315.

Schulte LA, Mladenoff DJ, Crow TR, Merrick LC and Cleland DT (2007) Homogenization of northern U.S. Great Lakes forests due to land use. *Landscape Ecology* **22**: 1089–1103.

Van Turnhout CAM, Foppen RPB, Leuven RSEW, Siepel H and Esselink H (2007) Scale-dependent homogenization: changes in breeding bird diversity in the Netherlands over a 25-year period. *Biological Conservation* **134**: 505–516.