



On defining and quantifying biotic homogenization

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ABSTRACT

Ongoing species invasions and extinctions are changing biological diversity in different ways at different spatial scales. Biotic homogenization (or BH) refers to the process by which the genetic, taxonomic or functional similarities of regional biotas increase over time. It is a multifaceted process that encompasses species invasions, extinctions and environmental alterations, focusing on how the identities of species (or their genetic or functional attributes) change over space and time. Despite the increasing use of the term BH in conservation biology, it is often used erroneously as a synonym for patterns of species invasions, loss of native species or changes in species richness through time. This reflects the absence of an agreed-upon, cogent definition of BH. Here, we offer an operational definition for BH and review the various methodologies used to study this process. We identify the strengths and weaknesses of these approaches, and make explicit recommendations for future studies. We conclude by citing the need for researchers to: (1) consider carefully the definition of BH by recognizing the genetic, taxonomic and functional realms of this process; (2) recognize that documenting taxonomic homogenization requires tracking the identity of species (not species richness) comprising biotas through space and time; and (3) employ more rigorous methods for quantifying BH.

Keywords

Beta-diversity, biological impoverishment, community change, extinction, invasion, species richness, taxonomic homogenization.

INTRODUCTION

In the wake of continued human enhancement of species invasions and extinctions, an emerging body of research reveals that biological diversity is changing in fundamentally different ways at different spatial scales. 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, so total species diversity increases over time (reviewed in Sax & Gaines, 2003). A much less recognized aspect of these trends is that although local or alpha (α) diversity has increased, this is typically at the expense of decreased beta (β) 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 (e.g. Loreau, 2000; Gering *et al.*, 2003) and more

broadly for the field of conservation biogeography (Whittaker *et al.*, 2005).

An emerging line of inquiry in this research area addresses how species invasions and extinctions increase taxonomic similarity of biotas among sites over time (i.e. decrease β diversity). This process, coined biotic homogenization (BH) (*sensu* McKinney & Lockwood, 1999), describes the gradual replacement of regionally distinct communities by cosmopolitan communities, and is seen to have important ecological and evolutionary consequences (Olden *et al.*, 2004). Recent work suggests that homogenization may be widespread in both aquatic and terrestrial systems (e.g. Rahel, 2000; Marchetti *et al.*, 2001; McKinney, 2004a; Rooney *et al.*, 2004; Taylor, 2004), and a recent synthesis (Lockwood & McKinney, 2001) and special symposium at the 2004 Society for Conservation Biology Annual Meeting (papers in a forthcoming issue of *Biological Conservation*) reflect that the study of BH is now considered an important research agenda (Olden, 2006).

Biotic homogenization represents a unique challenge to ecologists because it is a multifaceted process encompassing many

dimensions of the modern biodiversity crisis, including 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 (Olden & Poff, 2003). As important and illuminating as past efforts have been to understanding patterns of BH, two problems recur in the literature — many authors use BH erroneously as a synonym for species diversity loss, while others make no attempt to quantify (or quantify inappropriately) this process. Given these problems, it is not surprising that confusion continues to surround this research area, as reflected in the recent exchange between Wilkinson (2004) and Olden and Poff (2004a). This is an unfortunate circumstance, given the infancy of this research area and the need to advance our understanding of the patterns, mechanisms and impacts of BH.

We argue that progress in the study of BH is contingent upon an accurate characterization of this complex process and the use of defensible methods to quantify its existence. To help achieve this goal, our study has three primary objectives. We first explore the contemporary meaning of BH and provide an operational definition with respect to the different genetic, taxonomic and functional properties that are associated with this process. We then identify common misconceptions associated with BH, and offer both a theoretical illustration and empirical example for freshwater fishes and terrestrial plants in the United States to help dispel these misunderstandings. Lastly, we conduct a comprehensive literature review to examine how BH has been quantified in the past. We discuss the underlying assumptions and identify the strengths and weaknesses of each methodological approach, and make explicit recommendations for future studies. It is our hope that a common language and set of methodologies will facilitate greater progress in the study of BH and solidify its relevance to the field of conservation biology.

DEFINING BIOTIC HOMOGENIZATION

McKinney and Lockwood (1999) were the first to define BH contemporaneously as ‘the replacement of local biotas with non-indigenous species’, which ‘often replaces unique endemic species with already widespread species’. Later, Rahel (2002) extended this definition, stating ‘BH is the increased similarity of biotas over time caused by the replacement of native species with non-indigenous species’. Both studies advance the definition of BH as the *process* by which species similarity across space increases over time due to species invasions and extinctions, as opposed to the pattern resulting from this process. These definitions also reflect the common usage of the term BH in the literature, in which the species is the unit of investigation. More specifically, this process refers to taxonomic homogenization (TH), which we define broadly as an increase in the taxonomic similarity of two or more biotas over a specified time interval; in other words, a temporal decline in β diversity. Notably, taxonomic differentiation refers to the opposite process.

Taxonomic homogenization has been the primary focus of previous research and continues to be used interchangeably with the term BH throughout the literature. Imposing a narrow phylo-

genetically-based definition of BH, however, does not reflect accurately the truly multidimensional nature of this process. Rather, we suggest that BH should be defined pluralistically to describe the broader, overarching ecological process by which formerly disparate biotas lose biological distinctiveness at any level of organization, including in their genetic, taxonomic and functional characteristics (see Olden *et al.*, 2004). According to this view, we could identify a number of different forms of BH. At the molecular level, the term *genetic homogenization* can be used to describe an increase in the genetic similarity of gene pools over time resulting from intra- and inter-specific hybridization. This form of homogenization could be quantified in terms of the allelic composition or frequencies of a particular locus or set of loci (i.e. identity and relative abundance of genotypes). Genetic homogenization via the dilution of native gene pools by invading exotic genes may be pervasive (Petts, 2004), and is likely to be associated with a number of ecological and evolutionary effects (Rhymer & Simberloff, 1996; Olden *et al.*, 2004).

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 attributes of species that exhibit higher-order phylogenetic affinities (reviewed by McKinney, 1997; Kolar & Lodge, 2001). Functional homogenization can be 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’; see ecological homogenization described by McKinney and Lockwood (1999). For example, Duncan and Lockwood (2001) discussed how the transition from flowing rivers (lotic) to standing water habitats (lentic) due to dam construction is mirrored by changes from lotic-adapted to lentic-adapted fishes and the ‘wholesale replacement of functional groups’. Similarly, Blair (2004) reported that the homogenization of bird communities in response to urbanization (another form of anthropogenic disturbance) was the result of the replacement of specialist, urban-sensitive species by generalist, non-native species more adapted to urban environments. In a recent study, Devin *et al.* (2005) found that increased abundance of the alien species, zebra mussel (*Dreissena polymorpha*), was paralleled by depressed functional diversity of the macroinvertebrate communities.

In summary, advancement in our understanding of BH will be hastened by the recognition that this process probably operates across multiple levels of biological organization. In much the same way that BH increases biological similarity among communities (as noted above), homogenization may also occur within communities where the relative abundance of species (or genotypes or functional attributes) becomes uneven and skewed towards dominant species or other cosmopolitan forms (e.g. Rooney *et al.*, 2004). Certainly, we might expect that patterns of between- and within-community homogenization could vary in a way that communities may become differentiated with respect to each other but undergo homogenization within. A recent study by McKinney and Lockwood (2005) provides tentative evidence for a strong positive (equality) relationship between

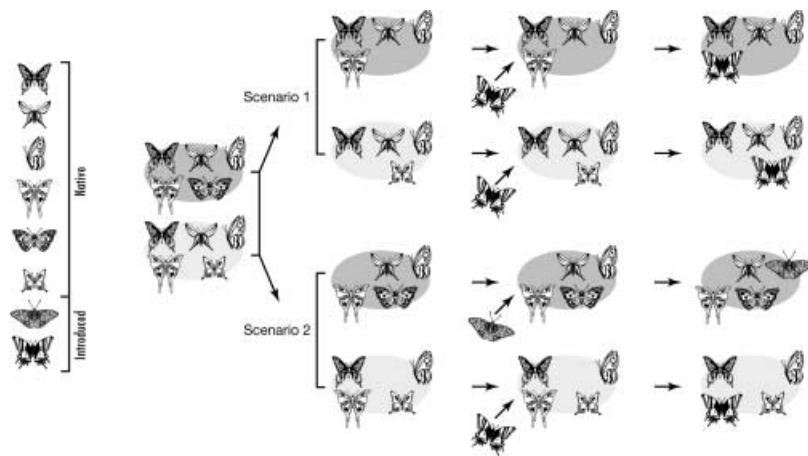
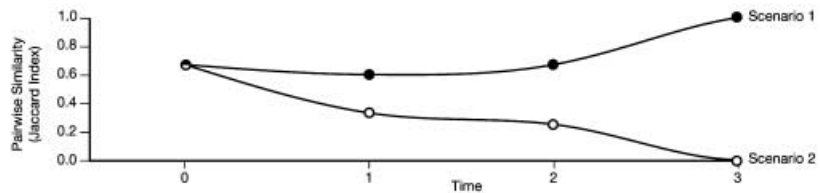


Figure 1 Illustration of how species invasions and extinctions can cause either taxonomic homogenization (scenario 1) or differentiation (scenario 2), depending on the identity of the species involved. A pair of communities (shaded ovals) for each scenario is illustrated where extinction events are represented by the disappearance of a species icon over a time step, whereas introduction events are represented by the arrow and appearance of a species icon. Importantly, both scenarios share the same species pool (six native butterflies, two exotic butterflies) and species richness and turnover through time are identical for both scenarios.

Time	0	1	2	3
Cumulative extinctions	0	1	1	2
Cumulative introductions	0	0	1	1
Species turnover	0.000	0.111	0.222	0.333
Species richness	5	4	5	4



patterns of community similarity based on species' presence/absence and species' abundance (according to a coarse measure of ranked abundance), which the authors use to suggest that species abundance may not play a large role in the homogenization process. In summary, future research is needed to explore the mechanisms, patterns and ecological consequences of BH, such as those manifested across genetic, taxonomic and functional levels both between and within communities.

COMMON MISCONCEPTIONS

While the study of BH is clearly still in its infancy, an examination of the literature shows that there is already a surprisingly high level of misconception regarding this process among ecologists. Previous studies have used BH incorrectly to describe *patterns* of species invasions, declining distributions and loss of native species, or changes in species richness over time. However, any one of these can occur without generating BH. Researchers need to appreciate that taxonomic homogenization is not synonymous with species invasions and extinctions, and therefore cannot be assumed to covary predictably with species richness. In fact, homogenization (or even differentiation) can arise when species invasions occur without commensurate loss of species, or conversely where only species extinctions occur (Rahel, 2000; Olden & Poff, 2004b). This has been illustrated conceptually by Rahel (2002) and Olden and Poff (2003).

Even when experiencing the same rate of extinctions and invasions, we cannot predict a priori whether a pair of communities

will undergo taxonomic homogenization or differentiation. To illustrate this, we simulate two scenarios with pairs of communities experiencing extinction and immigration events over three time steps (Fig. 1). At each time step, species richness, turnover and the cumulative number of extinctions and introductions are identical between scenarios, and both scenarios share the same species pool. Only the identity of species invading or going extinct differs between scenarios. Under scenario 1, the pair of communities undergoes taxonomic homogenization, while according to scenario 2 the pair of communities undergoes taxonomic differentiation. With this example we simply show that species additions and deletions need not both occur for the similarities among communities to change over time, and that TH is not synonymous with changes in species richness.

In fact, empirical evidence also suggests that a narrow focus on species invasions and extinctions fails to capture patterns of TH. The relationship between TH and species diversity is presented in Fig. 2 for freshwater fish (states) and plant communities (parks and natural areas) across the United States. For both taxonomic groups, native species richness exhibits a negative logarithmic association with mean percentage of TH (fishes: $R^2 = 0.82$, $P < 0.001$; plants: $R^2 = 0.57$, $P < 0.001$), whereas non-native species richness shows no relationship (fishes: $R^2 = 0.05$, $P = 0.125$; plants: $R^2 = 0.12$, $P = 0.129$). This illustrates that patterns of TH are clearly distinguishable from other components of biodiversity as they relate to native and non-native species richness. In summary, the final message is a simple one: biotic homogenization is not tantamount to species invasions and

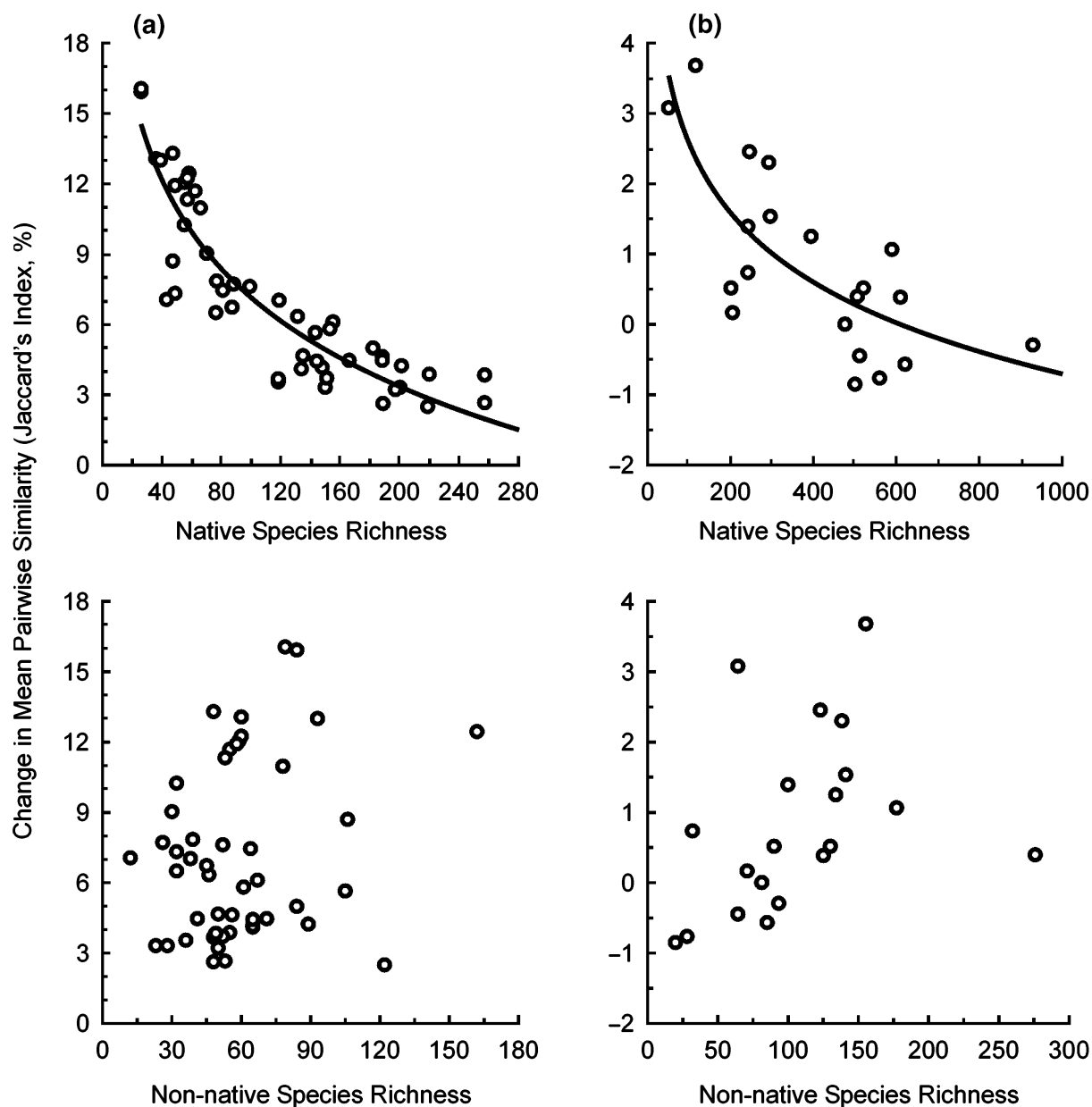


Figure 2 Association between mean percentage change in pairwise species similarity (i.e. taxonomic homogenization) based on Jaccard's index and (a) freshwater fish richness and (b) plant species richness for the United States. Data sources were Rahel (2000) for fishes (species lists for states) and McKinney (2004a) for plants (species lists for parks and natural areas). Statistically significant logarithm relationships were observed for native species richness, but not for non-native species richness (see text for details).

extinctions, and it does not refer merely to changes in species diversity. Rather, the various forms of BH (including genetic, taxonomic and functional) are distinct components of biodiversity that warrant explicit recognition and investigation by researchers.

HOW IS TAXONOMIC HOMOGENIZATION STUDIED?

Numerous measures and approaches have been used to quantify TH; to some extent like the numerous approaches used to

measure β diversity (Koleff *et al.*, 2003). TH 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). While the choice of similarity index can influence the

Table 1 A review of the methodological approaches used to quantify taxonomic homogenization

Approach	Metric	Reference
Species pools surveyed in two time periods		
<i>Minnesota, USA</i> : Fish community composition of 62 lakes surveyed in two time periods: 1940–55 and 1985–92	Jaccard's index	Radomski & Goeman (1995)
<i>Wisconsin, USA</i> : Plant community composition of 62 forest stands surveyed in two time periods: 1950 and 2000	Bray–Curtis index	Rooney <i>et al.</i> (2004)
Extant and reconstructed historical species pools (corrected for extinctions)		
<i>Canada</i> : Fish species lists for the 13 provinces/territories	Jaccard's index	Taylor (2004)
<i>British Columbia, Canada</i> : Fish species lists for eight aquatic ecoregions	Jaccard's index	Taylor (2004)
<i>United States</i> : Fish species lists for the 48 contiguous states	Jaccard's index	Rahel (2000)
<i>California, USA</i> : Fish species lists for six zoogeographical provinces	Jaccard's index	Marchetti <i>et al.</i> (2001)
<i>California, USA</i> : Fish species pools for 43 watersheds	Jaccard's index	Marchetti <i>et al.</i> (2001)
<i>Tennessee, USA</i> : Amphibian, fish and mussel species pools for seven terrestrial ecoregions	Index of spatial turnover	Duncan & Lockwood (2001)
Extant and reconstructed historical species pools		
<i>United States</i> : Plant surveys of 20 parks and local areas	Jaccard's index	McKinney (2004a,b)
<i>North America</i> : Plant species lists for selected states/provinces	Jaccard's index	Rejmánek (2000)
<i>New York, USA</i> : Fish species lists for 19 watersheds	Δ native and exotic spp. richness	Carlson & Daniels (2004)
Extant species pools — community similarity		
<i>California and Ohio, USA</i> : Bird surveys of six sites along a rural–urban gradient in two cities	Jaccard's index	Blair (2001)
<i>California and Ohio, USA</i> : Bird and butterfly surveys of six sites along a rural–urban gradient in two cities	Jaccard's index	Blair (2004)
<i>Finland</i> : Bird surveys of three sites along a rural–urban gradient in five towns	Sørensen's index	Jokimäki & Kaisanlahti-Jokimäki (2003)
Extant species pools — community metrics		
<i>American Samoa</i> : Land snail species lists for three national parks	Δ native and exotic spp. distributions	Cowie (2001)
<i>Tennessee, USA</i> : Fish community composition of 36 mid-order streams surveyed in one time period: 1995–98	% Endemic species vs. % cosmopolitan species	Scott & Helfman (2001)
<i>Georgia, USA</i> : Fish community composition of 30 small-order streams surveyed in one time period: 1999–2000	Ratio of endemic to cosmopolitan species	Walters <i>et al.</i> (2003)

magnitude of biological similarity computed (see 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 TH are also important, but are not discussed for the sake of brevity (see Olden & Poff, 2003 for discussion). Below we examine the underlying assumptions and strengths and weaknesses of the various approaches used thus far to quantify TH (Table 1). In so doing, we use a number of examples from the literature, but it is not our intent to undermine this existing body of work. Rather, we wish to highlight how TH has been defined in the past so that we can avoid previous shortcomings and build upon past advances.

Species pools surveyed in two time periods

The most straightforward method for quantifying TH 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, Rooney *et al.*'s (2004) resurveys 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 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 TH.

Extant and reconstructed historical species pools

A common approach to calculating TH 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 TH, it still provides a reasonable approach for assessing the overall level of homogenization associated with human settlement histories, assuming species gains and losses are recorded accurately.

Several other studies have reconstructed extant and historical species pools, but failed to account for native species extirpations by assuming erroneously that the historical species pool is 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 TH. 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 TH. Moreover, when species extirpations are not taken into account, the influence of exotic species introductions on TH will tend to be over-emphasized. Consequently, the assumptions of this methodology must be acknowledged when comparing the relative importance of exotic introductions vs. native extinctions in driving patterns of homogenization (e.g. McKinney, 2004b).

Extant species pool only

In contrast to the above approaches, a substantial (and unfortunately increasing) number of studies in the literature have quantified TH while either failing to account for species identity or examining only present-day species pools (Table 1). 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 TH, and Carlson and Daniels (2004) referred to changes in exotic and native species richness over time as TH. 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 TH: (1) simple examples and simulation experiments show that the two can be independent (Rahel, 2002; Olden & Poff, 2003); and (2) empirical data indicate that the form of the relationship between richness and homogenization is variable and differs between native and non-native species pools (this study; Olden, 2006). Therefore, despite the negative relationship between richness and homogenization implied in some empirical studies (e.g. Wilson, 1997), the association between different measures of diversity is highly variable (Koleff

& Gaston, 2002) and the loss of native biodiversity is not related universally to increased TH (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 TH (e.g. Blair, 2001). These studies examine spatial patterns in species identity, but provide only tentative evidence for TH because we are unaware of the historical degree of similarity among the communities. We might reasonably assume that it is low; however, this will depend on the proximity of the areas being compared and similarities in their biogeography. Without knowing levels of taxonomic similarity at some previous point in time, it is impossible to assess whether or how much biotas have converged in their species composition.

CONCLUSION

While many papers have depicted TH correctly as a replacement process leading to decreased β diversity, there are a great number of other papers where this concept (or more generally BH) is inappropriately applied. These offences range from the incorrect use of the term to the more serious violation where it is claimed falsely to be a primary objective of the study. Failure to appreciate the various components of biodiversity, including the multifaceted process of BH, could well undermine efforts to battle invasive species and sustain true biological diversity (McKinney, 2005; Olden *et al.*, 2005). By misrepresenting the homogenization process as a surrogate of species richness, we risk the possibility of overlooking the ecological and evolutionary effects of BH, which are likely to be manifested in the absence of major changes in species richness. Moreover, the implications of BH are likely to differ depending on what components are being simplified (Olden *et al.*, 2004), thus emphasizing the need for researchers to recognize and state explicitly the specific component of biotic homogenization under investigation.

Although the study of BH will probably profit from a diversity of methodologies, with no single line of inquiry being superior to all others, general patterns of BH have thus far proved elusive, which we believe stems from the lack of a consistent and rigorous methodological approach to its quantification. Unfortunately, without a standardized approach to the quantification of BH the interpretation of previous findings are greatly complicated, if not rendered impossible, because of the variety of ways used to measure homogenization. We recommend that BH be quantified by either revisiting locations that were historically surveyed or by utilizing pre-existing databases of extant and historical species lists and accounting explicitly for past species extirpations. Given the difficulties in estimating species extirpations (especially at finer spatial scales), the potential biases associated with the assumption of no extirpations should be made explicit.

In conclusion, we cite a need for researchers to: (1) consider carefully the broad, multifaceted definition of BH by appreciating the genetic, taxonomic and functional realms of this process; (2) recognize that TH refers to how the identities of species (not species richness) comprising biotas change over both space and

time; and (3) employ defensible methods for quantifying BH and explore its spatial and temporal dependency. Progress in these areas will ensure the better allocation of future efforts for understanding the mechanisms and predicting patterns of BH for different taxonomic groups, and facilitate the education of policy makers and the public regarding this important component of the modern biodiversity crisis.

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REFERENCES

- Blair, R.B. (2001) Birds and butterflies along urban gradients in two ecoregions of the United States: is urbanization creating a homogeneous fauna? *Biotic homogenization* (ed. by J.L. Lockwood and M.L. McKinney), pp. 33–56. Kluwer Academic/Plenum Publishers, New York.
- Blair, R.B. (2004) The effects of urban sprawl on birds at multiple levels of biological organization. *Ecology and Society*, **9**. Available at: <http://www.ecologyandsociety.org/vol9/iss5/art2/> [accessed July 2005].
- Carlson, D.M. & Daniels, R.A. (2004) Status of fishes in New York: increases, declines and homogenization of watersheds. *American Midland Naturalist*, **152**, 104–139.
- Collins, M.D., Vazquez, D.P. & Sanders, N.J. (2002) Species–area curves, homogenization and the loss of global diversity. *Evolutionary Ecology Research*, **4**, 457–464.
- Cowie, R.H. (2001) Decline and homogenization of Pacific faunas: the land snails of American Samoa. *Biological Conservation*, **99**, 207–222.
- Devin, S., Beisel, J.-N., Usseglio-Polatera, P. & Moreteau, J.-C. (2005) Changes in functional biodiversity in an invaded freshwater ecosystem: the Moselle River. *Hydrobiologia*, **542**, 113–120.
- Duncan, J.R. & Lockwood, J.L. (2001) Spatial homogenization of aquatic fauna of Tennessee: extinction and invasion following land use change and habitat alteration. *Biotic homogenization* (ed. by J.L. Lockwood and M.L. McKinney), pp. 245–258. Kluwer Academic/Plenum Publishers, New York.
- Gering, J.C., Crist, T.O. & Veech, J.A. (2003) Additive partitioning of species diversity across multiple spatial scales: implications for regional conservation of biodiversity. *Conservation Biology*, **17**, 488–499.
- Jackson, D.A., Somers, K.M. & Harvey, H.H. (1989) Similarity coefficients: measures of co-occurrence and association or simply measures of occurrence? *American Naturalist*, **133**, 436–453.
- Jokimäki, J. & Kaisanlahti-Jokimäki, M.-L. (2003) Spatial similarity of urban bird communities: a multiscale approach. *Journal of Biogeography*, **30**, 1183–1193.
- Kolar, C.S. & Lodge, D.M. (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution*, **16**, 199–204.
- Koleff, P. & Gaston, K.J. (2002) The relationship between local and regional species richness and spatial turnover. *Global Ecology and Biogeography*, **11**, 363–375.
- Koleff, P., Gaston, K.J. & Lennon, J.J. (2003) Measuring beta diversity for presence–absence data. *Journal of Animal Ecology*, **72**, 367–382.
- Lockwood, J.L. & McKinney, M.L. (2001) *Biotic homogenization*. Kluwer Academic/Plenum Publishers, New York.
- Loreau, M. (2000) Are communities saturated? On the relationship between α , β and γ diversity. *Ecology Letters*, **3**, 73–76.
- Marchetti, M.P., Light, T., Feliciano, J., Armstrong, T., Hogan, Z., Viers, J. & Moyle, P.B. (2001) Homogenization of California's fish fauna through abiotic change. *Biotic homogenization* (ed. by J.L. Lockwood and M.L. McKinney), pp. 259–278. Kluwer Academic/Plenum Publishers, New York.
- McKinney, M.L. (2004a) Measuring floristic homogenization by non-native plants in North America. *Global Ecology and Biogeography*, **13**, 47–53.
- McKinney, M.L. (2004b) Do exotics homogenize or differentiate communities? Roles of sampling and exotic species richness. *Biological Invasions*, **6**, 495–504.
- McKinney, M.L. (2005) New Pangea: homogenizing the future biosphere. *Proceedings of the California Academy of Sciences*, **56** (Suppl. 1), 119–129.
- McKinney, M.L. & Lockwood, J.L. (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, **14**, 450–453.
- McKinney, M.L. & Lockwood, J.L. (2005) Community composition and homogenization: evenness and abundance of native and exotic plant species. *Species invasions: insights into ecology, evolution and biogeography* (ed. by D.F. Sax, J.J. Stachowicz and S.D. Gaines), pp. 365–380. Sinauer Associates, Sunderland, MA.
- Olden, J.D. (2006) Biotic homogenization: a new research agenda for conservation biogeography. *Journal of Biogeography*, in press.
- Olden, J.D. & Poff, N.L. (2003) Toward a mechanistic understanding and prediction of biotic homogenization. *American Naturalist*, **162**, 442–460.
- Olden, J.D. & Poff, N.L. (2004a) Clarifying biotic homogenization. *Trends in Ecology & Evolution*, **19**, 283–284.
- Olden, J.D. & Poff, N.L. (2004b) Ecological mechanisms driving biotic homogenization: testing of a mechanistic model using fish faunas. *Ecology*, **85**, 1867–1875.
- Olden, J.D., Poff, N.L., Douglas, M.R., Douglas, M.E. & Fausch, K.D. (2004) Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology & Evolution*, **19**, 18–24.
- Olden, J.D., Douglas, M.E. & Douglas, M.R. (2005) The human dimension of biotic homogenization. *Conservation Biology*, **19**, 2036–2038.

- Petts, R.J. (2004) Biological invasions at the gene level. *Diversity and Distributions*, **10**, 159–165.
- Radomski, P.J. & Goeman, T.J. (1995) The homogenizing of Minnesota lake fish assemblages. *Fisheries*, **20**, 20–23.
- Rahel, F.J. (2000) Homogenization of fish faunas across the United States. *Science*, **288**, 854–856.
- Rahel, F.J. (2002) Homogenization of freshwater faunas. *Annual Review of Ecology and Systematics*, **33**, 291–315.
- Rejmánek, M. (2000) A must look for North American biogeographers. *Diversity and Distributions*, **6**, 208–211.
- Rhymer, J.M. & Simberloff, D. (1996) Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics*, **27**, 83–109.
- Rooney, T.P., Wiegmann, S.M., Rogers, D.A. & Waller, D.M. (2004) Biotic impoverishment and homogenization in unfragmented forest understory communities. *Conservation Biology*, **18**, 787–798.
- Sax, D.F. & Gaines, S.D. (2003) Species diversity: from global decreases to local increases. *Trends in Ecology & Evolution*, **18**, 561–566.
- Scott, M.C. & Helfman, G.S. (2001) Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. *Fisheries*, **26**, 6–15.
- Taylor, E.B. (2004) An analysis of homogenization and differentiation of Canadian freshwater fish faunas with an emphasis on British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, **61**, 68–79.
- Walters, D.M., Leigh, D.S. & Bearden, A.B. (2003) Urbanization, sedimentation, and the homogenization of fish assemblages in the Etowah River Basin, USA. *Hydrobiologia*, **494**, 5–10.
- Whittaker, R.H. (1972) Evolution and measurement of species diversity. *Taxon*, **21**, 213–251.
- Whittaker, R.J., Araujo, M.B., Jepson, P., Ladle, R.J., Watson, J.E.M. & Willis, K.J. (2005) Conservation biogeography: assessment and prospect. *Diversity and Distributions*, **11**, 3–23.
- Wilkinson, D.M. (2004) The long history of homogenization. *Trends in Ecology & Evolution*, **19**, 282–283.
- Wilson, K.-J. (1997) Extinct and introduced vertebrate species in New Zealand: a loss of biodistinctiveness and gain in biodiversity. *Pacific Conservation Biology*, **3**, 301–305.
- Wolda, H. (1981) Similarity indices, sample size, and diversity. *Oecologia*, **50**, 296–302.

BIOSKETCHES

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