



The varying role of population abundance in structuring indices of biotic homogenization

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ABSTRACT

Aim An important component of human-induced global change is the decrease or increase in community distinctiveness (taxonomic homogenization or differentiation, respectively) that follows the loss of native species and gain of non-native species. We use simulation approaches to assess the extent to which conclusions about the outcome of the homogenization process depend on whether or not abundance data are incorporated.

Location Data were produced through computer simulation.

Methods The frequency with which occurrence-based similarity indices and abundance-based similarity indices give different views of changes in community similarity, and the conditions under which such differences occurred were assessed using both deterministic and stochastic modelling approaches to simulate species assemblage states.

Results Occurrence-based and abundance-based indices were positively correlated across the set of simulations for both the deterministic and stochastic models. However, in both situations approximately one quarter (25%) of models resulted in contrasting outcomes for the two approaches of calculating changes in compositional similarity; that is, one data type showed a positive value (homogenization), whereas the other showed a negative value (differentiation).

Main conclusions In the majority of cases, species abundances will not change drastically enough after perturbation to produce large differences between homogenization scores measured using occurrence versus abundance information. However, in cases where these changes are large, it is important to recognize that the choice of metric to analyse homogenization trends will influence the qualitative and quantitative conclusions drawn. Studies of real assemblages are therefore necessary to evaluate the role of species abundance in defining the magnitude and direction of changes in community composition across space, and the implications of these changes for native biodiversity.

Keywords

Biotic homogenization, Bray–Curtis index, compositional similarity, extirpation, introduction, Sørensen index.

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INTRODUCTION

The arrival of humans at a location typically precipitates changes in the biota present through the opposing processes of species extirpation and the introduction of non-native species (Elton, 1958). These processes tend to increase local species richness because species gains typically outnumber

species losses (Sax & Gaines, 2003), but they also alter the species composition of the biota relative to that in other localities (McKinney & Lockwood, 1999). Recent theoretical and empirical research has shown that there are a number of ways in which the compositional similarity of locations can be altered by species invasions and extirpations (Olden & Poff, 2003; Cassey *et al.*, 2006). For major taxonomic groups such as

plants, birds and freshwater fishes, the widespread invasion of a limited number of cosmopolitan species and the extirpation of unique native populations has tended to decrease regional-scale biological distinctiveness – a process termed taxonomic homogenization (e.g. Rahel, 2000; McKinney, 2004b; Smart *et al.*, 2006; Cassey *et al.*, 2007; La Sorte *et al.*, 2007). However, in some cases, the establishment of different non-native species at different localities, combined with the extirpation of local populations of ubiquitous native species, has led to an increase in community distinctiveness, or taxonomic differentiation (McKinney, 2004a; Marchetti *et al.*, 2006; Cassey *et al.*, 2007; La Sorte *et al.*, 2007). Interest in these processes has been growing with the realization that extinction and invasion may change community similarity in a variety of non-intuitive ways, depending on the spatial grain and resolution of comparisons, the biogeographic and human histories of the locations, and the characteristics of the taxa concerned (Olden & Poff, 2003, 2004; McKinney, 2004a, 2005; Cassey *et al.*, 2006, 2007; La Sorte *et al.*, 2007; Olden *et al.*, 2007). Understanding the drivers and consequences of biotic homogenization is increasingly recognized as being important for conservation planning at both local and regional scales (Rooney *et al.*, 2007).

To date, the homogenization process has been studied primarily with respect to changes in the identities of species over time, despite the fact that locales may also differ in the population size (i.e. abundances) of those species. However, species that co-occur in the same locale often differ markedly in abundance, whereas the same species can differ substantially in abundance across locales. Changes in abundance can also affect the degree to which communities differ in composition, yet the potential role of abundance in driving taxonomic homogenization has been largely unexplored by previous studies, which have focused solely on presence–absence data to analyse changes in composition [reviewed in Olden (2006), but see Rooney *et al.* (2004) and examples below]. Recent empirical studies have suggested that considering spatiotemporal changes in species abundances may provide new insight into patterns and implications of the homogenization process. For example, Schulte *et al.* (2007) found strong evidence for the homogenization of regional forest types in the upper mid-west of the United States according to relative dominance, despite little change in the occurrence of tree species. Similarly, intense deer herbivory in Wisconsin forests is suspected to be the cause of the increased abundance of already common native species and the decline of other, usually rarer, native species (Rooney *et al.*, 2004; Wiegmann & Waller, 2006). McKinney & La Sorte (2007) recently suggested that ‘where abundance data are omitted, studies may significantly underestimate the impacts of invasive species on homogenization’. The authors argue that, if abundant non-native species tend to be shared to a greater degree than their rare counterparts, the increase in community similarity according to species abundances would be higher than estimates based on species presence–absence, especially when rare species are not detected during sampling. We posit that, depending on the relative

ecological roles of abundant versus rare species, the ecological consequences of biotic homogenization and its relevance to conservation planning will differ greatly (see Olden *et al.*, 2004; Rooney *et al.*, 2007).

Limited empirical evidence suggests that our perception of patterns (and perhaps the direction) of change in community composition over time may differ substantially depending on whether species presence–absence or abundance is examined. Figure 1 presents a simple hypothetical example to illustrate this point. In this case, if changes in similarity metrics were being used as a guide to the conservation status of these sites, evidence from species occurrence would suggest that taxonomic homogenization had occurred, whereas species abundance would, in contrast, suggest taxonomic differentiation. Clearly, if we are investigating the ecological or environmental drivers of homogenization (e.g. Marchetti *et al.*, 2006; Cassey *et al.*, 2007; Olden *et al.*, 2007), it is important to know whether communities have become more or less similar when trying to ascribe mechanisms to observed patterns. These results point to the importance of a systematic exploration of the circumstances in which we would expect changes in species abundance and occurrence to play similar or different roles in shaping patterns of homogenization.

Ideally, the influence of the relative roles of species abundance and composition in driving changes in taxonomic similarity or differentiation would come from a thorough assessment of species occurrence, abundance, and other population parameters in real ecological assemblages (e.g. Magurran, 1988). However, there are few animal or plant assemblages for which changes in species composition have been quantified over reasonably long time periods and across

	Historical			Extant	
	Locale 1	Locale 2		Locale 1	Locale 2
Sp. 1	35	75		2	80
Sp. 2	10	0		0	0
Sp. 3	55	25	— Perturbation →	8	15
Sp. 4	0	0		90	5
	Sørensen = 80%		(+ ΔCS_{Sor})	Sørensen = 100%	
	Bray–Curtis = 60%		(– ΔCS_{BC})	Bray–Curtis = 15%	

Figure 1 Schematic diagram of how our quantification of changes in composition can be affected by the choice of species data examined (either presence–absence or abundance). The abundances of four species are represented in an array for each assemblage. As a result of a perturbation (e.g. human colonization), all species are shared between the two assemblages and thus the Sørensen index increases from 80% to 100%, indicating an increase in homogenization (+ ΔCS_{Sor}). However, when we take species abundances into account, community similarity actually declines: the Bray–Curtis index decreases from 60% to 15%, thus indicating an increase in differentiation (– ΔCS_{BC}).

large spatial scales, and fewer still for which changes in abundance have also been quantified in a robust manner. Thus, we are likely to remain in the position of primarily using presence/absence information to examine the process of biotic homogenization. Given this, it would be advantageous to know how much, and when, our perception of homogenization (both in terms of direction and magnitude) changes in situations in which we can compare metrics based on presence–absence data alone, and metrics that additionally incorporate abundance data. In other words, how common is it to have a situation as depicted in Fig. 1? Here we use deterministic and stochastic simulation approaches to assess the extent to which conclusions about levels of homogenization depend on whether or not abundance data are incorporated. This allows us to assess the frequency with which occurrence-based indices and abundance-based indices give different views of changes in community similarity, and the conditions under which such differences occur.

METHODS

Simulation experiment

We simulated two distinct scenarios for distributing species abundances among two distinct assemblages (i.e. assemblages at two distinct localities). For each scenario, at each locality, we compared a historical assemblage with an extant assemblage, where the extant assemblage is the result of a perturbation of the historical assemblage. Both simulation scenarios were modelled in the Interactive Matrix Language of SAS v. 9.2. The first scenario is a deterministic model in which every possible outcome is realized (*sensu* Olden & Poff, 2003), and the second scenario is a stochastic model with a large number of possible outcomes that can be averaged to summarize overall patterns (*sensu* Cassey *et al.*, 2006). The two scenarios share a number of common features. The total abundance in each assemblage was always fixed, and both historic and extant assemblages

always contained at least one species. Both assemblages were always saturated, meaning that the total number of individuals across all species always reached the fixed cap.

A deterministic model of taxonomic homogenization

The first model considers two localities (j and k), each of which is inhabited by one or both of species X and Y . When the species co-occur, one has an abundance g and the other has an abundance h , and when only one species occurs, it has an abundance of $g + h$. Following a temporal perturbation, the two assemblages can take on any possible state as a combination of either the extinction of one species (where two were present), the invasion of a second species (where only one was present), or no change. Thus, each locality can have one of four possible states in terms of the species present and their abundances ($XgYh$; $XhYg$; $Xg+h$; $Yg+h$). Historical similarity can have one of 16 possible state combinations (because both localities can each have one of four possible states), and change in compositional similarity can be calculated for 256 distinct possible combinations of change (because each of the initial similarities can change to any of the other 16 similarities, including the one that results in no change). Values of g and h are arbitrary and can be set to any two positive numbers. We present an example for which $g = 25$ and $h = 75$ (Fig. 2); however, our conclusions do not change when these values are modified (see Discussion).

A stochastic model of taxonomic homogenisation

The second model considers two localities (j and k) containing p and q species, respectively, where the identities of the p and q species are randomly chosen (with probability α) from S species. The abundances of the S species are distributed according to a random broken stick process (MacArthur, 1957) from a common total abundance N . This allocation is performed separately for each community so that a given

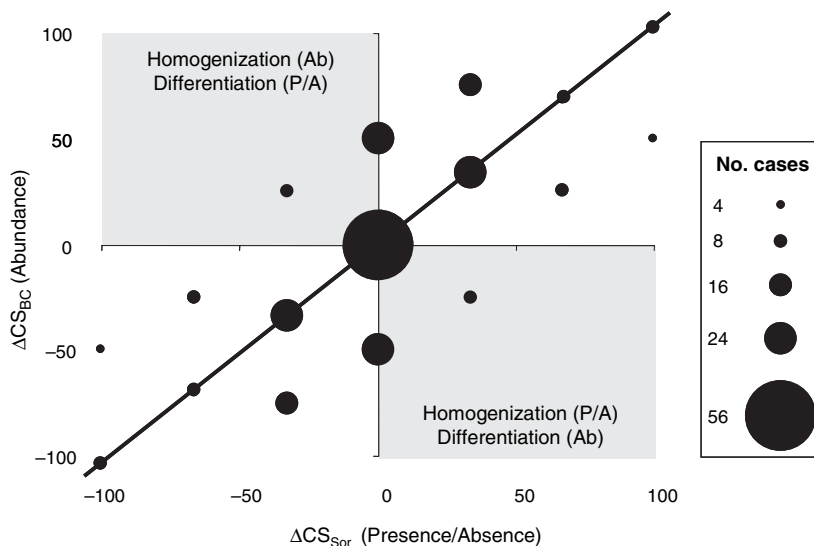


Figure 2 Bivariate relationship between ΔCS_{BC} and ΔCS_{Sor} compositional similarity for a deterministic model of assemblage composition. The number of possible outcomes is 256, and the size of each point represents the number of overlying points for each outcome. The upper-left quadrant of the plot represents the situation for which taxonomic homogenization is indicated by changes in species abundances, but taxonomic differentiation is indicated by changes in species presence–absence. The opposite pattern is represented in the lower-right quadrant of the plot.

species can have a different abundance in each community. The total abundance at each locality is the sum of the abundances of the p or q species randomly assigned to the localities. Thus, the total abundance at each locality can differ. Species that are not chosen for each locality (i.e. $S - p$ and $S - q$) constitute the possible invaders that can enter the localities following a temporal perturbation. Following a temporal perturbation, extant species are randomly subject to extirpation (with probability β_1), and possible invaders can be randomly successfully established (with probability β_2). Following the temporal perturbation, if the total abundance in the extant assemblage is greater (or less) than that in the historical assemblage, the distributed difference is randomly subtracted from (or added to) the extant species. Thus, the total abundances of the historical and extant assemblages at each locality are the same (remembering that this total can differ between localities). For brevity we present a single example, in which $S = 10$, $N = 1000$, $\beta_1 = 0.667$, and $\beta_2 = 0.333$.

Quantitative comparisons

We use the Sørensen index as our measure of compositional similarity (CS) between the two sampling locales (j and k) using only presence-absence information:

$$\text{Sørensen index} = 100 \left[\frac{2a}{b+c} \right], \quad (1)$$

where a is the number of species shared between the two communities, b is the number of species that are found in locale j but not in k , and c is the number of species found in locale k but not in j . We used the Bray-Curtis index as our measure of compositional similarity between the same two locales using species abundance information:

$$\text{Bray-Curtis index} = 100 \left[1 - \frac{\sum_{i=1}^r |\Psi_{ij} - \Psi_{ik}|}{\sum_{i=1}^r (\Psi_{ij} + \Psi_{ik})} \right]. \quad (2)$$

In this case, Ψ_{ij} and Ψ_{ik} are the respective abundances of species i in each of the two locales j and k .

Each index can take values ranging from 0 to 100, and both respond in a consistent monotonic way to changes in the number of species shared between locales (Legendre & Legendre, 1998). Both indices will take the value of 0 when no species are shared in common between locales j and k . The Bray-Curtis index will attain the value of 100 when all species are shared between the two locales and each species has exactly the same abundance in each. The Sørensen index will take the value of 100 when all species are shared between the two locales (Legendre & Legendre, 1998). We choose these two indices because: (1) they have been used in a number of past studies examining homogenization, and (2) the Sørensen index is simply the complement of the Bray-Curtis index when the abundance data are scored as 1 or 0 for presence/absence (Legendre & Legendre, 1998).

In homogenization studies (Olden & Rooney, 2006), similarity indices are calculated for all possible pair-wise comparisons within a single temporal window (e.g. historical

time period), producing a similarity matrix containing the similarity of each locale to all other locales. This process is repeated using the later temporal window (e.g. extant time period), producing a second matrix of pair-wise similarity scores. These two scores are simply subtracted from one another to generate a measure of compositional change over time ($CS_{\text{historical}} - CS_{\text{extant}} = \Delta CS$), which are then averaged across locales to produce a single average change for each locale ($\overline{\Delta CS}$).

We use $\overline{\Delta CS}$ to examine how historical similarity can change when the membership of assemblages is altered, and to correlate the direction and magnitude of change between ΔCS calculated with either abundance data or presence-absence data. If $\overline{\Delta CS}$ is positive, the locale has (on average) become more similar to the other locales after invasion and extirpation, i.e. taxonomic homogenization. If $\overline{\Delta CS}$ is negative, the locale has (on average) become less similar to the other locales, i.e. taxonomic differentiation. In the following examples we calculate ΔCS between only two locales, and we denote the ΔCS that was derived using the Sørensen index as ΔCS_{Sor} , and that using the Bray-Curtis index as ΔCS_{BC} .

For each model described above, we plot these two scores for each locale in a bivariate scattergram to illustrate their relationship to one another. We expect the two scores to be positively correlated in both models, since the underlying similarity indices share the same basic mathematical formulation and are based on the same underlying composition information. Thus, when one score indicates that the locales are homogenizing, the other should tend to report the same result. However, given the fact that the Sørensen index weights rare species and common species equally, it is possible that ΔCS_{BC} will be positive (indicating homogenization) while ΔCS_{Sor} remains unchanged, and vice versa. In addition, it is possible that one score will be positive (indicating homogenization) and the other negative (indicating differentiation; Fig. 1). We tally the number of occasions for which these discrepancies occur and note the changes in composition and abundance that produced them.

RESULTS

As expected, ΔCS_{Sor} and ΔCS_{BC} are positively correlated across the set of simulations based on both the deterministic (Fig. 2) and stochastic (Fig. 3) models of assemblage states. For the deterministic model, 136 out of the 256 (53%) possible ΔCS values were equal regardless of whether ΔCS was calculated using Bray-Curtis or Sørensen (i.e. they fall on the 1:1 line in Fig. 2). This indicates that analyses based on species occurrence and abundance data result in the same direction and level of change in compositional similarity. Results differed between the two similarity metrics for 56 cases for which either ΔCS_{BC} was greater than ΔCS_{Sor} (28 cases), or ΔCS_{Sor} was greater than ΔCS_{BC} (28 cases), but for which the direction of change (either indicating homogenization or differentiation) was the same. In 48 of the 256 cases (18.75%), the deterministic model produced a zero-value for ΔCS_{Sor} , whereas ΔCS_{BC}

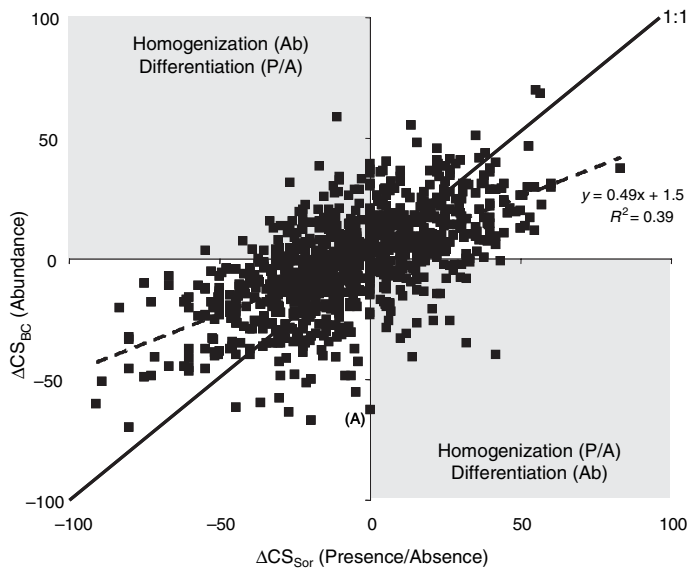


Figure 3 Bivariate relationship between ΔCS_{BC} and ΔCS_{Sor} compositional similarity scores for a stochastic model of assembly composition and temporal perturbation. The number of simulations is 1000, and the point (A) is the outcome specifically discussed in the text. The fitted line and statistics were obtained by ordinary least-squares regression.

was either positive or negative. These results stemmed from there being no change in the number of species shared between the two assemblages, but the abundances for these shared species becoming more, or less, similar. Finally, in 16 cases (6.25%), changes in compositional similarity according to species occurrence versus abundance were in opposite directions, indicating the extreme situation in which one data type indicated homogenization and the other differentiation, or vice versa (Fig. 2).

In the stochastic model (Fig. 3), the Pearson correlation coefficient between ΔCS_{BC} and ΔCS_{Sor} is highly positive and statistically significant ($r = 0.62$, $n = 1000$, $P < 0.001$). Similar to the deterministic model, in approximately a quarter of cases (290 out of 1000) the stochastic model resulted in outcomes for which ΔCS_{Sor} was non-positive when ΔCS_{BC} was positive, or ΔCS_{Sor} was non-negative when ΔCS_{BC} was negative (Fig. 3). In 221 cases (22.1%), the stochastic model resulted in contrasting outcomes for the two approaches of calculating changes in compositional similarity; that is, one data type showed a positive value while the other showed a negative value, or vice versa (Fig. 3). The average absolute difference between ΔCS_{BC} and ΔCS_{Sor} scores was 24.4% (SD = 13.6), ranging from 3.6% to 81.3%.

Given the broad congruence of results between the deterministic and stochastic models, we can use the deterministic model to inform us of the exact circumstances under which these differences in metrics occurred (Appendix 1). For brevity, these circumstances can be summarized as being most likely to occur: (a) when assemblages of different species richness converge to a similar number of species but with different abundances (ΔCS_{Sor} results in homogenization but ΔCS_{BC} results in differentiation); or (b) when assemblages of similar species richness diverge to a different number of species and, depending on the abundances of the species lost (or gained), the abundances of the remaining species either change or stay the same (ΔCS_{BC} results in homogenization but ΔCS_{Sor} results in differentiation). We

refer readers to Appendix 1 if they are interested in a more detailed treatment of these circumstances.

DISCUSSION

Despite the fact that numerical resolution (i.e. absolute abundance, abundance rankings, and species' presence or absence) has long been known to influence our perception of ecological phenomena (Rahel, 1990), there is surprisingly little analytical comparison of community similarity measures in the ecological literature (Legendre & Legendre, 1998; Koleff *et al.*, 2003). Similarity measures have surfaced mostly in studies of biogeographical gradients and of ecotones, and as the basis for multivariate statistical comparisons (Pielou, 1984; MacGarigal *et al.*, 2000). We thus have very little understanding of when two similarity indices will produce diametrically opposed results, much less of how these measures will inform our understanding of macroecological patterns and processes, including biotic homogenization.

Our results suggest that in the majority of comparisons the direction of change in species composition (i.e. homogenization or differentiation) does not depend on whether species' presence-absence or abundance is analysed. In support of this, McKinney & Lockwood (2005) found that the homogenization scores for plant assemblages across parks in the United States were the same regardless of whether the similarity metric used was based on species' presence-absence or species abundances. Indeed, the results from our simulation study are not surprising, given that both the indices we explored are influenced principally by the number of species shared between communities (Koleff *et al.*, 2003). Our results show, however, that there are instances when these two metrics can give results that are very different in their reported magnitude of change. Such differences will make it difficult to infer the mechanisms of observed changes in community composition, especially as abundance data suitable for exploring changes in community similarity are rare.

Modest discrepancies between the results from Bray–Curtis and Sørensen indices, where one index changes but the other does not, result from the equal weighting that rare and abundant species receive within presence–absence metrics. If the number of shared species between communities does not change, but the abundances do, the Bray–Curtis index (i.e. a similarity index based on species abundance) will show changes that depend on the magnitudes of shifts in abundance, whereas the Sørensen index (i.e. a similarity index based on species presence–absence) will show no change. La Sorte *et al.* (2007) succinctly captured the influence this difference will have on our ecological or conservation perspective in the idea of ‘perceived homogenization’. Perceived homogenization explicitly takes into account an increase in the abundance of shared species that are typically detectable to humans (i.e. that are numerically dominant). Thus, two communities will be perceived as more similar to one another because the species they share become the dominant species, or because they tend to share only dominant species after perturbation. Indeed, if the abundant species are the widespread and shared ones, even a small differentiation in species composition may result in perceived homogenization because the species that drive differentiation are only the rare, less visible ones. We extend this result to include ‘perceived differentiation’, in which case the species shared between locales end up with very different abundances relative to one another after perturbation. Thus, the species that humans readily observe (the numerically abundant ones) will be quite different in abundance between the two locales where before they were very similar. This change can occur in the absence of any non-native species invasion or native species extinction, or may even occur if the two communities come to share only rare species (i.e. they homogenize). The changes leading to this difference in perception can be quite large, as indicated, for example, by the simulation result labelled (A) in Fig. 3. This iteration has a Sørensen index score of 0 and a Bray–Curtis differentiation score of 62.6%.

More troublesome are the situations in which one similarity metric indicates homogenization while the other indicates differentiation. In our simulations, 1% of cases (10 out of 1000) had ΔCS_{BC} and ΔCS_{Sor} values with an absolute difference greater than 50% (Fig. 3). In fact, the size of this difference is dependent on the observed differences in the magnitude of abundances among species (results not shown). The more over-dispersed the abundances are, the greater this difference can become. For the deterministic model we present an example in which $g = 25$ and $h = 75$ (Fig. 2). The more similar these two values are, the smaller the magnitude of the difference between metrics. However, our overall conclusions do not change.

Nevertheless, there are reasons to believe that situations for which one similarity metric indicates homogenization and the other differentiation will be uncommon in nature. A general feature of natural assemblages is that those species that are widespread in the distribution are more likely to be common at the sites they occupy, whereas narrowly distributed species

tend to be rare at all sites (Järvinen & Sammalisto, 1976; Hanski, 1982; Brown, 1984; Gaston, 1996; Blackburn *et al.*, 2006). If homogenization results from rare, narrowly distributed native species becoming extinct, or from invasive species becoming widespread in a novel environment, while widespread species tend also to be abundant, we might expect similar conclusions on homogenization from indices that do incorporate abundance and those that do not. The abundance–occupancy relationship may in fact be a fruitful context in which to consider homogenization processes more generally, linking them to studies that have explored how changes in abundance and occupancy may be associated in species contracting or spreading across the environment (e.g. Gregory, 1998; Gaston *et al.*, 1999; Freckleton *et al.*, 2005, 2006).

Our results indicate that, although cases for which presence–absence and abundance data produce opposing conclusions about homogenization are uncommon (*c.* a quarter of occurrences), when they do occur they could drastically change the ecological or conservation conclusions drawn. The Bray–Curtis index will show homogenization where the Sørensen index will show differentiation when the abundance of a newly arriving non-native species varies considerably between two locales while at the same time the abundances of the native species are themselves drastically changing. The reverse will happen when a rare native is locally extirpated from one community, while the abundances of the species in the other community are also radically changing. These scenarios may be typical of communities that are driven far from their ‘native’ equilibrium, such as after a major disturbance event (e.g. the deposition of pollutants, the addition or subtraction of ecosystem engineers, or large-scale urbanization or deforestation). Such perturbations tend to induce species invasions and extinctions while at the same time re-ordering the relative abundance patterns of species already present. If the abundance patterns are largely reversed after the perturbation such that formerly rare species become dominant or vice versa, the choice of metric used to evaluate similarity changes will be extremely important.

The other condition that promotes large differences involves the loss of a numerically abundant species from one community and not another, when previous to this loss the two locales were exactly the same in composition and in the abundance of these shared species. In this case, the Bray–Curtis index will show homogenization whereas the Sørensen index will show differentiation. There is much evidence to indicate that numerically rare species are more likely to become extirpated than common ones (Pimm *et al.*, 1988; Lande, 1993; Lawton & May, 1995). However, there are certainly instances for which a formerly abundant species is driven locally extinct (Gaston & Fuller, 2007), or when new invading species establish large populations and then crash to extinction (Simberloff & Gibbons, 2004). This situation is likely to occur for native species when a threatening agent is species-specific and highly localized. A possible example is the introduction of a predatory mammal to an oceanic island that causes the extinction of one or more formerly abundant ground-nesting birds. One island

in an archipelago may have the non-native mammal, whereas another may not, and the effect of the mammal is specific to ground-nesting birds only. Another potential example is the effect of emerging infectious diseases that are highly virulent for one species, but not others, and that may remain local in their impacts.

Finally, the quantification of community similarity change using species abundance may yet prove to be particularly important for enhancing our understanding of the ecological consequences of biotic homogenization/differentiation. Patterns of species abundance in biological communities, for example, play a critical role in defining ecosystem function and resilience (Hooper *et al.*, 2005). As a result, the ecological and evolutionary implications of biotic homogenization/differentiation will depend, in large part, on spatiotemporal patterns of change in the abundance and ecological functions of those species gained and lost among the communities (Olden *et al.*, 2004). Given the differential contributions of dominant and rare species to a variety of ecosystem processes (e.g. Walker *et al.*, 1999; Lyons & Schwartz, 2001), it may be necessary to examine patterns of change in species abundance in order to fully appreciate the ecological implications of taxonomic and functional homogenization.

CONCLUSIONS

As the stochastic simulation model illustrates, there are myriad gradations of potential differences in estimates of biotic homogenization/differentiation depending on whether species presence–absence or abundance is examined. The degree of these differences will depend on the conformity of the real-world situation to the rigid conditions we described using the deterministic model (Fig. A1). We suggest that the key to avoiding this situation is to determine how abundance is likely to change relative to changes in species composition over time. In the majority of cases, abundances will not change drastically enough to produce large differences. However, in situations for which these changes are large, it is important to recognize that the metric used to analyse homogenization trends will have a large influence on the qualitative and quantitative conclusions drawn. Nearly all texts on ecological statistics suggest careful consideration of the question(s) asked when deciding on what measure of community similarity to use (e.g. Magurran, 1988; Legendre & Legendre, 1998; Koleff *et al.*, 2003). We extend this caution to studies of homogenization, and further modify it to include careful consideration of the perturbation that produced changes in species identities and abundances at each locale. Finally, we cite the need for additional studies that evaluate the role of species abundance in defining the magnitude and direction of changes in community composition across space, and the implications of these changes for native biodiversity.

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APPENDIX 1

Recall that in the deterministic model there are only two species (X and Y), and that each can have an abundance of $g + h$ (in this case $g + h = 100$) if they exist alone at a locale (j or k). Alternatively, if the two species co-exist in the same locale, they can only take abundances of either g (in this case $g = 75$) or h (in this case $h = 25$) (Fig. A1). Thus, changes in composition involve either adding or subtracting a single species (i.e. adding being an invasion and subtracting being an extirpation). Changes in abundance, given that both species remain in the community after perturbation, can only involve switching abundances from g to h and the reverse for the other species.

Given these constraints, the value of ΔCS_{BC} can be negative when ΔCS_{Sor} is positive (negative skew) when a rare species historically found in locale k invades locale j and becomes numerically dominant in j while the composition and abundance in locale k do not change (Fig. A1). Alternatively, the value of ΔCS_{BC} can be negative when ΔCS_{Sor} is positive if a rare species historically found in locale k invades locale j and remains numerically rare in j while the composition in locale k remains the same, but the two species change in abundance so

that the formerly dominant species becomes rare in k (Fig. A1). The same difference in metrics occurs if the locales are switched so that a rare species historically present in j invades k , or if the invading species is reversed from X to Y.

The value of ΔCS_{BC} can be positive when ΔCS_{Sor} is negative (positive skew) if locales j and k historically share the same species but they are of different abundances, the rare species in locale j is extirpated, and the two species in locale k switch abundances (Fig. A1). The same difference in metrics occurs if the locales are switched, or if the extirpated species is reversed from Y to X. Alternatively, ΔCS_{BC} can be positive when ΔCS_{Sor} is negative when the numerically abundant species in both locales j and k is extirpated from j but not from k , and the species in k do not themselves change in abundance (Fig. A1).

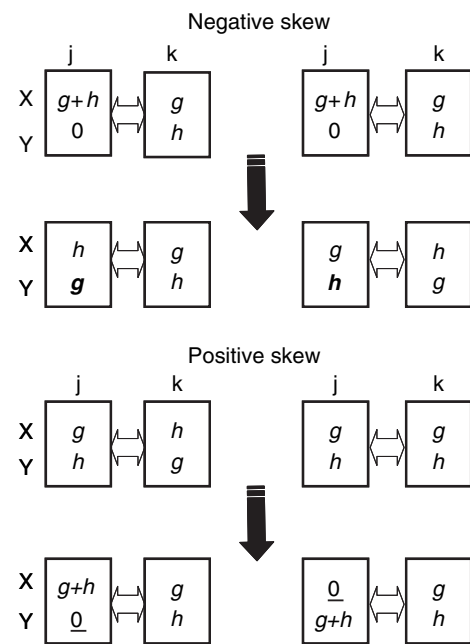


Figure A1 Graphical representation of deterministic model outcomes in which contrasting estimates of change in compositional similarity (i.e. homogenization versus differentiation) are produced. Open arrows represent the calculation of compositional similarity scores (Bray–Curtis or Sørensen), and closed arrows represent changes in assemblage composition resulting from perturbation (invasions or extinctions). Thus, the top two squares in each set are historical compositions for the two locales, and the bottom squares are extant compositions. Bold letters represent the abundance of invasive species. Underlined zeroes represent extirpation of native species.