Assessing the suitability of diversity metrics to detect biodiversity change

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ABSTRACT

A large number of diversity metrics are available to study and monitor biodiversity, and their responses to biodiversity changes are not necessarily coherent with each other. The choice of biodiversity metrics may thus strongly affect our interpretation of biodiversity change and, hence, prioritization of resources for conservation. Therefore it is crucial to understand which metrics respond to certain changes, are the most sensitive to change, show consistent responses across different communities, detect early signals of species decline, and are insensitive to demographic stochasticity. Here we generated synthetic communities and simulated changes in their composition according to 9 scenarios of biodiversity change to investigate the behaviour of 12 biodiversity metrics. Metrics showed diverse abilities to detect changes under different scenarios. Sørensen similarity index, arithmetic and geometric mean abundance, and species and functional richness were the most sensitive to community changes. Sørensen similarity index, species richness and geometric mean abundance showed consistent responses across all simulated communities and scenarios. Sørensen similarity index and geometric mean abundance were able to detect early signals of species decline. Geometric mean abundance, and functional evenness under certain scenarios, had the greatest ability to distinguish directional trends from stochastic changes, but Sørensen similarity index and geometric mean abundance were the only indices to show consistent signals under all replicates and scenarios. Classic abundance-weighted heterogeneity indices (e.g. Shannon index) were insensitive to certain changes or showed misleading responses, and are therefore unsuitable for comparison of biological communities. We therefore suggest that separate metrics of species composition, richness, and abundance should be reported instead of (or in addition to) composite metrics like the Shannon index.

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1. Introduction

In a period of rapid global change, monitoring biodiversity changes is key to detect early warning signals of decline, infer the causes of such decline, and develop effective conservation strategies to mitigate it (Ash et al., 2009; Balmford et al., 2003, 2005; Buckland et al., 2005; Butchart et al., 2010; Gregory et al., 2005; Nichols and Williams, 2006; Tittensor et al., 2014). The multifaceted nature of biodiversity (Gaston, 1996; Purvis and Hector, 2000) is studied through a large number of metrics. Different metrics measure different components of biodiversity such as species richness, abundance, evolutionary history (i.e. phylogenetic diversity; Faith, 1992), and functional traits (Mason et al., 2005). However, as no single metric captures all relevant aspects of biodiversity, none of them taken individually can provide a full picture of the patterns of change. Further, metrics can even be misleading if considered individually. For instance, the geometric mean abundance can increase if rare species increase in abundance, while total abundance is decreasing (Schipper et al., 2016). Similarly, invasive species can increase species richness or functional and phylogenetic diversity, while having negative impacts on the abundances of native species (Thomas, 2013; Winter et al., 2009). The rate and direction of change in a metric may also depend on idiosyncrasies in the state of the initial community, and/or natural ecological succession. Moreover, in addition to directional changes in biodiversity, species relative abundances may fluctuate over shorter time frames due to demographic stochasticity or competitive and predator-prey dynamics. This "noise" can confound the signal of interest (i.e. directional change in response to a specific driver).

The choice and response of biodiversity metrics may strongly affect our interpretation of biodiversity change and, hence, prioritization of resources for conservation (Gaston and Spicer, 2004; Purvis and Hector, 2000). Thus, it is crucial to understand how alternative metrics respond to specific changes, which metrics are the most sensitive in order to detect early signals of biodiversity decline, and which ones respond consistently to changes. Empirical datasets allow investigating how metrics change in space and time, but have several limitations. These include the limited number of possible scenarios and communities represented, and the lack of control on the underlying cause of change, the likely co-existence of several mechanisms of decline (e.g., decline of habitat specialists due to the loss of their habitat type and decline of large species due to overexploitation). This complicates the attempts to link the behaviour of a diversity metric to a definite mechanism of biodiversity change. Virtual datasets allow full control of both the community composition and the mechanism of decline, and thus allow the comparison of the relative responses of the diversity metrics (Zurell et al., 2010) by simulating ecological processes under alternative scenarios (Dornelas, 2010; Lamb et al., 2009; Münkemüller and Gallien, 2015; Olden and Poff, 2003; Supp and Ernest, 2014).

In this study, we explored the behaviour of a set of diversity metrics under different scenarios of biodiversity change. To this end, we generated synthetic communities and simulated changes in their composition to investigate the responses of the metrics. We recorded how metrics changed over time under each scenario, and identified those that were most sensitive to these community changes and showed a consistent response irrespective of the state of the original community. We also assessed non-linearity in metrics responses, and their effect on our ability to detect early warning signals of biodiversity change. Finally, we measured the signal-to-noise ratio (SNR) of the metrics under each scenario to compare the metrics' ability to detect directional changes in biological communities.

2. Methods

2.1. Virtual dataset

We assumed a landscape area of 10,000 km^2 consisting of two habitats, one dominant and one secondary. For convenience we will refer to these habitats as forest and grassland, respectively. The size of the landscape was chosen such that it was large enough to allow each species to form a population from ~15 to >50,000 individuals. Forest covered a random proportion between 0.7 and 0.9 of the entire landscape.

We generated 150 species, and randomly assigned to each a diet, body mass, population density, and affinity level for each of the two habitats. The number of species was chosen as a compromise between representativeness of a biological community and computation time for the simulations. For simplicity, we simulated static assemblages with no interactions among species, and restricted the species pool to the consumers in the community.

To simulate realistic communities, we followed established macroecological rules. Specifically, our synthetic communities had the following properties: 1) species in higher trophic levels tended to be larger than species in lower trophic levels; and 2) smaller species tended to be more common than large species (Fig. 1). This was implemented as follows. We sampled a diet category for each species, where herbivores (H), omnivores (O) and carnivores (C) had relative probabilities of 0.5, 0.3 and 0.2 respectively. The body masses (kg) were then sampled from log-normal distributions (Loder et al., 1997) reflecting the negative relationship between trophic level and body mass (H: log-mean = 0.5, log-SD = 1.5; C: log-mean = 0.5 multiplied by a random value between 0.5 and 4, log-SD = 1.5; O: log-mean = mean between the log-mean for H and C, log-SD = 1.5; see predator-prey body mass ratio reported by Brose et al., 2006). Based on the species' body mass and diet category, we estimated population density (ind/km^2) for each species using allometric relationships (log population density vs. log body mass), where the slope of the relationship was sampled from a normal distribution (mean = −0.75, SD = 0.1; Blackburn and Gaston, 1997).

We assumed forest habitat to be richer in species than grassland habitat: within the community, 40% of the species were exclusively forest specialists (affinity of 1 to forest and 0 to grassland), 20% were exclusively grassland specialists (affinity of 1 to grassland and 0 to forest), and 40% were ubiquitous. The affinity value of ubiquitous species to forest habitat was sampled from a symmetric beta distribution (shape parameters = 2; so that central values were more frequent than extreme values), and the habitat affinity to grassland was equal to 1-affinity to forest (i.e. the two affinity values summed to 1). The affinity values were multiplied by the estimated species population abundance (in turn obtained by multiplying density by habitat area) in each of the two habitats to produce a realized abundance for each species.

Finally, we simulated two phylogenetic trees that described the relatedness among the species in the dataset. The first phylogenetic tree assumed that species with similar traits are more phylogenetically similar. For this, for each community we randomly sampled one or more biological traits (body mass, diet, and affinity for the two habitats), and used them to generate a distance matrix based on Gower's distance, as it allows using both continuous and categorical data types (Gower, 1971). The phylogenetic tree was obtained by applying a neighbour joining approach on the distance matrix. The second phylogenetic tree assumed no dependency on biological traits. For this, we followed the same procedure as described above, yet with biological traits randomly shuffled across species before calculating the distance matrix.

2.2. Biodiversity change scenarios

To explore how metrics behave under diverse conditions, we prepared nine scenarios of biodiversity change. Scenarios (Table 1) ranged from the uniform or proportional decline of all species in the community, to the decline of a subset of species sharing certain characteristics (e.g. traits and relative abundance), to the change in the area available for different species (i.e. extent of habitat). These scenarios span the range of disturbances considered by Dornelas (2010), and expand it to accommodate different susceptibilities to change among different types of species. To measure metrics' sensitivity to noise, we considered