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Short communication

Biotic homogenization and conservation prioritization

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ABSTRACT

Quantitative studies of biotic homogenization can provide useful insights into conservation problems when used appropriately, but can be dangerously misleading when they are not. By separating the concept of biotic homogenization at the global scale from the study of biotic homogenization at spatially- and temporally-explicit scales, researchers can avoid many of the subtle pitfalls inherent in homogenization studies.

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As human activities accelerate rates of species invasion and extinction, biological diversity changes in fundamentally different ways at different spatial scales. While species richness is declining globally, species gains are frequently observed at regional and local scales as range-expanding habitat generalists (both native and non-native in origin) invade new species pools typically at the expense of rare, and often endemic, native species that disappear (Hobbs and Mooney, 1998). The process describing this non-random reshuffling of species pools is coined biotic homogenization (McKinney and Lockwood, 1999); referring to an increase in the taxonomic similarity of two or more species pools through time as the result of species invasions and extinctions (Olden and Poff, 2003; Olden and Rooney, 2006).

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. It extends beyond the narrow focus on elevated extinction rates to incorporate the other side of the equation: species introductions are also well above background levels. Biotic homogenization conjures the image of Quammen's (1998) dystopian "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, it is anything but. Most importantly, extinction and invasion events at sub-global scales do not automatically increase

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the taxonomic similarity among species pools through time. Depending on species identities, taxonomic similarity could increase, decrease (i.e., biotic differentiation), or remain unchanged (Olden and Poff, 2003), thus highlighting the complexity and challenge of studying biotic homogenization and applying findings to conservation strategies. Olden et al. (2004) recently discussed the negative ecological implications of biotic homogenization, thereby supporting that idea that biotic homogenization and biotic impoverishment go hand-in-hand. This begs the central question addressed in our paper: does biotic homogenization always reflect biotic impoverishment, and correspondingly, does biotic differentiation reflect a conservation improvement? In other words, can we use measures of biotic homogenization to assess changes in biota in a manner that is relevant to conservation efforts? We view the quantitative analysis of biotic homogenization and differentiation as a tool that is useful when used properly, and dangerously misleading when it is not. Here, we explore some of the potentials and pitfalls that are not immediately apparent by (1) illustrating the danger of drawing conservation inferences solely from changes in pairwise similarity through time; and (2) recommending approaches that would increase the utility of similarity measures in conservation planning.

To date, biotic homogenization has been used almost exclusively as an assessment tool. Researchers have provided evidence that biotic homogenization is underway in urban areas (e.g. Crooks et al., 2004; McKinney, 2006; Schwartz et al., 2006), among states in the United States (e.g. Rahel, 2000), and among local communities within metacommunities (e.g. Radomski and Goeman, 1995; Rooney et al., 2004). However, it may be unreasonable to assume that biotic homogenization has important conservation implications in all of these cases. Consider the study of Rooney et al. (2004) who sampled 62 local communities in temperate forests of the upper Midwestern United States, and found the mean Bray-Curtis pairwise floristic similarity among sites to increase slightly over a 50 year period, from 30.8% to 33.5%. Not every site lost distinctiveness. The mean similarity of Brunet Island State Park (Wisconsin) to all other sites declined from 25.4% to 22.0%, and the average similarity of Gogebic State Park (Michigan) to all other sites declined from 33.7% to 22.6%. Does this increased biotic differentiation in floral communities reflect conservation success of state parks? In this example we argue this is not the case. Biotic differentiation in these state parks was driven by the loss of native species: a 65% decline at Brunet Island and a 63% decline at Gogebic. Sites with very high extinction rates and no counterbalancing colonization will differentiate from similar sites with few extinctions; a fact that many researchers overlook. Similarly, Marchetti et al. (2006) observed increasing biotic differentiation in California fish assemblages as a function of increasing watershed urbanization. In Germany, the neophyte flora in highly urbanized areas showed strong patterns of differentiation, even while the archaeophyte and native flora tended to exhibit biotic homogenization (Kühn and Klotz, 2006). In these later cases, high colonization rates with idiosyncratic invaders and low corresponding extinction drove differentiation. Clearly, both biotic homogenization and differentiation can reflect conservation failures.

To interpret changes in pairwise community similarity, we need to understand why biotic homogenization occurs, and by extension, we must recognize the identity of species responsible for the changes. Olden and Poff (2003) report that extinction can increase or decrease similarity among sites, depending on whether the same species or different species disappear. The initial fraction of sites occupied by a species also matters. Consider this hypothetical example: we examine pairwise changes in fish community similarity in 20 lakes where a fish species once common to all lakes begins to disappear. According to Jaccard's index of similarity, each extinction event will always increase pairwise differentiation if we hold the rest of the species pool constant. This will continue until it remains in only half of the lakes. Once it is present in fewer than half of the lakes, each subsequent extinction event will tend to increase pairwise homogenization. We use this simple example to illustrate that the exact outcome depends on the species composition of each lake; differentiation is likely if the similarity in pairwise species composition among lakes is very low. The converse is also true. An invading species will tend to increase pairwise differentiation until half of the sites examined are occupied, after which it will always increase pairwise homogenization.

Studies of biotic homogenization often exhibit scale dependence, which further complicates the applicability of this concept in conservation biology (Olden, 2006). Marchetti et al. (2001) provide a good example; they observed homogenization at regional and local spatial scales, but biotic differentiation at intermediate scales. In a follow-up study, Marchetti et al. (2006) note that idiosyncratic patterns of fish introductions associated with increased human development contribute to the patterns of biotic differentiation at intermediate scales. Scale-dependence might simply reflect the reshuffling in site occupancy by a species that occurs when the system is re-scaled. One species might occupy the majority of reaches sampled within a particular watershed, and at the same time occupy a minority of watersheds within a larger zoogeographic province. This species would have a homogenizing effect within the watershed it occupies, and a differentiating effect in among-watershed comparisons. Scale clearly matters, even if the interpretation of the conservation significance of biotic homogenization is less than straightforward. There is no single "correct" scale for analyzing the conservation significance of biotic homogenization. It will be up to researchers to determine if homogenization matters in their particular system.

Yet, biotic homogenization does have relevance for conservation, as it has utility in reserve selection and management. Regional conservation planning is both a key strategy and top priority in conservation biology (Margules and 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 recent review, Ferrier (2002) highlights the complementarity approach to conservation planning. By using information on the taxonomic similarity among different areas, biologists can identify combinations of sites that maximize the representation of regional species biodiversity while minimizing economic, political, or social costs. While this approach is based on the assumption that taxonomic composition will remain constant through time, regional

species pools can and do change, even in protected areas (Gurd et al., 2001; Sax and Gaines, 2003), with endemics, habitat specialists, species with large home range requirements, and migrants especially prone to extirpation. Invasive, range-expanding, and weedy species are likely to invade all reserves, keeping managers busy with containment and eradication plans.

We think the application of the concept of biotic homogenization 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. 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 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.

We hope these examples highlight the danger of uncritically applying similarity measures as a conservation index, for example, using biotic homogenization as a sole measure of ecosystem integrity. How then do we decide what level of homogenization or differentiation ‘matters’ in terms of conservation? For it to be informative, there has to be careful justification for selecting and comparing compositional similarity among areas *a priori* at scales relevant to conservation. There are a few studies that reflect thoughtful and meaningful site selection. Duncan and Lockwood (2001) examined patterns of biotic homogenization within ecoregions, and Kühn and Klotz (2006) confined their analysis to sites within a similar bioclimatic region. By limiting their analysis to areas with a common species pool and similar historical biogeography, the authors account for the fact that biotas change across ecoregional boundaries and as a function of distance (McKinney, 2006). Likewise, local species assemblages reflect constraints imposed by the regional species pool and local processes such as management or habitat alteration. In many cases, it would be useful to know the degree of temporal turnover, or taxonomic similarity at a site through time. When combined with estimates of biotic homogenization or differentiation, we will be able to compare differences among systems while controlling for turnover rates. Using such an approach we can determine if similar degrees of homogenization simply reflect a similar rate of turnover between systems. If not, it could provide important insights into the drivers of homogenization.

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. Does biotic homogenization or differentiation always lead to biotic impoverishment? Probably not. Should biotic homogenization be considered an

important component of the broader biodiversity crisis? We think so. Ultimately, we need to separate the concept of biotic homogenization at the global scale from the study of biotic homogenization at explicit scales. By doing so, we can better appreciate its nuances and recognize that we have much to learn about its utility for identifying robust conservation strategies and evaluating conservation success.

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