



Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/bioc

Assessing the suitability of diversity metrics to detect biodiversity change

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ARTICLE INFO

Article history:

Received 30 March 2016

Received in revised form 3 August 2016

Accepted 22 August 2016

Available online xxxx

Keywords:

Abundance

Biodiversity indicators

Biodiversity monitoring

Similarity index

Functional diversity

Phylogenetic diversity

Shannon index

Simpson index

Synthetic community

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 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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<http://dx.doi.org/10.1016/j.biocon.2016.08.024>

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Please cite this article as: Santini, L., et al., Assessing the suitability of diversity metrics to detect biodiversity change, Biological Conservation (2016), <http://dx.doi.org/10.1016/j.biocon.2016.08.024>

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 km² 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/km²) 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

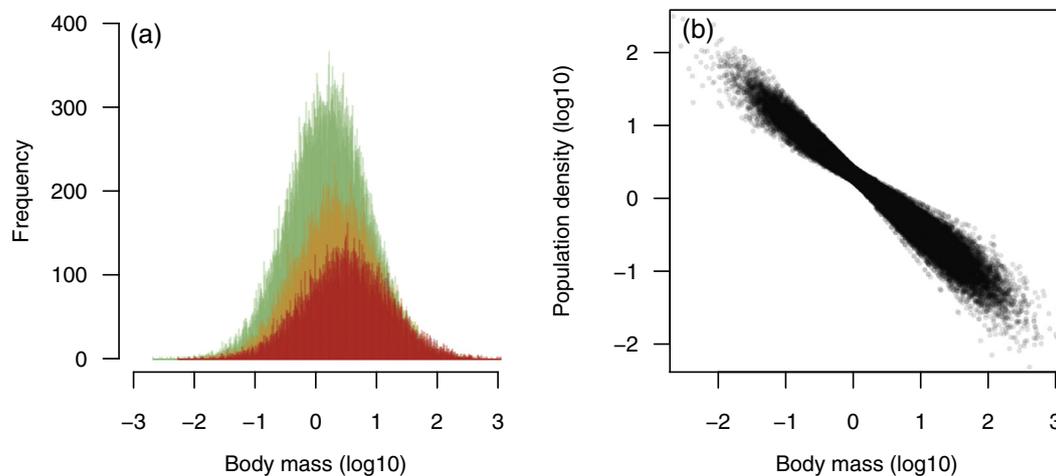


Fig. 1. (a) Distribution of body mass (\log_{10} kg) in the virtual community. (b) Relationship between body mass (\log_{10} kg) and population density (\log_{10} ind/km²). Green = herbivores; orange = omnivores; red = carnivores. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

an additional scenario of stochastic demographic fluctuations (see Section 2.4; Table 1). The simulations consisted of 10 time steps, whereby the first step represented the initial community and the nine subsequent time steps were used to simulate change until reaching an equilibrium (e.g. extinction of a given group of species). Each scenario was deterministic, but was replicated 1,000 times over independently sampled initial communities to account for stochasticity in the simulation parameters (% of forest, body-mass distribution, density distribution, diet categories distribution, and habitat preferences).

2.3. Diversity metrics

We recorded a set of metrics (Table 2) encompassing change in community composition from an initial community (temporal turnover), species abundance, taxonomic diversity, functional diversity and phylogenetic diversity. The set included 12 metrics: Sørensen similarity to the species composition of the original community (i.e. time step 1), arithmetic mean abundance, geometric mean abundance, species richness, Simpson diversity index, Shannon index, Faith's phylogenetic diversity, weighted Faith's phylogenetic diversity, functional evenness, functional divergence, functional dispersion and functional richness. Functional diversity metrics covered four traits: body mass, diet category, and the affinity levels for the two habitats.

Sørensen similarity index measures the change composition between two or more communities. It is commonly used to compare the composition of different communities in space (β diversity), but can also be used to compare the same community between consecutive time steps, or to a single baseline time period (temporal turnover; Dornelas et al., 2014; Shimadzu et al., 2015). The geometric mean abundance tends to be more sensitive to changes in abundances of rare species than the arithmetic mean, and acts as a composite measure of evenness and abundance (Buckland et al., 2011; Gregory and van Strien, 2010; Gregory et al., 2005; Schipper et al., 2016; van Strien et al., 2012). Because the geometric mean cannot handle zero values, it is common to add a small constant to all values prior to the calculation, and to remove the constant from the result (Buckland et al., 2005, 2011). Here, we added 1 to all abundances prior to the calculation, and removed 1 from the geometric mean. The Simpson and Shannon indices measure species diversity on the basis of species richness and evenness in abundance. Simpson diversity index tends to be more sensitive than Shannon index to the dominant species in the community (Nagendra, 2002). Faith's phylogenetic diversity is calculated as the total length of all branches of the phylogenetic tree linking species in the community (Faith, 1992). The weighted Faith's phylogenetic diversity is weighted by species' relative abundance (Swenson, 2014).

Functional richness represents the amount of functional trait space filled by the community and is calculated as the volume of the convex hull of the trait space (Villéger et al., 2008). Functional dispersion also measures the trait diversity in the community, but differs from functional richness in being less sensitive to outliers. Functional dispersion is calculated as the weighted mean distance in multidimensional trait space of individual species to the weighted centroid of all species, where weights correspond to the relative abundances of the species (Laliberté and Legendre, 2010). Functional evenness describes the evenness of abundance distribution in the functional trait space (Mason et al., 2005). Functional divergence represents how abundance is spread along a functional trait axis, within the range occupied by the community (Mason et al., 2005); it takes lower values when the most abundant species have functional traits that are close to the community centre of functional trait space, and higher when at the extremes.

2.4. Analyses

To quantify the sensitivity of biodiversity metrics under different scenarios, for each of the 1,000 replicates, we fitted a linear regression model between the biodiversity metric values and time (10 time steps). Biodiversity metrics were first standardized to a mean of zero and a SD of one across all replicates and scenarios, to obtain comparable slopes among the metrics under alternative scenarios. Trends are thus represented as standardized slopes, which indicate the rate of change in the metrics. The higher the slope values, the higher the sensitivity of the metrics to a given scenario of biodiversity change. We evaluated the consistency of the slope sign over all replicates, and considered metric responses significantly consistent if the slope sign was the same in >95% of the replicates. Thus, the response of metrics showing significant slopes can be considered more consistent across diverse communities. In order to detect differential abilities of the metrics to catch early (EWS) vs. late warning signals (LWS) of biodiversity change (non-linear responses), we also calculated the standardized slopes for the first two and the following eight time steps separately.

Finally, to compare the metrics' abilities to detect directional changes rather than stochastic fluctuations in species abundances, we computed the signal-to-noise ratio (SNR) by dividing the slope of each replicate under each scenario by the standard deviation of the slopes of all replicates in the scenario of "Neutral community with stochastic fluctuations". SNR was computed only for those metrics that are weighted by species abundance, and not for other metrics such as species richness that are by definition insensitive to stochastic demographic fluctuations unless these lead species to extinction. However, under the "Neutral community with stochastic fluctuations" we assumed

Table 1
Description of the scenarios of biodiversity change. Each of the scenario is simulated for 9 consecutive steps (from the 2nd to the 10th).

Scenario	Description	Rationale
Uniform decline	At each time step all species are reduced by 1/9 of the mean abundance of all species (i.e. species decline at different rates). By the end of the simulation half of the species have gone extinct.	Extreme scenario to investigate metric behaviour where all species are losing the same number of individuals.
Proportional decline	At each time step all species are reduced by 1/9 of their original population size (i.e. species decline at the same rate). By the end of the simulation all species have gone extinct.	General decline of all species, e.g. in response to the loss of natural areas.
Large species decline	At each time step all large species are reduced by 1/9 of their original population size. By the end of the simulation all large species have gone extinct. Large species are defined as those having a body mass larger than the 75th percentile of the body mass of all species in the initial community.	Large species are generally more vulnerable to extinction (Cardillo et al., 2005; Purvis et al., 2000), and are often targeted for subsistence or trophy hunting.
Rare species decline	At each time step all rare species are reduced by 1/9 of their original population size. By the end of the simulation all rare species have gone extinct. Rare species are defined as those having a population size lower than the 25th percentile of the population size of all species in the initial community.	Trophy hunting/collection of rare animals (e.g. seashells, corals, butterflies.), together with higher genetic/demographic or environmental stochasticity, can easily trigger extinction vortex (Courchamp et al., 2006; Gilpin and Soulé, 1986).
Common species decline	At each time step all common species are reduced by 1/9 of their original population size. By the end of the simulation all common species have gone extinct. Common species are defined as those having a population size higher than the 75th percentile of the population size of all species in the initial community.	Common species may be those more commonly hunted/fished. Common grassland species are also impacted by agricultural intensification (Gaston and Fuller, 2008).
Toward evenness	At each time step abundance is added to the rarer and or removed from the more common species. The increase/decrease in abundance was set to 1/9 of the species difference to the mean abundance of the community. By the end of the simulation all species have the same abundance.	The decline of common species may be partly compensated by an increase in rare species (Schipper et al., 2016). We consider an extreme case to assess how metrics respond to an increase in evenness.
Habitat loss	At each time step forest habitat is reduced by 1/9 of its original extent. At each time step species abundance in forest is recalculated according to the new extent. The habitat is not replaced, it is just lost (i.e. converted to unsuitable habitat for all species). By the end of the simulation forest habitat is entirely lost.	Habitat loss is one of the first cause of biodiversity loss (Hoffmann et al., 2010).
Habitat replacement	At each time step, 1/9 of the original forest habitat extent is replaced by grassland. At each time step species abundance is	Often habitat is replaced by habitat suitable to different species. Land cover change can be induced by climate change

Table 1 (continued)

Scenario	Description	Rationale
	recalculated according to the new extent of the two habitats. By the end of the simulation forest habitat is entirely lost and grassland habitat covers the entire landscape.	or human disturbance (e.g. fire).
Invasive species	In the second step a new species (invasive species) is added to the community. The species originally has 1/9th of its potential population size, and at each step it is increased by an additional 1/9th. Meanwhile, a sample of five species in the community (sensitive species), decline by 1/9th of their population size. By the end of the simulation, the invasive species has reached its carrying capacity, while the sensitive species have gone extinct. The invasive species is sampled randomly from ubiquitous species living at high population density (>75th percentile of the population density of all species in the community). Sensitive species are sampled randomly from the community.	Invasive species are one of the main cause of biodiversity loss and homogenization (Hoffmann et al., 2010). We consider the scenario as one case of confounding effect on the metrics due to the population growth of alien species.
Neutral community with stochastic fluctuations	Species abundances fluctuate randomly while the total biomass remains constant, where the extent of the fluctuation depends on species body mass (Brown et al., 2004; Korhonen et al., 2010; Abundance $t = 1 =$ Abundance $t \times \exp[N(\mu = 0, \sigma = 0.1 \times (\text{body_mass}) - 1 / 4)]$; Peters, 1983). When a species is lost from the community, an individual of a species with the exact same characteristics colonizes the community (i.e. trait distribution remains stable).	Demographic stochasticity where species are characterized by demographic rates (Hubbell, 2001; Rossberg, 2013).

that extinctions were compensated by colonizations of species with similar characteristics (see Table 1). We considered the SNR sign significantly consistent if it was the same in >95% of the replicates.

The simulation was entirely done in R v. 3.0.3 (R Core Team, 2016). We calculated the Simpson, Shannon and Sørensen indices using the ‘vegan’ package v. 2.2. (Oksanen et al., 2012), Faith’s phylogenetic diversity using ‘picante’ package v. 1.6 (Kembel et al., 2010) and functional diversity metrics using ‘FD’ package v. 1.0. (Laliberté et al., 2014).

3. Results

3.1. Metric behaviour under alternative scenarios

The diversity metrics exhibited different temporal trends under the nine scenarios of biodiversity change (Figs. 2, 3, Figs. A1–A8). Under the “Uniform decline” scenario, where all species decreased by the same number of individuals and rare species went extinct first, all metrics showed a decrease, especially species richness, functional richness and functional dispersion (Fig. 2). The “Proportional decline” scenario,

Table 2

Description of the diversity metrics employed in the simulation. Ab = population abundance; n_{sp} = number of species; BL = branch length of the phylogenetic tree. In the Sørensen similarity formula: $_1$ = original community and $_2$ = community at time step x .

Diversity metric	Formula/definition	Reference
Sørensen similarity	$x = 1 - \frac{\sum_{i=1}^{n_{sp}} Ab_{i1} - Ab_{i2} }{\sum_{i=1}^{n_{sp}} Ab_{i1} + Ab_{i2} }$	Sørensen (1948)
Species richness	$x = n_{sp}[Ab > 0]$	
Arithmetic mean abundance	$x = \frac{\sum_{i=1}^{n_{sp}} Ab_i}{n_{sp}}$	
Geometric mean abundance	$x = \exp\left(\frac{\sum_{i=1}^{n_{sp}} \ln Ab_i}{n_{sp}}\right)$	
Simpson Index	$x = 1 - \sum_{i=1}^{n_{sp}} Ab_i^2$	Simpson (1949)
Shannon Index	$x = - \sum_{i=1}^{n_{sp}} Ab_i * \ln Ab_i$	Shannon and Weaver (1949)
Faith's phylogenetic diversity	$x = \sum_{i=1}^{NB} BL_i$	Faith (1992)
Weighted Faith's phylogenetic diversity	$x = NB * \frac{\sum_{i=1}^{NB} BL_i * Ab_i}{\sum_{i=1}^{NB} BL_i}$	Swenson (2014)
Functional richness	The convex hull volume of the individual species in multidimensional trait space (Villéger et al., 2008).	Villéger et al. (2008)
Functional dispersion	The weighted mean distance in multidimensional trait space of individual species to the centroid of all species. Weights are species relative abundances (Laliberté and Legendre, 2010)	Laliberté and Legendre (2010)
Functional evenness	The regularity with which species abundances are distributed along the minimum spanning tree which links all the species in the multidimensional functional space (Villéger et al., 2008).	Villéger et al. (2008)
Functional divergence	Species deviance from the mean distance to the centre of gravity weighted by relative abundance within multidimensional trait space (Villéger et al., 2008).	Villéger et al. (2008)

where all species declined but their relative abundance remained unchanged until extinction, was characterized by a decrease in all metrics, especially the Sørensen similarity index, Simpson index and functional divergence (Fig. A1). When common species declined, the Sørensen similarity index and arithmetic mean abundance decreased most, followed by geometric mean abundance and species and functional richness. Conversely, the Simpson and Shannon indices increased, as did functional dispersion, evenness and divergence, and weighted phylogenetic diversity (Fig. A2). In the “Toward evenness” scenario, where the community gradually converged to an even abundance distribution, geometric abundance, richness and functional metrics weighted by abundance increased; arithmetic abundance and species richness remained stable; and Sørensen similarity index decreased (Fig. A4). Both the “Rare species decline” and “Large species decline” scenarios were characterized by a slight decrease in geometric mean abundance, species richness and functional richness (Figs. A3, A5). Under the “Invasive species” scenario, metric responses were weak, with some negative and some positive changes but all close to zero (Fig. A6). In the “Habitat

loss” scenario, where forest extent was gradually decreased, the Sørensen similarity and the arithmetic mean abundance decreased, followed by the geometric mean abundance, species richness and functional richness, while functional dispersion, evenness and divergence, and the weighted phylogenetic diversity (using the trait-based tree) increased (Fig. A7). When the forest habitat loss was replaced by grassland, the metrics behaved similarly to the “Habitat loss” scenario, with the exception of the arithmetic mean abundance, which, despite decreasing, was partly balanced by the increase in abundance of grassland species (Fig. A8).

3.2. Metric sensitivity

In general, the responsiveness of the metrics was mostly determined by the specific change in the community: richness-based metrics (species richness, functional richness, and phylogenetic diversity) showed stronger responses when the change led to a higher number of extinctions, abundance metrics (arithmetic and geometric mean) responded

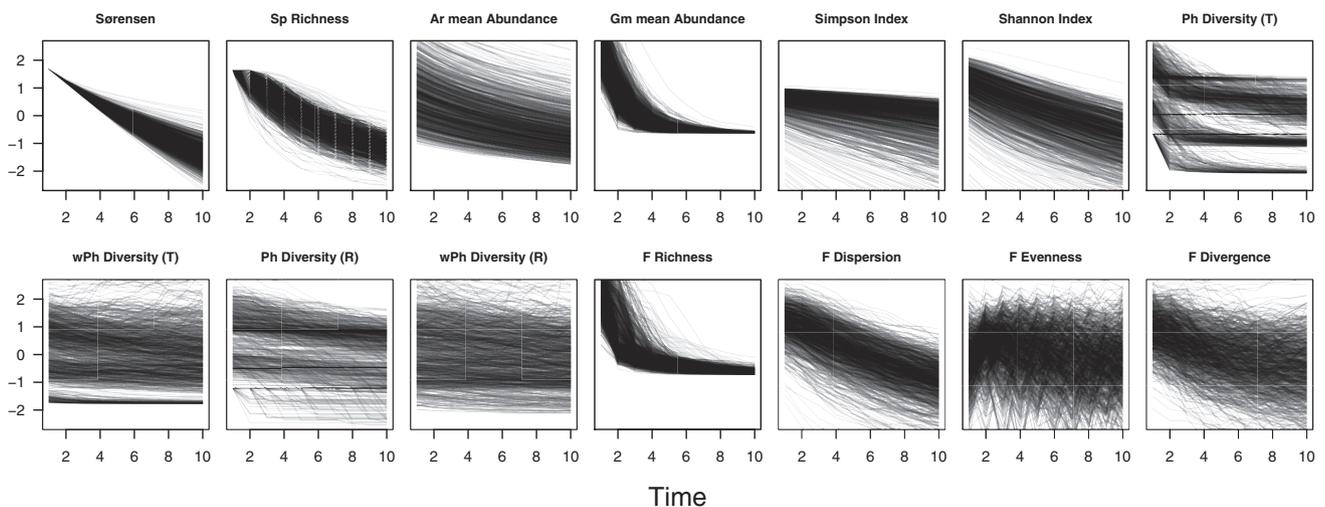


Fig. 2. Temporal trends in biodiversity metrics under the “Uniform decline” scenario. Each line represents one of the 1,000 replicates. Metrics values are standardized on the same scale for comparability (mean = 0; SD = 1). Ar = arithmetic; Gm = geometric; Ph = phylogenetic; Div = diversity; wPh = phylogenetic weighted by abundance; F = functional; T indicates phylogenetic trees based on Traits; R indicates Random phylogenetic trees.

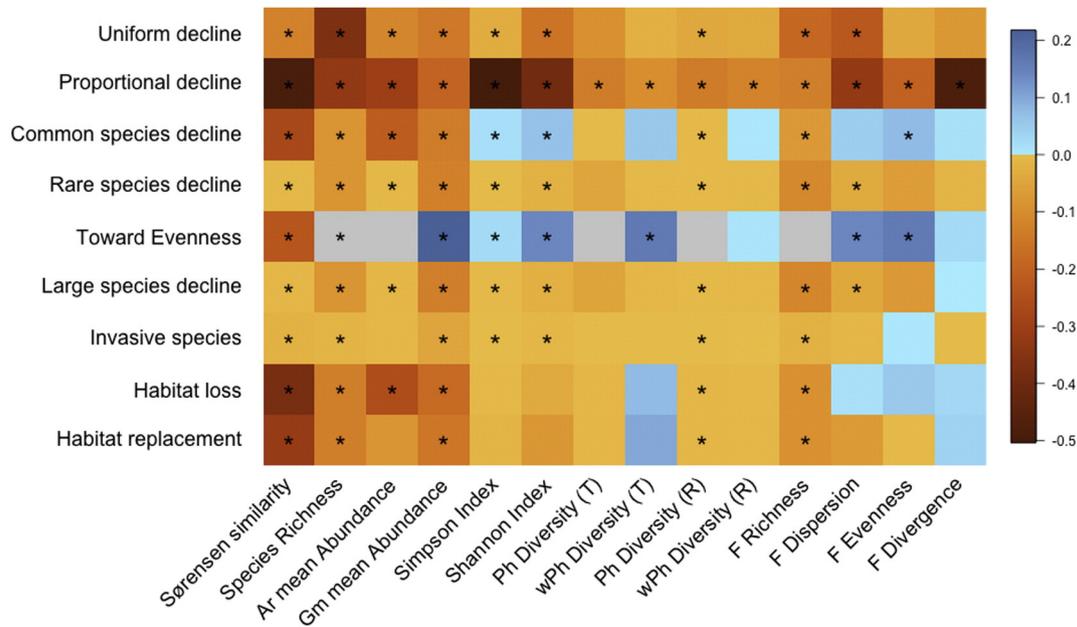


Fig. 3. Heatmap representing the mean trend (standardized mean slopes over time; color bar) of biodiversity metrics for the alternative scenarios of biodiversity change. Standardized slopes represent the rate of change in the metrics. * indicate metrics that show consistent trends (same sign) in >95% of the replicates. The heatmap can be read by row or by column, depending on whether one wants to compare metric behaviour in a given scenario or a given metric's behaviour across scenarios. Ar = arithmetic; Gm = geometric; Ph = phylogenetic; Div = diversity; wPh = phylogenetic weighted by abundance; F = functional; T indicates phylogenetic trees based on Traits; R indicates Random phylogenetic trees. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

strongest when abundance declined in many species, and abundance-weighted metrics (Simpson, Shannon, weighted phylogenetic diversity, and functional dispersion, evenness and divergence) mainly responded

to changes in species abundance distributions. The metrics most sensitive to biodiversity change (i.e., those with steeper slopes) were the Sørensen similarity index, arithmetic and geometric mean abundance,

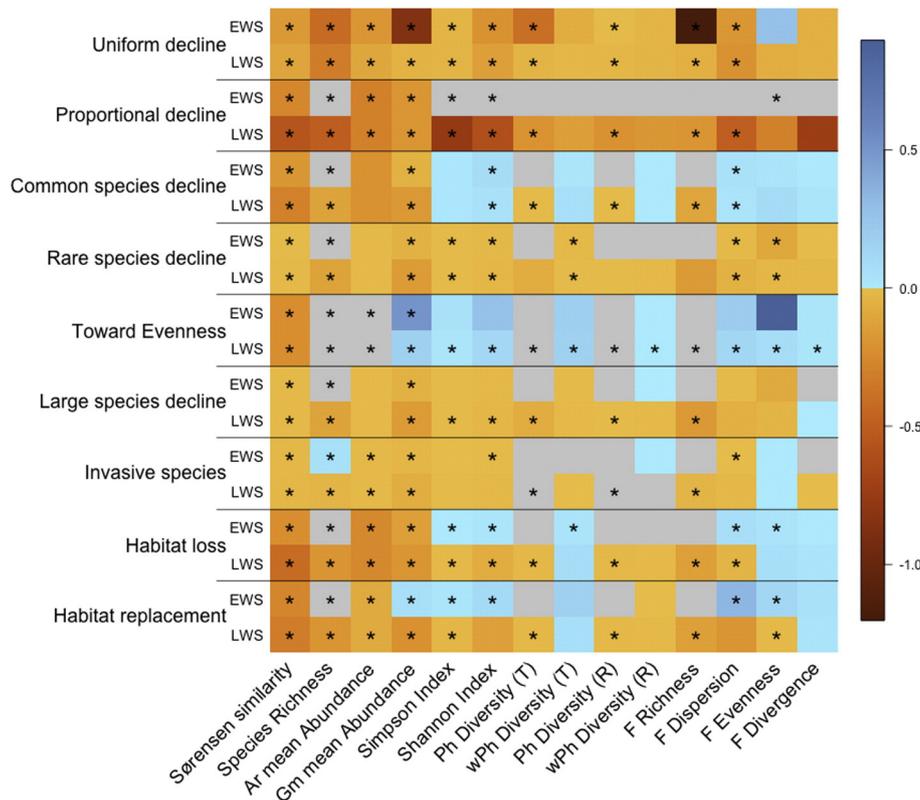


Fig. 4. Heatmap representing the early (EWS) vs. late warning (LWS) signals of biodiversity change for the alternative scenarios of biodiversity change. Both are represented as standardized mean slopes over time, where EWS are calculated in the first 2 steps, and LWS in the second 8 steps. The heatmap can be read by comparing the color (standardized slopes) of EWS and LWS within a given metric for a given scenario; the colors differ if the metric response is non-linear. Ar = arithmetic; Gm = geometric; Ph = phylogenetic; Div = diversity; wPh = phylogenetic weighted by abundance; F = functional; T indicates phylogenetic trees based on Traits; R indicates Random phylogenetic trees. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

species richness and functional richness. The weighted phylogenetic diversity metrics and functional divergence were less sensitive in most scenarios (Fig. 3).

3.3. Metrics' consistency across iterations

Sørensen similarity index, species richness and geometric mean abundance were the only metrics that exhibited consistent responses in >95% of the replicates under all scenarios. Arithmetic mean abundance, Simpson and Shannon indices, and functional richness were consistent in most of the scenarios, whereas phylogenetic diversity, weighted phylogenetic diversity, functional dispersion, evenness and divergence often showed inconsistent responses across replicates (Fig. 3).

3.4. Early versus late warning signals of biodiversity change

Many metrics showed non-linear responses (Fig. 4): some showed convex (accelerating) or concave (decelerating) responses, or inverted their trend. Species richness and functional richness generally showed a convex response, remaining stable until species went extinct. Under the “Proportional decline” scenario all abundance-weighted metrics behaved similarly, with a stable initial pattern followed by a steep decline when species went extinct. Similarly, geometric mean abundance response was stronger at later stages under the “Habitat replacement” scenario. Concave responses were rare, and only occurred in particular instances, such as geometric mean abundance and species richness and functional richness under the “Uniform decline” scenario (Fig. 2). In other instances, the trend reversed during the simulation, for example functional evenness under “Rare species decline” and “Large species decline”, which decreased at first, but increased when species went extinct (Figs. A3, A5). Similarly, under the “Habitat replacement” scenario the geometric mean abundance, Simpson and Shannon indices, and functional evenness and dispersion first increased influenced by grassland species growth, but later decreased as a

consequence of forest species decline and extinction (Figs. 4, A8). Among the metrics considered, Sørensen similarity index and geometric mean abundance showed more consistent responses in the first two and last eight time steps.

3.5. Sensitivity to demographic fluctuations

The metrics which were least confounded by demographic stochasticity (highest SNR) were the geometric mean abundance (to a lesser extent under the “Invasive species” scenario), the functional evenness under the “Proportional decline” and “Toward evenness” scenarios, and the functional divergence under the “Proportional decline” (Fig. 5). The other metrics did not show evident differences in SNR. The SNRs of the Sørensen similarity index and the geometric mean abundance exhibited consistent responses under all scenarios. Arithmetic mean abundance was also fairly consistent in most scenarios, whereas Shannon and Simpson indices, weighted phylogenetic diversity and functional dispersion, divergence and evenness were often inconsistent.

4. Discussion

Simulating biodiversity change through time allowed us to explore the behaviour of a set of biodiversity metrics and assess their suitability for monitoring biodiversity change, including declines in species' abundances that can be of conservation concern. Richness-based metrics require presence data, which is less time-consuming and costly to collect than abundance data (Costello et al., submitted for publication). Knowing which species are present, particularly those that are ecologically important, or may be of conservation concern, is fundamental to biodiversity data analysis (Asaad et al. submitted for publication; Latombe et al. 2016). Functional richness can also provide important complementary information that can be more directly related to ecosystem function and stability. However, richness-based metrics are not sufficient on their own for biodiversity monitoring, because they only respond to

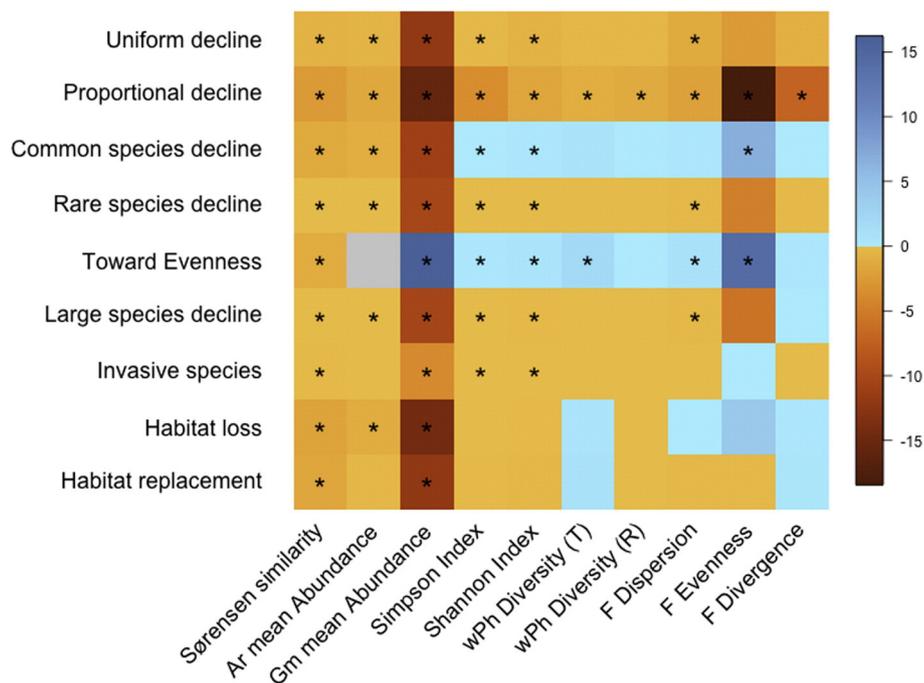


Fig. 5. Heatmap representing signal to noise ratio (SNR) (color bar) of biodiversity metrics weighted by abundance for alternative scenarios of biodiversity change. SNR is the strength of the signal (biodiversity change measured as standardized slopes) relative to the noise in the metric resulting from demographic fluctuations (SD in metric values under the “Neutral community with stochastic fluctuations” scenario). * indicates SNR that shows consistent trends (same sign) in >95% of the replicates. The heatmap can be read by row or by column, depending on whether one wants to compare metric behaviour in a given scenario or a given metric's behaviour across scenarios. Ar = arithmetic; Gm = geometric; Ph = phylogenetic; Div = diversity; wPh = phylogenetic weighted by abundance; F = functional; T indicates phylogenetic trees based on Traits; R indicates Random phylogenetic trees

species extirpations or colonizations. Hence, they are inadequate for detecting early warning signals of biodiversity change.

The Sørensen similarity index was used as a temporal beta-diversity index, and showed high sensitivity to changes, as it detects any change in composition and abundance of the species relative to the initial community. The extent of its change is proportional to the magnitude of the change, which, although desirable in some instances, may underestimate small but significant change. For example, the decline of elephants in Savanna would have little impact on the Sørensen similarity index, but potentially large indirect impacts on the habitat structure and the community. Interpretation of why this, and other beta-diversity indices, are changing requires knowing which species occurrences and abundances are changing.

Abundance metrics are appealing for biodiversity monitoring, because a change in abundance of one or more species may lead to a change from one community to another, may reflect the decline or recovery of a threatened species, or an alien species becoming invasive. However, trends in population abundance can be easily confounded by two factors: demographic and environmental stochasticity, and abundance compensations. Populations of some species, such as microbes, invertebrates and plants, may live at high population densities and fluctuate by orders of magnitude due to natural reproductive cycles and weather events (Damuth, 1987; Sinclair, 2003). As a consequence, such species may dominate the arithmetic mean abundance of a given community, either being common or during outbreaks, and can easily confound temporal trends by natural demographic fluctuations. In this respect, the geometric mean abundance appears to be more useful by being more sensitive to the rare species of the community (van Strien et al., 2012), whether this is because they live at low densities or are close to extinction. Less abundant species, such as top predators or large herbivores, may be keystone species (Estes et al., 2011; Leleu et al., 2012; Ripple et al., 2014, 2015) that tend to be more vulnerable to extinctions (Cardillo et al., 2005; Purvis et al., 2000) and hence deserve particular conservation attention. On the other hand, small common species may be fundamental for ecosystem functioning and services (Gaston and Fuller, 2008).

Abundance compensation may occur, for example when the increase of one species leads to the decline of another (e.g. invasive species), or conversely when the decline of one species prompts the increase of another one (e.g. competitive release), or just by the occurrence of two simultaneous but unrelated events. In any of these cases, arithmetic mean abundance may be easily confounded, while geometric mean abundance would respond by being sensitive to the change in the rarer of the two species. An example is given by the “Toward evenness” scenario where the arithmetic mean was unresponsive, but the geometric mean abundance increased in response to the growth of populations of rare species. For these reasons abundance metrics on their own may not provide sufficient information for biodiversity monitoring. It is therefore essential that the identities of the species whose abundance is changing are also recorded.

Abundance-weighted heterogeneity indices carry more information than richness alone and are sensitive to population changes. However, their weighting of richness and relative abundance varies (Magurran, 2004) and these components can vary independently (e.g. Costello and Myers, 1987). Thus they may exhibit counter-intuitive trends and non-linear responses. An illustrative example is presented by the Shannon and Simpson indices, which increase if common species decline but abruptly change when these species go extinct (Fig. A2). This questions the reliability of such metrics for biodiversity monitoring (van Strien et al., 2012). In addition, our results question the validity of such metrics for the comparison of the biodiversity state between biological communities. Evenness is certainly an aspect of diversity, but we should also recognize that abundance distributions are naturally skewed (Magurran and Henderson, 2003) and an increase of evenness does not necessarily indicate greater ‘biodiversity’ (Schipper et al., 2016; van Strien et al., 2012). This problem is further exacerbated in metrics

that cannot account for extinct species, such as functional diversity metrics (i.e. that do not allow for zero abundance values). Functional diversity metrics weighted by abundance might increase after the loss of rare and particular species (in terms of traits), thus leading to the conclusion that an impoverished community is actually more diverse than an intact community. All in all, we consider that phylogenetic and functional diversity metrics can only be informative when considered in relation to the more fundamental variables of species composition, richness and abundance and where they have been studied for long enough to relate their dynamics to actual changes in community structure.

In this study, we employed a simplified model of biological communities where the decline or loss of a certain biodiversity component does not prompt an increase or decrease in another. Such interactions can be highly complex and unpredictable (Rossberg, 2013; Yodzis, 1988), and are likely to complicate interpretation. The trends that we have depicted are thus useful to investigate metrics’ behaviour under controlled conditions, but may not be considered realistic representations of community change under specific pressures. We considered one form of noise deriving from population demographic stochasticity, but in practice, another form of noise is errors in abundance estimates due to e.g. detection bias. The influence of error in abundance estimates on diversity metrics is treated in Lamb et al. (2009). In our simulations, we simulated communities characterized by certain macroecological patterns in order to simulate realistic species assemblages (e.g. body mass distribution, trophic levels, and body mass-density relationship). However in practice, another source of uncertainty is the choice of the empirical sample of species monitored (Maurer and McGill, 2011). These samples often focus on a given taxon or are collected on an opportunistic basis. Further research is needed to investigate the extent to which incomplete samples can inform about overall changes in a biological community.

The Convention on Biological Diversity (CBD) has renewed the commitment to halt or at least reduce the rate of biodiversity loss (CBD, 2010). To this end, it is necessary to collect biodiversity data in a systematic way, capturing those key biodiversity dimensions that allow us to monitor biodiversity change through time (Pereira et al., 2013), and prevent further biodiversity loss by prioritizing conservation funding and actions. Our results clearly indicate that no single metric should be employed for biodiversity monitoring. However, Sørensen similarity index and geometric mean abundance share several ideal properties for biodiversity monitoring such as the sensitivity to most scenarios of change, consistency in their responses irrespective of the original community composition, the ability to capture early signals of biodiversity change, and robustness to demographic stochasticity. Species richness and functional richness also share several of these properties. Therefore we recommend that biodiversity monitoring include the following primary data: (1) presence of species in the community (i.e. species composition), and (2) species abundance. From these at least the geometric mean abundance, Sørensen’s similarity index (or similar turnover measures) and species richness should be calculated. While metrics such as phylogenetic and functional diversity may also be useful, scientists should consider whether they provide added value in terms of conveying useful information to end-users such as conservation managers. For example, phylogenetic diversity and functional richness are often correlated with species richness (Schipper et al., 2016). Generally, a small set of complementary and conceptually simple metrics is more transparent, intuitive and informative for policy makers on the underlying causes of changes in biodiversity (e.g. Latombe et al., 2016 for invasive species).

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2016.08.024>.

Acknowledgements

We thank R D Gregory and another anonymous reviewer for providing constructive comments on earlier versions of the manuscript. This

article is based upon work from COST Action ES1101 “Harmonising Global Biodiversity Modelling” (Harmbio), supported by COST (European Cooperation in Science and Technology).

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