

# Biotic Homogenisation

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Based in part on the previous version of this eLS article 'Biotic Homogenization' (2008) by Julian D Olden.

## Advanced article

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**Biotic homogenisation 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. Recent years have witnessed enhanced interest and research effort in the study of biotic homogenisation across taxonomic groups and geographic regions, with the first article published over 20 years ago. Despite sustained interest, past research efforts have been unevenly distributed with regard to taxonomic groups and ecosystems. Biotic homogenisation of vertebrate and plant communities have been studied the most, while invertebrates have received little attention. Concurrent with heightened quantification of biotic homogenisation, is continued clarification on the significant ecological, evolutionary and social consequences of this phenomenon. Biotic homogenisation 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.**

## Introduction

Humanity's migrations across, and subsequent modification of, the landscape have had innumerable effects on the many organisms with 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 often increased because the establishment of nonnative species can outpace the loss of native species. Species gains are also 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 latter process, by which species invasions and extinctions increase the genetic, taxonomic or functional similarity of two or more locations over a specified time interval, or in other words the decrease in  $\beta$ -diversity over time, is called biotic homogenisation (McKinney and Lockwood, 1999). By contrast, biotic differentiation describes the process of decreased biological similarity over time (i.e. increased  $\beta$ -diversity) (Olden and Poff, 2003). See also: [Biodiversity–Threats](#); [Conservation of Biodiversity](#); [Conservation Biology and Biodiversity](#); [Species Richness: Small Scale](#)

Biotic homogenisation is now considered a distinct facet of the broader biodiversity crisis, resulting in significant ecological, evolutionary and social consequences (Olden *et al.*, 2004, 2011). However, biotic homogenisation is not a new phenomenon in the earth's history. Indeed, the palaeontological record is replete with examples of episodic mixing of biotas causing homogenisation 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 recognise 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](#)

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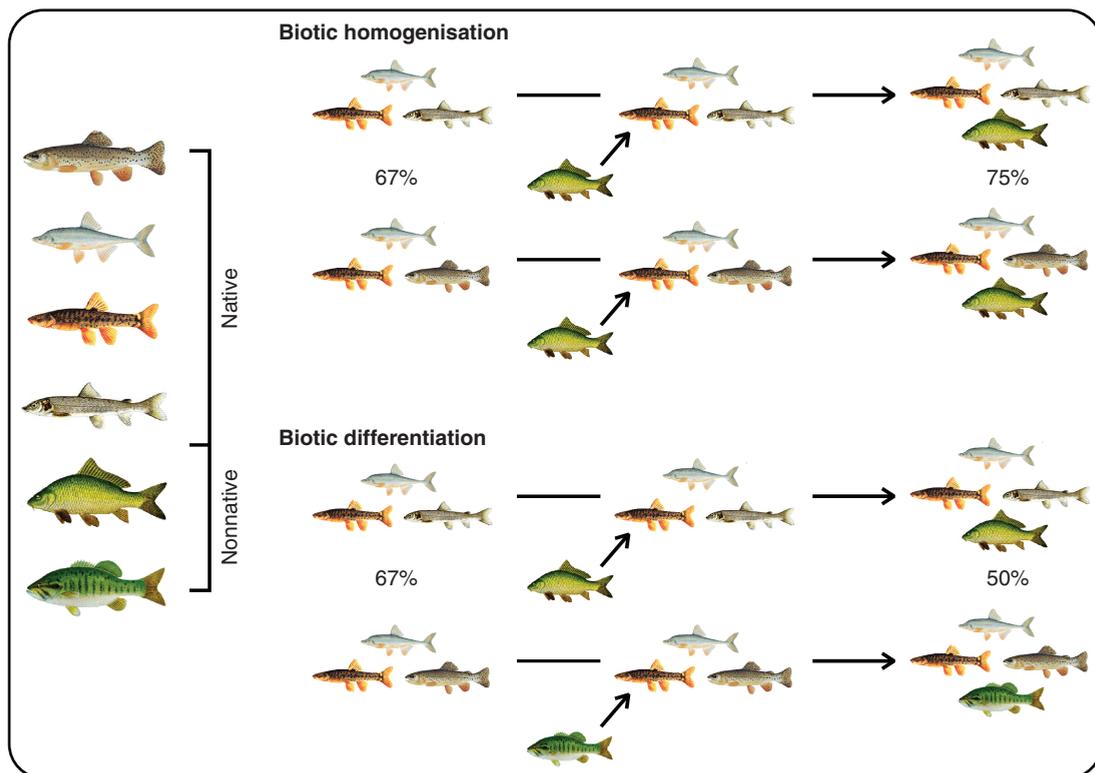
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## The Process of Biotic Homogenisation

The study of biotic homogenisation 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 homogenisation 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 homogenisation can occur, both empirical data and theoretical modelling suggest 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 (homogenisation) and decreases (differentiation) in community similarity.

Biotic homogenisation is considered as an overarching ecological process that encompasses 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 homogenisation throughout the literature (as it is throughout this article). However, imposing a narrow phylogenetically based definition of biotic homogenisation does not reflect accurately the truly multidimensional nature of this process. Consequently, biotic homogenisation should be defined pluralistically to describe the broader ecological process by which formerly disparate biotas lose biological distinctiveness at any level of organisation, including in their genetic and functional characteristics. According to this view, two additional forms of biotic homogenisation can be recognised.

Genetic homogenisation refers to a reduction in genetic variability within a species or among populations of a species, and it can occur through at least three mechanisms (Olden *et al.*, 2011). First, the intentional translocation of populations from one part of the range to another enhances the potential for intraspecific hybridisation (i.e. hybridisation between different subspecies within a species), with the end result being the assimilation of gene pools that were previously differentiated in space. Second, introduction of species outside of their original range(s) increases the likelihood of a founder effect and reduced levels of genetic variability, as well as sets the stage for interspecific



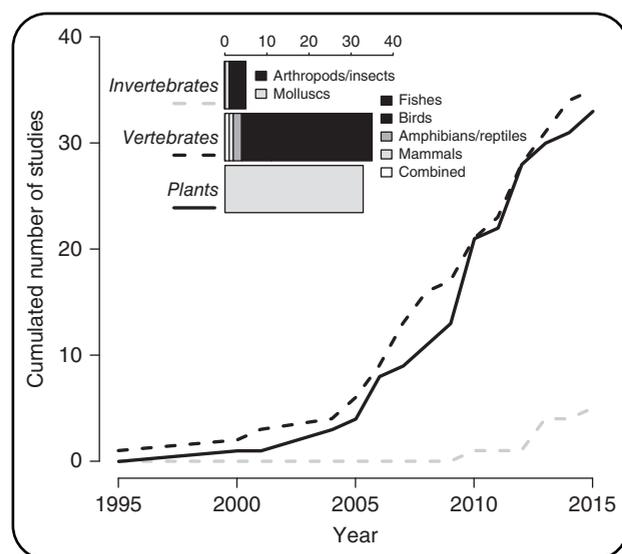
**Figure 1** Illustration of how species invasions and extinctions can cause either biotic homogenisation or differentiation, depending on the identity of the species involved. A pair of communities for each scenario is illustrated where introduction events are represented by the arrow and appearance 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.

hybridisation (i.e. hybridisation between different species within the same genus). Third, if extirpations were a cause for faunal homogenisation, then one consequence might be bottleneck(s) in local populations of the impacted species, along with lowered effective population size(s).

At a higher level of organisation, functional homogenisation 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.

## Patterns and Drivers of Biotic Homogenisation

Recent years have witnessed enhanced interest and research effort in the study of biotic homogenisation across taxonomic groups and geographic regions, with the first article quantifying temporal changes in community similarity published in 1995 (Figure 2).



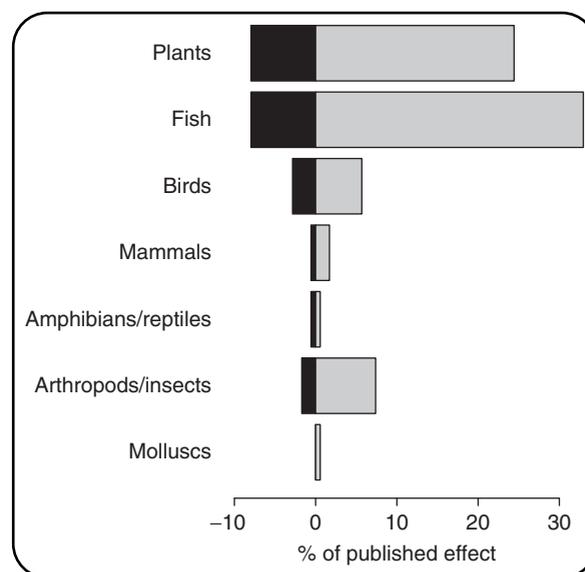
**Figure 2** Cumulative number of published articles through time quantifying patterns of biotic homogenisation between at least two separate time periods and classified according to major taxonomic groups. Results from a search of the literature using ((*biotic OR taxonomic OR functional OR phylogenetic*) AND (*homogenization or homogenisation*) AND (*similarity OR Jaccard OR Sorensen OR Sørensen OR Bray-Curtis OR raup-crick*)) as search terms on ISI Web of Knowledge<sup>SM</sup> (10 March 2016). Only studies reporting changes in community similarity between at least two separate time periods were included.

Despite sustained interest, a review of the peer-reviewed literature reveals that research efforts have been unevenly distributed with regard to taxonomic groups and ecosystems. Biotic homogenisation of vertebrate and plant communities has been studied the most, while invertebrates have received little attention. Among those, fishes and vascular plants are by far the most studied groups. Surprisingly, all the studies have been conducted in terrestrial and freshwater ecosystems with no investigation of marine organisms. Among the different facets of biotic homogenisation, most effort has been directed towards quantifying patterns of taxonomic homogenisation, whereas the processes of genetic and functional homogenisation have received considerably less attention. Out of the 69 articles identified in our literature review, only seven and three have quantified changes in trait and phylogenetic composition, respectively.

To date, the majority of studies have documented an increase in taxonomic homogenisation of biological communities through time (Figure 3). Despite this overall trend, observed variability both within and across taxonomic groups is also apparent – a phenomenon that may be partially explained by the use of different metrics to quantify community similarity, as well as studies being conducted over varying temporal and spatial extents. Below we highlight a number of studies that have examined the homogenisation of different taxonomic groups, and refer the reader to Olden (2006), Olden *et al.* (2011) and Baiser *et al.* (2012) and the Further Reading list for additional examples.

## Fishes

Freshwater fishes were perhaps the first taxonomic group in which the process of biotic homogenisation was formally examined. Rahel (2000) compared the species similarity of present-day



**Figure 3** Number of studies (expressed as a percentage) reporting a positive (homogenisation) or negative (differentiation) change in taxonomic community similarity according to the literature review (Figure 2).

versus pre-European settlement in the United States and found that pairs of states averaged over 15 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. Patterns of fish homogenisation were primarily the result of species introductions associated with fish stocking for recreational purposes (brown trout, rainbow trout and smallmouth bass) or aquaculture (common carp), and to a smaller degree the extirpation of endemic species. Olden *et al.* (2008) found strong evidence for the homogenisation 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%. Geographical patterns of homogenisation were highly concordant with levels of disturbance associated with human settlement, infrastructure and land use. At the global scale, strong historical differences have resulted in the fairly low (0.5%) taxonomic homogenisation of major watersheds in response to species invasions, although it is high (up to 10%) in some highly invaded river basins from the Nearctic and Palearctic realms (Villéger *et al.*, 2011).

Clavero and García-Berthou (2006) used distributional data for freshwater fish in four time periods to assess the temporal dynamics of biotic homogenisation among river basins in the Iberian Peninsula. The authors found strong evidence for biotic homogenisation, with faunal similarity among river basins increasing 17.1% from historical times to the 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 homogenisation in some regions and the continuing addition of newly introduced species led to biotic differentiation in others.

There is also strong evidence that freshwater fish faunas have demonstrated functional homogenisation over time. In southwestern United States, Pool and Olden (2012) found that fish assemblages homogenised over the twentieth century in terms of both taxonomy (species composition) and function (trait composition); however, the rate and magnitude of change varied substantially, as did the roles of the native and nonnative species driving those processes. For major watersheds of Europe, functional homogenisation exceeded taxonomic homogenisation six-fold, and only a moderate positive correlation existed between these changes (Villéger *et al.*, 2014). For instance, 40% of assemblages that experienced taxonomic differentiation were actually functionally homogenised. Translocated species (i.e. nonnative species originating from Europe) played a stronger role than exotic species (i.e. those coming from outside Europe) in the homogenisation process, while extirpation did not play a significant role.

Research over the past two decades has shown that urbanised regions are often characterised by greater increases in taxonomic similarity, suggesting that humans are playing a central role in promoting the homogenisation process by introducing new species and favouring the persistence of nonnative species over native species. A striking example are the Mediterranean-climate regions, which harbour among the highest levels of biodiversity

but also human populations, and for which an average increase in taxonomic and functional similarity of freshwater fish fauna of 7% have been documented as a result of human activities (Marr *et al.*, 2013). All Mediterranean regions around the world showed taxonomic and functional homogenisation in more than 50% of their catchments, with the exception of the southwestern Cape, Central Anatolia and Aegean Sea drainages. Overall, catchments exhibiting taxonomic homogenisation are also homogenised in terms of their functional trait composition, which may have important consequences for the functioning of these ecosystems.

Other studies investigating the homogenisation of fish communities include Taylor (2004), Hermoso *et al.* (2012), Glowacki and Penczak (2013), Li *et al.* (2013) and Vargas *et al.* (2015).

## Plants

Mounting evidence suggests that biotic homogenisation of plant communities might be widespread. 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 homogenisation of plant communities, this study revealed that plant traits related to dispersal ability and canopy height occurred more frequently 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 homogenisation), whereas species identities remain relatively constant. At a smaller spatial scale, Rooney *et al.* (2004) re-surveyed 62 upland forest stands in northern Wisconsin to assess the degree of floral homogenisation 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 homogenisation were greatest in areas without deer hunting, suggesting that selective grazing by overabundant deer populations was a key driver of flora homogenisation.

At a continental scale, Winter *et al.* (2009) demonstrated that although the number of plant introductions has exceeded the number of native plant extinctions within European regions since 1500, resulting in an overall increase in species richness, European floras have become taxonomically and phylogenetically impoverished. The homogenisation effect of species introductions was seven times higher than the differentiation effect due to species losses, indicating that species extinctions only played a minor role in defining current compositional patterns of regional floras. At a much larger temporal extent, Feurdean *et al.* (2010) quantified vegetation dynamics over the last 11 500 years based on pollen records in Romania. The authors found evidence for distinct episodes of differentiation and homogenisation, highlighting that homogenisation patterns can also result from non-anthropogenic factors. In contrast to previous results, they also found that recent human occupation (i.e. 200 years) has resulted in increased regional vegetation differentiation, raising awareness about the influence of the temporal extent when studying changes in community similarity through time.

Other studies investigating the homogenisation of bird communities include Qian and Ricklefs (2006), Schwartz *et al.* (2006), Lôbo *et al.* (2011) and Durak *et al.* (2015).

## Birds

Avifauna homogenisation 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 homogenisation 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. Patterns in taxonomic homogenisation were dependent on the spatial scale. At smaller spatial scales (islands within archipelagos), the expected pattern of low initial similarity leading to greater homogenisation was observed, whereas this relationship reversed at the larger spatial scale of islands between archipelagos.

There is also evidence of functional homogenisation in avian communities. Within different landscapes in France, local communities have become functionally more similar over a span of 23 years (1989–2012) (Monnet *et al.*, 2014). It is important to note that this trend is not linear; functional diversity actually increased in the first 9–10 years before subsequently decreasing. Functional homogenisation is also likely to be trait dependent. In the United States, Baiser and Lockwood (2011) demonstrated that bird communities became 0.9% more similar in terms of breeding traits but diverged (1.8% less similar) with respect to their foraging traits over a period of 40 years. Recently, studies have begun to investigate whether taxonomic and functional homogenisation are concomitant. Baiser and Lockwood (2011) concluded that this was indeed the case in US bird communities and suggested that low trait redundancy might be driving this phenomenon. By contrast, Monnet *et al.* (2014) showed that there is little temporal synchrony between trends in taxonomic and functional homogenisation among bird communities in France, a pattern that was similarly evident for freshwater fishes (Pool and Olden, 2012; Villéger *et al.*, 2014).

Other studies investigating the homogenisation of bird communities include La Sorte and Boecklen (2005), La Sorte *et al.* (2007) and Van Turnhout *et al.* (2007).

## Mammals

Evidence for the homogenisation of mammal communities is also mounting. In a compelling study, Spear and Chown (2008) examined the effects of ungulate introductions on biotic similarity across four spatial scales, at three spatial resolutions within South Africa and among 41 nations located worldwide. They found that between 1965 and 2005, ungulate assemblages had become 2% more similar for countries globally and 8% more similar at the coarsest resolution within South Africa. Interestingly, species introduced from other continents, as opposed to those introduced from within Africa, were found to have different effects on patterns of homogenisation.

## Insects

There are relatively few studies examining biotic homogenisation of insects compared to plants, birds and fish. However, a recent study focusing on multiple taxa (bees, hoverflies and butterflies) within three different countries (the Netherlands, Belgium and Great Britain) advanced our understanding of both the basic ecology and the conservation aspects of biotic homogenisation (Carvalho *et al.*, 2013). The degree of taxonomic homogenisation differed among different taxa, countries and spatial extents. For example, homogenisation of hoverfly communities occurred in all three countries whereas homogenisation of bees and butterflies was strongly observed in Netherlands and Great Britain, and Netherlands and Belgium respectively. Homogenisation is also strongly scale dependent. For bees and butterflies in the Netherlands and bees in Great Britain, homogenisation occurred at both the finest (0–50 km) and the coarsest spatial scales (>200, 300 and 800 km for the Netherlands, Belgium and Great Britain, respectively), whereas for others such as hoverflies and bees in Belgium, homogenisation occurred only at coarser spatial scales. Importantly, Carvalho *et al.* (2013) demonstrated that functional homogenisation had slowed or even reversed for certain taxa post-1990, providing support for continued conservation investments in these countries. Another study investigating the homogenisation of insect communities is Shaw *et al.* (2010).

## Amphibians and reptiles

Investigations of herpetofaunal homogenisation are limited. For counties in the state of Florida, Smith (2006) reported that the presence of nonnative amphibians and reptiles has not caused changes in the similarity of the herpetofauna. However, this study found a positive relationship between taxonomic similarity and distance among counties, suggesting that the scale of comparison influences the perception of homogenisation, with no effect or slight homogenisation at small scales (neighbouring counties) and differentiation at larger scales (distant counties). This pattern is broadly reflected in studies of fish, bird and plant homogenisation. In a very interesting study, Smith *et al.* (2009) showed that the widespread pathogenic agent of amphibian decline, *Batrachochytrium dendrobatidis* (Bd), has resulted in selective extinction and homogenisation of Lower Central American amphibian biotas. The authors found that Bd-associated extinctions have caused a substantial loss of  $\beta$ -diversity in amphibian assemblages, resulting in taxonomic homogenisation of the regional amphibian biota. The pattern of extirpations also resulted in phylogenetic homogenisation at the family level and functional homogenisation of reproductive mode and habitat association.

## Ecological, Evolutionary and Social Consequences of Biotic Homogenisation

Although it is generally acknowledged that a loss of species diversity brings ecological, evolutionary and social costs, an understanding of the consequences of biotic homogenisation is

still lacking. In the absence of research demonstrating these consequences, Olden *et al.* (2004) made a number of broad predictions, which are briefly summarised below.

In situations where genetic homogenisation arises from inter-specific hybridisation between genetically distinct species, we might expect elevated probabilities that 'hybrid swarms' will form and threaten native taxa. Similarly, intraspecific hybridisation 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 in the western United States currently threatens the genetic distinctiveness of endemic subspecies of native trout. Taxonomic and functional homogenisation 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 synchronising 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 homogenisation 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 homogenisation 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 homogenisation may jeopardise 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 homogenised communities.

**See also:** [Speciation: Genetics](#)

Biotic homogenisation is also likely to be associated with a number of social consequences. Some have likened this process to the now global distribution of fast-food restaurants, coffee houses and big-box retailers (Olden *et al.*, 2005). From a purely ethical perspective, one could argue that biotic homogenisation 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 well-being 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 homogenisation as endemic elements of the landscape that typify geographic regions and cultures are slowly replaced by ubiquitous forms. Biotic homogenisation may influence not only how we view the world but also affect our motivation to experience it. Thus one might expect biotic homogenisation 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 homogenisation 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 homogenisation in both aquatic and terrestrial ecosystems (McKinney and Lockwood, 1999; Olden and Poff, 2003; Olden, 2006). Increasing globalisation 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 homogenisation.

The most effective conservation of biodiversity involves reducing and, where possible, preventing the two processes generating biotic homogenisation – species invasions and extinctions. The conundrum is determining the best way to achieve this goal. Because the key factors facilitating homogenisation include people and habitat transformation (through extinctions or the establishment of nonnative species), a first step towards achieving biodiversity conservation goals is to focus efforts in areas subject to human activities and to reduce human-related impacts.

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