# Components, Processes and Consequences of Biotic Homogenization: a Review

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**ABSTRACT**

Among the major changes induced by human beings, biotic homogenization is gaining popularity at regional as well as global level. Biotic homogenization is a multifaceted process which results from species extinction, introduction and environmental modification often induced by human beings. This human mediated introduction of alien species and the extirpation of native species, either independently or in combination have caused loss of taxonomic regional distinctiveness among formerly disparate faunas and floras. Ample evidence reveals that extent of homogenization differed between various ecosystems and taxa, as well as in different regions. Although biotic homogenization leads to increase in species richness at local level but it also causes loss of diversity at global level (i. e., paradox of gaining species but loosing diversity). Potentially biotic homogenization could affect any of the many processes in communities that vary in space and time, such as spatial subsidies and food-web dynamics, and thereby have cascading effects elsewhere on the landscape. Biotic homogenization does have relevance to conservation as it has utility in reserve selection and management. Current knowledge pertaining to patterns, mechanisms and implications of biotic homogenization is highly variable across taxonomic groups, but in general is incomplete. This article is an attempt to review literature pertaining to patterns, mechanisms and implications of biotic homogenization.

**Key words:** biological invasion; species extirpation; ecological and evolutionary consequences; conservation; urbanization.

Biotic homogenization is an important component of current biodiversity crisis and is assumed to have a significant influence on future trends in biodiversity. McKinney and Lockwood [1999] were the first to define biotic homogenization as "the replacement of local biotas with non-indigenous species", which "often replaces unique endemic species with already widespread species". Later, Rahel [2000] extended this definition by stating that "biotic homogenization is the increased similarity of biotas over time caused by the replacement of native species with non-indigenous species". In simple terms, biotic homogenization is the increased similarity of biotas over time caused by the replacement of native species with non-indigenous species, usually as a result of introduction of such species by human-beings. The central aspect of the homogenizing process is the ability of species to overcome natural biogeographic barriers, either through intentional transport by humans or through colonization routes created by human activities. According to McKinney and Lockwood [1999], biotic homogenization occurs when a widespread environmental change promotes the geographic expansion of some species ("winners") and the geographic reduction of others ("losers"). Homogenization is the outcome of three interacting processes: introductions of non-native spe-
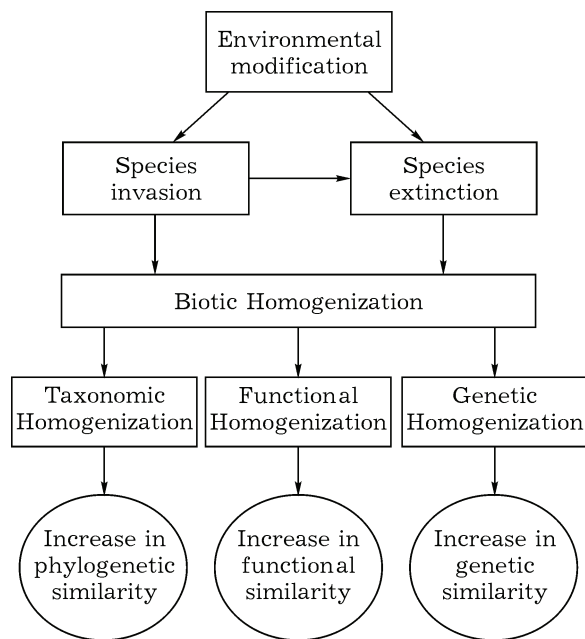
Components of biotic homogenization and processes involved in it

cies, extirpation of native species, and habitat alterations that facilitate these two processes (see Figure).

The introduction of non-native species and the extirpation of native species either independently or in combinations have caused loss of taxonomic regional distinctiveness among formerly disparate faunas and floras [Olden, Rooney, 2006]. Biotic homogenization is not a new phenomenon in the history of the Earth. Episodic mixing of historically isolated taxa has occurred throughout the paleontological record [Vermeij, 1991]. The phenomenon, however, has been a topic of wide discussion in the scientific literature only since the turn of millennium, because it is now occurring on a global scale at an accelerated rate as a result of three influences: environmental modification, transportation of exotic species and extinction of endemic species [Rahel, 2002]. Environmental modification promotes the loss of local endemic species that cannot tolerate anthropogenic pressures. On the other hand, increasing global transport promotes the spread of non-indigenous species [Vitousek et al., 1996; Williamson, 1996; Lockwood, 1999]. Although many of these non-indigenous species thrive in disturbed environments, some also invade, and thus homogenize relatively undisturbed natural areas

[Williamson, 1996]. The homogenization process is particularly distinct in island biotas where the loss of endemic species and their replacement by widespread exotic species result in decreased beta diversity among the islands [Harrison, 1993]. The projected rise in species extinctions [Myers, 1997; Russell et al., 1999] and species introductions [Williamson, 1996] will almost certainly increase homogenization at continental scales as well. Brown [1989] also stated that geographically restricted native species with sensitive requirements will continue to have high extinction rates, while those widespread tolerant species that can live with humans, and benefit from their activities, will spread and become increasingly dominant.

Many studies have shown that the outcome of biotic homogenization depends on the balance of invasion/extinction between regions [Olden, Poff, 2003] and the spatial scales analyzed [Cassey et al., 2006]. In addition to homogenization, biotic change, driven by species invasions and extinctions may lead to decreased similarity – a process called biotic differentiation, or no change at all – a process called biotic tracking [Castro, Jaksic, 2008]. Castro and Jaksic [2008] defined biotic tracking in the context of biotic change, as a process where a particular combination of invasion/extinction events results in the maintenance of similar patterns of biotic (floristic in this case) similarity between areas.

Emerging evidence suggests that biotic homogenization is a major response to global environmental change [Devictor et al., 2008]. Many studies have emphasized that specialist (unique endemic) species are more likely to be negatively affected by current global changes than generalists [McKinney, Lockwood, 1999; Warren et al., 2001; Julliard et al., 2004; Rooney et al., 2004]. Urbanization, an important component of modernization, is increasing dramatically around the world and it is considered as one of the strong forces causing biotic homogenization and the loss of biodiversity [Blair, 2001; Miller, Hobbs, 2002; McKinney, 2006]. Because biotic change is driven by unequally distributed human influence [Vitousek et al., 1997; Chapin et al., 2000; Sala et al., 2000], it is expected that regions located in different hemispheres will exhibit different rates of biotic

homogenization, or even different trends. The latter may occur because recent theoretical [Olden, Poff, 2003; Cassey et al., 2006] and empirical studies [Rejmánek, 2000; Marchetti et al., 2001, 2006] have revealed that when changes in taxonomic similarity among regions are characterized, complex outcomes may occur.

The consequences of biotic homogenization are predicted to be a more species-poor biosphere, where local ecosystems and communities are also more similar from place to place as a result of the non-random turnover of species populations in response to human activity [McKinney, Lockwood, 1999, 2001]. Biotic homogenization driven by alien species is likely to pose serious ecological and evolutionary consequences for regional biotas, including reduced genetic variability among populations of several species, limited potential for future speciation [Rosenzweig, 2001], reduced functional diversity, and altered ecosystem resilience leading to limited capacity for adaptation in the face of further environmental changes [Olden et al., 2004]. Given that species invasions and extirpations may act in concert at all trophic levels, biotic homogenization could affect any of the many processes in communities that vary in space and time, and thereby have cascading effects elsewhere on the landscape. For example, increased spatial similarity in the species identity of predators and competitors could have direct and indirect effects on species at lower and higher trophic levels, by increasing extirpation rates via intensified species-specific interactions (i. e. functionally similar species might utilize the same resources). Besides, more and more species are likely to become extinct as a result of genetic and functional homogenization. Also, from a purely ethical perspective, it is assumed that biotic homogenization will degrade the quality of human life by enriching biological communities with an aesthetically unappealing uniformity [Olden et al., 2005].

Recent work suggests that homogenization may be widespread in both aquatic and terrestrial systems [Rahel, 2000; Marchetti et al., 2001; McKinney, 2004a; Rooney et al., 2004; Taylor, 2004], and recent syntheses reflect that the study of biotic homogenization is an important research agenda [Olden, 2006; Lôbo et al., 2011]. In addition, biotic homogeniza-

tion has received increased attention in recent years for numerous taxonomic groups, including plants [Rooney et al., 2004], birds [Lockwood et al., 2000; Jokimäki, Kaisanlahti-Jokimäki, 2003], insects [Blair, 2001], reptiles and mammals [Wilson, 1997], marine algae [Carlton, 1996], mussels and amphibians [Duncan, Lockwood, 2001], snails [Cowie, 2001], zooplankton [Beisner et al., 2003], and fish [Radomski, Goeman, 1995; Rahel, 2000; Marchetti et al., 2001; Scott, Helfman, 2001].

While human activities have led to decreased global species diversity, the opposite pattern is often observed at regional and local scales, where the establishment of exotic species frequently outweighs the loss of native species, and hence total species diversity increases over time [Sax, Gaines, 2003]. Although local or alpha ($\alpha$) diversity increases; it is typically at the expense of beta ($\beta$) diversity − a measure describing the spatial turnover or change in the identities of species between two or more assemblages [Whittaker, 1972]. Beta diversity is a fundamental component of biodiversity, and change in species composition along spatial or environmental gradients is not only a topic of theoretical interest, but also has important implications for regional biodiversity planning [Loreau, 2000; Gering et al., 2003] and more broadly for the field of conservation biogeography [Whittaker et al., 2005].

### Components of biotic homogenization

According to Olden et al. [2004] biotic homogenization has three components: taxonomic, genetic and functional (see Figure).

**Taxonomic homogenization.** Taxonomic homogenization refers to an increase in similarity of species composition across a set of communities [Olden, Rooney, 2006]. Most commonly, taxonomic homogenization has been documented as a result of the spread of non-native species across a region, resulting in the loss of native species [McKinney, Lockwood, 1999]. Taxonomic homogenization is quantified as the change in the pair-wise community similarity (based on species presence or absence) over a specified time interval [Rahel, 2002]. Evidence for taxonomic homogenization comes primarily from regional or national comparisons of the

similarity between introduced and native species pools [Castro et al., 2007; Hoagstrom et al., 2007; McKinney, La Sorte, 2007; Magee et al., 2008] and community similarities along large-scale spatial gradients [Kühn, Klotz, 2006; Dormann et al., 2007; Blair, Johnson, 2008]. However, contrasting evidence is also available [Beck, Khen, 2007]. For example, species invasions were found not to simplify taxonomic composition of Mediterranean floras [Lambdon et al., 2008], while the flora of two US States showed more instances of differentiation than homogenization [Qian et al., 2008].

Conflicting evidence for taxonomic homogenization partly reflects variation in the methods used. As per Olden and Rooney [2006], the most powerful method for detecting taxonomic homogenization involves the comparison of complete species pools from the same sites at different times. However this method has rarely been employed because it is dependent on the availability of suitable historical data, which are usually lacking [Olden, Rooney, 2006]. Application of this approach demonstrated taxonomic homogenization over five decades in Wisconsin (USA) woodland plant communities, as a result of local extinction [Rooney et al., 2004]. In contrast, Smart et al. [2006] found no evidence of taxonomic impoverishment in a sample of plant communities throughout Britain over a 20-year period. Different results have, therefore, been obtained in terms of both the occurrence of taxonomic homogenization and the processes responsible. Variation among studies might also be attributable to the contrasting time scales investigated.

Keith et al. [2009] quantified taxonomic homogenization of woodland plant communities over 70 years. Whether over time the patches decreased in species richness, homogenized, or shifted towards novel communities was also explored by them. They observed that the similarity in species composition among woodlands increased over time and also observed that the woodlands have undergone taxonomic homogenization without experiencing declines in the local diversity or shifts towards novel communities. Analysis of species characteristics led them to suggest that these changes were not driven by non-native species invasions or climate change, but instead reflected recognization of the novel plant communities in response to eutrophication and increasingly shaded conditions.

Winter et al. [2009] analyzed the large-scale effects of plant extinctions and introductions on taxonomic and phylogenetic diversity of floras across Europe, using data from 23 regions. They observed that plant invasions since AD 1500 exceeded extinctions, resulting in: i) increased taxonomic diversity (i. e. species richness) but decreased phylogenetic diversity within European regions, ii) increased taxonomic and phylogenetic similarity among these regions.

**Genetic homogenization.** The term genetic homogenization is used to describe an increase in the genetic similarity of gene pools over time, resulting from intra- and inter-specific hybridization. So far, information about genetic homogenization is only available from fishes. According to Olden et al. [2004], this form of homogenization can be quantified using a variety of genetic characteristics, such as the allelic composition of a particular locus or set of loci (i. e. identity of genotypes), their frequencies (i. e. relative abundance of genotypes), or by one of many metrics derived from the above parameters, such as percent polymorphic loci, mean number of alleles per locus and mean heterozygosity. In addition, levels of population divergence can also be assessed by indices of genetic similarity, such as $F_{st}$ or using a variety of cluster analyses (e. g. Bayesian inference). These measures of genetic diversity are usually assessed in a comparative spatial framework (i. e. introduced versus source population, or disturbed versus non disturbed populations), but they are rarely examined in a temporal framework (i. e. pre- and post disturbance), simply because no genetic baseline data were collected before the homogenization event. Furthermore, the choice of genetic markers (i. e. level of resolution) could be crucial to detect the potential subtle genetic differences inherent to homogenization.

The possible mechanisms of genetic homogenization are:

i) intentional translocation of populations from one part of the range to another,

ii) intentional introductions of species outside of their normal ranges, and

iii) extirpation of local or regional floras/faunas.

Genetic homogenization is a serious, but often less recognized threat to the integrity of endemic gene pools, and can have several important implications. Translocation of population(s) would enhance the potential for intraspecific hybridization, which in the end would result in assimilation of previously differentiated gene pools [Stockwell et al., 1996; Storfer, 1999]. Introductions of species outside of their original range(s) could result in a founder effect and yield reduced levels of genetic variability, as well as setting the stage for interspecific hybridization [Rhymer, Simberloff, 1996]. And finally, if extirpations were a cause for homogenization then one consequence might be bottleneck(s) in local populations of the impacted species, along with lowered effective population size(s) [Lee, 2002]. This would occur directly via removal of individuals from source populations, or indirectly by habitat modifications.

Olden et al. [2004] argued that mechanisms driving genetic homogenization are actually synergistic, and that human interventions simply amplify the potential for hybridization within a given system. Human-mediated, long-distance dispersal and colonization events, for example, elevate the probability that pairwise interactions between species will yield hybrids, whilst human-provoked environmental disturbances will likewise provide habitats that are suitable for hybrid progeny [Ellstrand, Schierenbeck, 2000]. This human-dimension aspect enhances the probability that "hybrid swarms" will genetically extirpate native taxa [Rhymer, Simberloff, 1996]. Although such events are thought to occur over many years, even decades (as with trout), examples do exist where genetic swamping has occurred within abbreviated time frames. For example, within a four-year period following its introduction, the exotic pupfish, *Cyprinodon variegates,* was involved in a large-scale introgressive hybridization event with the endemic *C. pecosensis* across 430 km of the Pecos river in New Mexico [Echelle, Connor, 1989]. Genetic swamping can occur relatively rapidly and over extended distances, and the seriousness of this phenomenon cannot be underestimated simply because its effects are deemed slower than, say, overt predation.

**Functional homogenization.** Functional homogenization is defined as an increase in the functional similarity 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". For example, Devin et al. [2005] found that increased abundance of the alien species zebra mussel (*Dreissena polymorpha*) was paralleled by reduced functional diversity of the macro invertebrate communities. Recently Clavel et al. [2010] suggested that the replacement of geographically local specialist species by geographically local generalist species is central to the ongoing process of functional homogenization. According to them long-term persistence of specialist species is adversely affected by past and current global changes, and generalist species have effectively replaced specialist species, causing functional homogenization at the community level.

According to Olden et al. [2004], functional homogenization can be calculated by first calculating the site-by-trait matrix (calculated as the product of the species-by-site matrix and the trait-by-species matrix), and then examining community similarity using one of the approaches which are used for quantifying taxonomic homogenization. The frequency distribution of traits or simply the presence or absence of species traits in the community could be used to assess community similarity in functional characteristics. The choice of similarity coefficient or multivariate statistical approach to be used will be in turn determined by the fact whether the species traits are discrete (binary or multi-state) or continuous.

Although functional homogenization is considered to be one of the most prominent forms of biotic impoverishment induced by the current global changes yet this process has hardly been quantified on a large-scale, and the connection between landscape disturbance and functional homogenization has hardly been established. To date, scientific research on homogenization has been pursued largely from a phylogenetic perspective [Lockwood, McKinney, 2001; Rahel, 2002], where the term "taxonomic homogenization" is used to describe an increase in the compositional similarity among communities, owing to the successful invasion of "winning" species and the extirpation of "losing" species [McKinney, Lockwood, 1999].

Accounting for taxonomic change in communities is important and achieved relatively easily [Olden, Poff, 2003]; however, ecologically profound functional changes might occur in homogenized communities that are largely independent of taxonomic identity. Thus, a more subtle ecological examination of homogenization is required. Species contribute individually and collectively to the functional stability of communities and ecosystems [Elton, 1958; Hurd et al., 1971; Hooper et al., 2005]. Winners and losers in the homogenization lottery are not randomly distributed taxonomically; rather, invasion success and extirpation vulnerability are primarily defined by the interaction between intrinsic species traits and extrinsic environmental characteristics [McKinney, Lockwood, 1999]. Ecological implications of biotic homogenization might be more profitably examined by considering "functional diversity" (i. e. the composition of and variation in community traits, and its spatial distribution across landscapes). Modifying the functional diversity of a community might result in functional homogenization, involving the replacement of ecological specialists by the same widespread generalists. Although functional diversity is recognized as a determinant of ecosystem processes [Díaz, Cabido, 2001], the importance of functional homogenization has received inadequate attention.

According to Olden et al. [2004], modifications to within- and between community trait compositions will probably impinge upon community and ecosystem function, and resistance to environmental change. A decrease in functional diversity might reduce overall community and ecosystem functioning [Tilman et al., 1997], stability [Sankaran, McNaughton, 1999] and resistance to environmental change by simply narrowing the available range of species specific responses [Stachowicz et al., 2002]. Historical communities, with much greater breadth in functional space, should exhibit higher resistance or resilience when compared with homogenized communities.

### Processes driving biotic homogenization

At present, the understanding of the process driving biotic homogenization is very limit-

ed. It is because of the fact that biotic homogenization can arise from a number of ecological mechanisms representing specific, often quite distinct, interactions among native species, non-native species, and the environment [Olden, Poff, 2004]. Although several factors such as type of habitats being homogenized [Qian, Guo, 2010; Lososová et al., 2011], level of disturbance [Abadie et al., 2011] and attributes of alien species such as growth form, life span, invasiveness [Qian, Guo, 2010] and residence time [Lososová et al., 2011] have been shown to influence patterns and rates of homogenization yet the complete understanding of factors influencing biotic homogenization is still wanting.

In addition to environmental modification, the two distinct processes that result in biotic homogenization are: species gains, for example through invasions or range expansions (winning species); and species losses, through extinctions or range contractions (losing species) [McKinney, Lockwood, 1999]. The interplay of both processes can result in increasing, decreasing or unchanged taxonomic similarity [Olden, Poff, 2003]. Specifically, communities can become more similar through the loss of rare species, leading to biotic homogenization, especially when they are replaced by widespread species. In contrast, species invasion can also lead to biotic differentiation due to different species colonizing different regions [Winter et al., 2010].

The first mechanistic investigation of biotic homogenization was provided by Olden and Poff [2003], who developed a predictive model that forecasts trajectories of biotic homogenization or differentiation (i. e., decreased community similarity) according to a series of distinct mechanisms that describe the outcomes of various interactions between native species, non-native species, and the environment. Olden and Poff [2004] tested this mechanistic model using freshwater fish faunas, the only taxonomic group for which quantitative estimates of homogenization are published. They analyzed three data sets at three spatial scales: the continental United States [Rahel, 2000], zoogeographic provinces in California [Marchetti et al., 2001], and the watersheds within these Californian provinces [Marchetti et al., 2001]

to evaluate which specific mechanisms would best describe the interactions between native fish species, non-native fish species, and environmental modification at the three scales.

The model of Olden and Poff [2003] describes 14 ecological mechanisms by which different rates and patterns of species invasions and extinctions can cause changes in community similarity. These 14 scenarios represent possible outcomes resulting from unique combinations of interactions among species and the environment that are well supported in the aquatic and terrestrial literature. They divided invasion − extinction scenarios into three groups, depending on whether only species invasions, only species extinctions, or both species invasions and extinctions occur in the recipient communities.

Effects of scale dependencies are well known for biodiversity patterns, in general [Levin, 1992; Whittaker et al., 2001], and invasion processes, in particular [Rouget, Richardson, 2003; Pauchard, Shea, 2006; Kühn, Klotz, 2007]. Thus, biotic homogenization has also been shown to be scale-dependent [Olden, Poff, 2003]. Usually the number of introduced species exceeds the loss of natives [Sax et al., 2007], but it is disproportionately high at a smaller scale. At a fine spatial resolution, it is less likely that the same alien species will be introduced and the same native species will go extinct in all the locations [McKinney, Lockwood, 2005; Olden, 2006]. This results in biotic differentiation across regions over time. Conversely, at coarser scales, homogenizing effects are implicitly favoured due to a greater number of sampled habitats and communities, and hence an increasing probability of finding any given species [Olden, 2006]. However, using geographical distance to explain scale-dependent homogenization patterns has resulted in conflicting conclusions [Rejmánek, 2000; McKinney, 2005; Qian, Ricklefs, 2006]. McKinney [2005] found that the species introduced from less distant sources (within the USA) have a greater homogenizing effect on community composition than species from more distant sources (outside the USA). In contrast, Rejmánek [2000] and Qian and Ricklefs [2006] found a differentiation effect of alien plant species among the floras of neighbouring North American re-gions, but a homogenization effect among floras at greater distance.

Although many human activities promote biotic homogenization, urbanization is one of the most homogenizing activities of all. One reason for this is the exceptionally uniform nature of urban areas; cities, for example, are habitats constructed almost exclusively to meet the relatively narrow demands of just one species, *Homo sapiens*. As a result, cities are physically very similar throughout the world: roads, skyscrapers, and residential housing in the suburbs are almost indistinguishable. Also, cities typically grow by accretion and their homogenizing influence expands as land-use alteration intensifies.

### *Quantification of biotic homogenization*

Taxonomic homogenization has been the primary focus of previous research and continues to be used interchangeably with the term "biotic homogenization" in literature [Olden, Rooney, 2006]. As such much of the literature is available about quantification of taxonomic homogenization. Numerous measures and approaches have been used to quantify taxonomic homogenization [Koleff et al., 2003]. Taxonomic homogenization is quantified as the change in the pairwise species similarity between two time periods [Olden, Poff, 2003], often computed using species presence or absence. Jaccard's similarity index or measures of spatial turnover [Duncan, Lockwood, 2001] are used most frequently for occurrence data, while the Bray − Curtis similarity index (when sampling effort is equivalent among communities) or Morisita's index of similarity (when sampling effort differs among communities) are appropriate for data based on relative abundance [Wolda, 1981] (see Table). While the choice of similarity index can influence the magnitude of biological similarity computed [Jackson et al., 1989], a more pressing issue involves the appropriate collection of data. How community similarity is compared between the time periods (i. e. absolute vs. relative) and the influence of spatial and temporal grain and extent of investigation on patterns of taxonomic homogenization are also important [Olden, Poff, 2003].

**Indices used for computation of biotic homogenization**

| S. N | Name of Index | Equation | Legends | Reference |
|---|---|---|---|---|
| 1 | Jaccard's Index* | $J = \dfrac{a}{(a+b+c)}$ | $a$ is the number of species common to both sites; $b$ and $c$ are the numbers of species only present in one of the sites | Radomski and Goeman [1995]; Rahel [2000]; Rejmánek [2000]; Blair [2001]; Marchetti et al. [2001]; Blair [2004]; Mckinney [2004a, b]; Taylor [2004] etc. |
| 2 | Sorenson index | Sorenson index $= 100\left[\dfrac{2a}{b+c}\right] = 100\left[\dfrac{2a}{b+c}\right]$ | $a$ is the number of species common to both sites; $b$ and $c$ are the numbers of species only present in one of the sites | Jokimäki and Kaisanlahti – Jokimäki [2003]; Lougheed et al. [2008] |
| 3 | Bray-Curtis index# | Bray-Curtis index $= 100\left[1 - \dfrac{\sum_{i=1}^{r}\left|\Psi_{ij} - \Psi_{ik}\right|}{\sum_{i=1}^{r}\left|\Psi_{ij} + \Psi_{ik}\right|}\right]$ | $x_{ij}$ and $x_{ik}$ are the abundances of species $i$ at sites $j$ and $k$, respectively | Rooney et al. [2004]; Cassey et al. [2008]; Feurdean et al. [2010] |
| 4 | Beta-sim index# | $\beta_{sim} = \dfrac{\min(b,c)}{a + \min(b+c)}$ | $a$ is the number of species common to both sites; $b$ and $c$ are the numbers of species only present in one of the sites; min $(b, c)$ refers to the smaller value of $b$ and $c$ | Lennon et al. [2001]; Villéger, Brosse [2012] |
| 5 | Association index | Association index $S(t) = \dfrac{n_{i=1,j=1}}{\min(n_{i=1,j=1})}$ | Where X is the status group (A = alien, N = native), $n_{i=1}$ is the number of species occurring in site $i$, $n_{j=1}$ is the number of species occurring in site $j$, and $n_{i=1,j=1}$ is the number of species "shared", i. e. occurring in both sites $i$ and $j$ | Lambdon et al. [2008] |
| 6 | Raup and Crick measure of beta diversity ($\beta_{RC,\,xy}$) | Calculated as the proportion of pairs of null communities that share the same number or more species in common than sites $x$ and $y$ | | McKinney and Lockwood [1999]; Vellend et al. [2007]; Lobo et al. [2011] |
| 7 | Morisita – Horn dissimilarity index (MH) | $D_{MN} = \dfrac{2\sum(x_{ij}x_{ik})}{(\lambda_i + \lambda_k)\sum x_{ij}\sum x_{ik}}$ with $\lambda_j = \dfrac{\sum x_{ij}^2}{\left(\sum x_{ij}\right)^2}$ and $\lambda_j = \dfrac{\sum x_{ij}^2}{\left(\sum x_{ij}\right)^2}$ | Where $x_{ij}$ and $x_{ik}$ are the frequencies of species $i$ in sites $j$ and $k$ | Winter et al. [2008; 2009] |

*A homogenization Index H $= J_{\text{total}} - J_{\text{native}}$ derived from Jaccard's Index has been used by many authors such as Rahel [2000]; Qian & Guo [2010]; Lososová et al.[2011].
#Difference between the $\beta_{sor}$ and the $\beta_{sim}$ index ($\beta_{nes} = \beta_{sor} - \beta_{sim}$) expresses the nestedness component of the compositional differentiation between a pair of sites [Baselga, 2010; Baeten et al., 2012].

The most straightforward method for quantifying taxonomic homogenization involves surveying the species pool across multiple sites at two points in time, and examining temporal changes in pairwise species similarity. For example, using fisheries survey data for 62 lakes in Minnesota, USA, Radomski and Goeman [1995] demonstrated an increase in fish assemblage similarity over a 43-year time period (1940−55 to 1985−92). Similarly, resurveys of Rooney et al. [2004] of 62 upland forest plant communities in northern Wisconsin, USA revealed floral homogenization between 1950 and 2000. The advantage of this method lies in the quantification of homogenization based on observations at two distinct points in time, and, therefore, the rates of homogenization can be quantified explicitly. However, this approach suffers from the typical concerns associated with sampling communities, such as the assumption that comparable sampling techniques and effort are employed in both time periods. Violation of this assumption, for example, may result in differential probabilities of false absences for rare species that contribute to historical differences, thus leading to erroneous estimates of taxonomic homogenization.

A common approach to calculating taxonomic homogenization is based on reconstructing species pools from published lists of native and non-native species. The historical fauna is represented by extant native species plus known extirpations and the contemporary species pool is represented by extant native species plus established non-native species. For example, Rahel [2000] and Taylor [2004] compared species similarity before European settlement (only native faunas plus known extirpations) to present-day (native plus non-native faunas) to assess the degree of fish fauna homogenization for US states and Canadian provinces, respectively. While this approach does not provide the specific time interval of taxonomic homogenization, it still provides a reasonable approach for assessing the overall level of homogenization associated with human settlement histories, assuming that species gains and losses are recorded accurately. While several other studies have reconstructed extant and historical species pools, but have failed to account for native species extirpations by assuming erroneously that the historical species pool was

equivalent to the extant native species pool. These studies assume that species extirpations have not occurred since human settlement. If extirpations have occurred, this approach will over-estimate the level of species similarity of the historical species pool, and as a result under-estimate the level of taxonomic homogenization. This bias increases as the ratio of extirpations to the extant native species pool increases. As the spatial grain of the analysis decreases, the probability of recording an extirpation event rises, as does the likelihood of underestimating taxonomic homogenization. Moreover, when species extirpations are not taken into account, the influence of exotic species introductions on taxonomic homogenization will tend to be over-emphasized. Consequently, it has been suggested that the assumptions of this methodology must be acknowledged when comparing the relative importance of exotic introductions vs. native extinctions in driving patterns of homogenization [McKinney, 2004b].

In contrast to the above approaches, a substantial (and, unfortunately, increasing) number of studies in the literature have quantified taxonomic homogenization while either failing to account for species identity, or examining only the present-day species pools. This approach is of limited utility, and could generate misleading results. For fish faunas, Scott and Helfman [2001] and Walters et al. [2003] equated the present-day relative abundance and richness of species classified as either "cosmopolitan" or "endemic" to levels of taxonomic homogenization. Unfortunately, these studies provide only limited insight into patterns of homogenization because there is no indication of how species compositions (that is species identity and not richness) have changed. In fact, two lines of evidence suggest that species richness is a poor indicator of taxonomic homogenization: i) simple examples and simulation experiments show that the two can be independent [Rahel, 2002; Olden, Poff, 2003], and ii) empirical data indicate that the form of the relationship between richness and homogenization is variable and differs between native and non-native species pools [Olden, 2006]. Therefore, despite the negative relationship between richness and homogenization implied in some empirical studies [Wilson, 1997], the association between different measures of diver-

sity is highly variable [Koleff, Gaston, 2002] and the loss of native biodiversity is not related universally to increased taxonomic homogenization [Collins et al., 2002; Olden et al., 2004].

Other studies looking at the effects of urbanization on bird communities have used present-day avifauna similarity along rural − urban gradients to investigate the effects of land use intensity on taxonomic homogenization [Blair, 2001]. These studies examine spatial patterns in species identity, but provide only tentative evidence for taxonomic homogenization because of lack of information about the historical degree of similarity among the communities.

### Consequences of biotic homogenization

Biotic homogenization results in the paradox of gaining species but losing diversity because local richness often increases with the introduction of cosmopolitan species while, at the same time, regional and global diversity decrease as endemic species are driven to extinction. Given that species invasions and extirpations may act in concert at all trophic levels, biotic homogenization could affect any of the many processes in communities that vary in space and time, such as spatial subsidies and food-web dynamics, and thereby have cascading effects elsewhere on the landscape. For example, increased spatial similarity in the species identity of predators and competitors could have direct and indirect effects on species at lower and higher trophic levels by increasing extirpation rates via intensified species-specific interactions (i. e. functionally similar species might utilize the same resources).

The negative consequences of both processes, i. e. species invasion and extinction, apply to the process of homogenization [Tilman, 1999; Mack et al., 2000], as it is a combined result of the same. Although concerns about introductions typically center on species that become pests or reduce the abundance of more desirable species but most introduced species do not have major detectable effects on native species, and in some cases they provide economic benefits related to sport fishing or aquaculture [Horak, 1995]. For instance, Mills et al. [1993] estimated that only 10 % of the 139 in-

troduced species in the North American Great Lakes have had demonstrably substantial impacts. In a review of the literature on invasive species, Lodge [1993] noted that between 2 and 40 % of introduced species had an impact large enough to be detected. But the minority of introduced species that prove harmful can have major ecological and economic impacts [Pimental et al., 2000]. For example, Vivrette and Muller [1977] showed that the crystalline iceplant, an annual invader from South Africa, dramatically altered the composition and density of coastal grassland species in California. Simialrily, Zebra mussels have had negative economic effects by clogging water intake structures, and they appear to have major ecological effects by causing the extinction of native mussel species in North America [Ricciardi et al., 1998]. Although in view of the dangers of introducing non-native species, the rate of official introductions has declined [Townsend, Winterbourn, 1992; Rahel, 1997] but unofficial and often illegal introductions continue to be a problem.

The possible consequences of biotic homogenization are likely to be diverse because of the diverse nature of this process. One possible consequence is loss of genetic diversity which results from genetic homogenization. On account of this process, large spatial component to genetic variation of many species is lost when one or a few stocks are used to replace extirpated populations or supplement declining populations [Allendorf, Leary, 1988; Nehlsen et al., 1991]. This genetic homogenization also reduces the ability of species to adapt to changing environmental conditions or new diseases [Allendorf et al., 2001] and as such more and more species are driven to extinction. Genetic homogenization is especially a problem for cultured species that are widely distributed into the natural environment through intentional stocking or escapes from aquaculture facilities [Hindar et al., 1991; Beveridge et al., 1994]. Also, introduction of genotypes outside of their native range can disrupt native gene pools [Philipp et al., 1993; Bulak et al., 1995]. In addition to genetic homogenization at the intraspecific level, a similar process can reduce biotic diversity at the species level. Hybridization with introduced species is thought to have been a major factor in the extinction of several fish species in North America and hybridization

with introduced rainbow trout currently threatens several native trout species in the southwestern United States [Miller et al., 1989; Rhymer, Simberloff, 1996].

Similarly, functional homogenization of all local communities within a region (i. e. metacommunities) can increase vulnerability to large-scale environmental events by synchronizing local biological responses across the individual communities. This, in turn, would reduce variability among communities in their response to disturbance and would compromise the potential for landscape- and regional-level buffering. Because community composition defines the range of functional traits that influence ecosystem functions such as, nutrient retention or energy flow [McGrady-Steed et al., 1997], biotic homogenization might jeopardize ecosystem functioning by limiting the pool of species that can compensate for local extinctions (i. e. reduce spatial patterns in functional redundancy). Homogenized communities might, therefore, exhibit a decreased resilience to environmental disturbance because elevated similarities among communities might dampen or eliminate potential recolonizations by species with locally extirpated trait(s). Susceptibility of homogenized communities to environmental alteration might be particularly high in areas, such as urban ecosystems that experience more frequent and severe disturbance events [Rebele, 1994].

Simplification via homogenization is expected to play a significant role in influencing the rate of species spread and community resistance to future invasions [Olden et al., 2004]. García-Ramos and 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. Furthermore, species extinction associated with simplification via homogenization might make a community susceptible to further invasions as species deletions make more resources available to be used by invaders [Davis et al., 2000].

### Biotic homogenization and conservation

The study of biotic homogenization is a young and rapidly emerging research area in the emerging field of conservation biology.

Because species invasions and extirpations all too often result in the wake of environmental degradation, biotic homogenization seems an important dimension of the biodiversity crisis. Biotic homogenization conjures the image of Quammen's [1998] distopian "Planet of Weeds" scenario and the prospect of Kunstler's [1993] "The Geography of Nowhere" in which biotic distinctiveness is gradually dissolving over time.

While the application of biotic homogenization to conservation problems may appear relatively straightforward, but it is more complex than it appears. Most importantly, extinction and invasion events at sub-global scales do not automatically increase the taxonomic similarity among species pools through time but depending on species identities, taxonomic similarity could increase, decrease (i. e., biotic differentiation), or remain unchanged [Olden, Poff, 2003], thus highlighting the complexity and challenge of studying biotic homogenization and applying findings to conservation strategies. Olden et al. [2004] discussed the negative ecological implications of biotic homogenization, thereby supporting the idea that biotic homogenization and biotic impoverishment go hand in-hand.

Biotic homogenization does have relevance to conservation as it has utility in reserve selection and management. Regional conservation planning is both a key strategy and a top priority in conservation biology [Margules, Pressey, 2000] that relies on measures of species richness, rarity, endemism and complementarity in space [Prendergast et al., 1993; Reyers et al., 2000]. In a review, Ferrier [2002] highlighted the importance of complementarity approach to conservation planning. Information on the taxonomic similarity among different areas can be used to identify combinations of sites that maximize the representation of regional species biodiversity while minimizing economic, political, or social costs. Although this approach is based on the assumption that taxonomic composition will remain constant through time but regional species pools can and do change even in protected areas [Gurd et al., 2001; Sax, Gaines, 2003], with habitat specialists especially prone to extirpation and generalists likely to invade ever greater ranges as a result of anthropogenic activities.

Rooney et al. [2007] suggested that the application of the concept of biotic homogeniza-

tion and its measurement can be used to monitor if complementarity goals are maintained through time, or if additional strategies need to be designed and implemented. According to them biologists would be wise to limit their analysis of complementarity to a subset of the regional species pool, focusing only on native species. It would also be useful to know in advance of reserve acquisition as to how biotic homogenization might occur and how that, in turn, would affect conservation planning. Simulation models can be used to analyze the sensitivity of a set of candidate reserves to ongoing extinctions, extirpations, and colonizations with the idea that the complementarity of some candidate reserves might be more robust to future homogenization. Such simulations could also identify species that required additional management, either in the form of population recovery, or control efforts that would further limit homogenization.

Urban biotic homogenization is a huge challenge to conservation for at least two fundamentally different but important reasons. One reason is its dominant role in the loss of native species and the consequent homogenization of the world's biota. Another reason is the impact of urbanization on human perceptions of nature. Because so many people live in cities, and because so many urban flora and fauna are not indigenous to the local urban environment, the human species is becoming increasingly unfamiliar from their native biological environment. Olden et al. [2005] argued that the social repercussions resonating in the wake of biotic homogenization must not be ignored and there is an urgent need to consider the idea that the increasingly global uniformity in biological life may be linked to the loss of traditional values and quality of life, and have considerable consequences for conservation-oriented advocacy and ecotourism. Thus the concept of biotic homogenization is not only important for conservation of biodiversity but is also important for maintaining the quality of human life which may otherwise get degraded if not looked into.

## CONCLUSIONS

Biotic homogenization is a multifaceted process that results from species invasions and extinctions often induced by human beings. Although homogenization has occurred in the past but the same process is now occurring at an accelerated pace on account of anthropogenic activities and as such needs to be addressed on priority basis. In particular the mechanisms underlying the process need to be understood at both local as well as global scale. It seems likely that homogenization will continue and will eventually produce a biosphere that is more homogenized. This process is going to have grave consequences for ecosystem functioning and stability. Despite the growing literature on biotic homogenization, confusion still confounds the distinction between biotic homogenization and taxonomic homogenization. There is an urgent need to address the multidimensional nature of this process as this multidimensional nature is going to determine what possible consequences it is going to have? In addition, the growing realization that species composition (not richness) defines the role that biodiversity plays in maintaining ecosystem function highlights the need for conservation biologists to consider the many threats to the biological diversity, including biotic homogenization. As such biotic homogenization is likely to play an important role in determining conservation policies.

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