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RESEARCH ARTICLE*

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Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring

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Abstract

1. Global concern about human impact on biological diversity has triggered an intense research agenda on drivers and consequences of biodiversity change in parallel with international policy seeking to conserve biodiversity and associated ecosystem functions. Quantifying the trends in biodiversity is far from trivial, however, as recently documented by meta-analyses, which report little if any net change in local species richness through time.
2. Here, we summarise several limitations of species richness as a metric of biodiversity change and show that the expectation of directional species richness trends under changing conditions is invalid. Instead, we illustrate how a set of species turnover indices provide more information content regarding temporal trends in biodiversity, as they reflect how dominance and identity shift in communities over time.
3. We apply these metrics to three monitoring datasets representing different ecosystem types. In all datasets, nearly complete species turnover occurred, but this was disconnected from any species richness trends. Instead, turnover was strongly influenced by changes in species presence (identities) and dominance (abundances). We further show that these metrics can detect phases of strong compositional

shifts in monitoring data and thus identify a different aspect of biodiversity change decoupled from species richness.

4. *Synthesis and applications*: Temporal trends in species richness are insufficient to capture key changes in biodiversity in changing environments. In fact, reductions in environmental quality can lead to transient increases in species richness if immigration or extinction has different temporal dynamics. Thus, biodiversity monitoring programmes need to go beyond analyses of trends in richness in favour of more meaningful assessments of biodiversity change.

KEYWORDS

biodiversity change, biodiversity loss, diversity, dominance, human impact, monitoring, richness, species composition, species turnover, time series

1 | INTRODUCTION

Human modification of Earth's ecosystems has led to altered biodiversity in many regions of the world, across marine, terrestrial and freshwater ecosystems, and further shifts are expected as a consequence of rapid environmental change (Sala et al., 2000). Research has documented declining state variables of biodiversity such as increasing numbers of endangered (red-listed) species (Butchart et al., 2010) or decreasing abundance of key organism groups (Lotze et al., 2006). These changes in biodiversity have led to what is often called a “biodiversity crisis,” with warnings that current rates of extinctions are exceptionally high (Mace et al., 2005; Pimm et al., 2014), indicating a global mass extinction phenomenon (Barnosky et al., 2011, 2012).

Science and policy have responded to the need to address the extent of biodiversity change, the drivers of this change and its functional consequences. Most prominently, these efforts have led to the formulation of the Aichi biodiversity targets under the umbrella of the Convention on Biological Diversity (CBD), aiming to halt further biodiversity decline by 2020 (Tittensor et al., 2014). Important components of these assessments are international agreements on monitoring and systematically reporting the status of ecosystems and biodiversity (Pereira & Cooper, 2006), which in Europe are exemplified by the Water Framework Directive and the Marine Strategy Framework Directive (Borja, Elliott, Carstensen, Heiskanen, & van de Bund, 2010; Hering et al., 2010). While it is clear that documenting and understanding biodiversity change is critical to these assessments, there is little agreement on how to monitor and quantify biodiversity change (Buckland, Magurran, Green, & Fewster, 2005; Hill et al., 2016; Proença et al., 2016; Vačkář, Ten Brink, Loh, Baillie, & Reyers, 2012).

Although there is little doubt that biodiversity is declining at the global scale, assessing biodiversity change at scales smaller than the globe is not as straightforward as often assumed (McGill, Dornelas, Gotelli, & Magurran, 2015). Indeed, a series of recent publications synthesising time series on biodiversity change have suggested that local-scale biodiversity—typically measured as species richness—is not systematically declining (Dornelas, Gotelli, et al., 2014; Elahi et al., 2015; Vellend et al., 2013). The results of these meta-analyses have been criticised for a variety of technical issues (Gonzalez et al., 2016; see reply by Vellend et al., 2017), and other meta-analyses have shown decreasing trends of local species richness in the face of intensive land-use (Newbold et al., 2015). Nevertheless, it is evident that local species richness does not always, or even often, decline in concert with global biodiversity loss. Even positive trends have been observed in multiple time series, likely as a result of global change leading to favourable conditions for multiple species, whereas negative trends occurred only in subsets with distinct negative human impacts (Elahi et al., 2015). Likewise, the rate of introduction of alien species often exceeds the (either consequent or independent) rate of extinction of native species in the same habitat (Ellis, Antill, & Kreft, 2012; Sax, Gaines, & Brown, 2002), leading to stasis or increases in local biodiversity.

On the surface, the result that the most commonly used metric to detect biodiversity trends—species richness—does not appear to be systematically declining locally might be taken to suggest that the “biodiversity crisis” has been overblown, or at least is not as straightforward as often implied (Thomas, 2013; Vellend, 2017). On the contrary, however, we posit here that the paucity of empirical evidence for biodiversity change stems from the widespread use of inadequate tools to capture and quantify the ongoing change caused by humans, rather than the non-existence of exceptional biodiversity change. It is important to note that biological diversity is a multifaceted construct, which includes (according to the CBD) “the variability among living organisms […] and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.”

Biodiversity thus not only includes richness, i.e., the number of species, but also aspects of identity, dominance and rarity. Consequently, biodiversity *change* comprises more than a reduction in species richness; for example, the decline of long-lived foundation species and their replacement by smaller, weedy ones (Lotze et al., 2006) may not change total species number, but changes the identity of species and consequently the functional traits (structure, longevity) associated to these. Thus, even if local extinction is balanced by immigration, the extinction is not random with regard to identity and functional performance, such that changing composition will have major consequences for ecosystem functioning. There are many tools already being developed allowing better interpretation of patterns in temporal biodiversity, including scale-explicit approaches and those that include functional, phylogenetic and genetic information (Hill et al., 2016; Pereira et al., 2013; Scholes & Biggs, 2005). Rather than reinventing such measures, which are available for change in taxonomic (Chao, Chazdon, Colwell, & Shen, 2005; Magurran et al., 2010) or functional composition (Petchey & Gaston, 2002), our emphasis here is primarily on establishing an interpretation framework for monitoring data on biodiversity change that moves away from a focus on changes in species richness and towards a more robust, management-relevant measure of change.

Monitoring agencies, which provide the primary information for assessing biodiversity status and trends, face the inherent problem of how to detect multiple aspects of biodiversity change and how to disentangle phases of rapid compositional shifts from naturally occurring turnover in species composition. This is especially linked to the demand for managing ecosystems towards an unimpaired environmental status, as biodiversity trends are used as an indicator of changes in environmental quality, responding to impacts (e.g. the use of natural resources) and protection measures (e.g. a restoration project).

In the following sections, we briefly summarise the known limitations of species richness as a biodiversity metric in general, and present a simple simulation showing that richness trends (negative, neutral or positive) carry incomplete information on biodiversity change and serve as limited indicators of ecosystem status, because a directional change in environmental quality does not necessarily lead to corresponding trends in species richness. Using these same data, we identify an approach that can be implemented for readily available monitoring data to quantify different aspects of biodiversity change. This quantification of temporal dynamics in the number and identity of species as well as their relative dominance will assist managers in early detection and mitigation of biodiversity changes.

1.1 | Trends in richness do not capture biodiversity change

Biodiversity is a multifaceted construct, comprising genetic, taxonomic, phylogenetic and ecological components. Unfortunately, a single facet of biodiversity, species richness, has become the most dominant measure of biodiversity and its change (Appendix S1), as it is easily observed and recorded, making it a relatively affordable means to monitor change in natural ecosystems. This superficial ease of calculation is misleading as richness poses a number of technical, statistical and ecological issues which have frequently been raised in the scientific literature (e.g. Brose, Martinez, & Williams, 2003; Gotelli & Chao, 2012; Gotelli & Colwell, 2001; Magurran, 2004). Technically, taxonomic resolution differs among—and even within—monitoring programmes, as categorisation or taxonomic knowledge changes over time (Pomati et al., 2015).

Statistically, there are two interrelated problems that render analyses of changes in species richness quite limited. First, species richness is a highly scale-dependent measure owing to the ubiquitous species-area relationship (Drakare, Lennon, & Hillebrand, 2006; Jost, 2007; Lande, 1996). As a result, any comparisons of species richness from different sites or time periods will depend on the scale at which observations are made (e.g. Chase & Knight, 2013; Powell, Chase, & Knight, 2013). Keeping the sampling scale constant does not suffice to make the absolute difference in species richness among sites or time periods comparable when the size of the regional species pool differs, as the same observed absolute change creates a higher relative difference in a community consisting of a few species than in a diverse community (e.g. Chao and Jost, 2012; Chase & Knight, 2013).

Second, at any given scale, species richness estimates vary with changes in one or more of the following four components: (1) the total abundance of individuals (i.e., the more individuals hypothesis), (2) the relative abundance of individuals, including their dominance or evenness (i.e., the SAD, species abundance distribution), (3) the intraspecific spatial aggregation (clumping) of individuals and (4) the total number of species in a given spatial extent (Chase & Knight, 2013; He & Legendre, 2002; McGill, 2011). Thus, simply comparing changes in species richness, or the lack thereof, tells us little about which of the components that underlie species richness estimates actually changed (i.e., whether the numbers of rare species, the numbers of individuals or the entire SAD changes) (Collins et al., 2008; Hallett et al., 2016).

Ecologically, changes in species richness and its underlying components (i.e., the shape of the SAD) do not necessarily correlate with species compositional turnover, which can be a strong indicator of how communities respond to global change. The lack of a temporal trend in species richness (e.g. Dornelas, Gotelli, et al., 2014; Elahi et al., 2015; Vellend et al., 2013) does not mean that species composition remains unchanged, but only that immigration and extinction events are equally frequent. Indeed, the above mentioned meta-analyses all mention this fact and Dornelas, Gotelli, et al. (2014) provide an explicit analysis showing large changes in species composition over time despite relative stasis in species richness (see also Brown, Ernest, Parody, & Haskell, 2001; Supp & Ernest, 2014).

The rates of change in species composition are often decoupled from changes in richness for a number of reasons. First, immigrations and extinctions can be equally high, leading to strong—even complete—turnover with little concomitant change in species richness. This can happen both for stochastic reasons, as in the case of the MacArthur and Wilson's (1967) equilibrium theory of island biogeography (Brown et al., 2001; Diamond, 1969), or for deterministic reasons if environmental change favours some species, and disfavours others, but the equilibrium numbers of species remains the same (Dornelas, Gotelli, et al., 2014). Second, species immigrations can exceed extinctions, for example, if human-mediated dispersal of alien organisms is high (Sax et al., 2002), or global changes allow species to invade areas in which they previously could not persist (Elahi et al., 2015). Here, we would expect high rates of turnover and increases in species richness. Third, extinctions can exceed invasions, for example, when global changes make sites less favourable to species in the pool or reduce the number of potential niches (Harpole et al., 2016; Newbold et al., 2015). Here, we would expect high turnover and decreases in species richness.

In a monitoring context, it is important to acknowledge that such expected increases or decreases in species richness would not necessarily be seen until the system reached equilibrium, which can take a long time or may not occur at all in a continuously changing environment. During the transient phase towards an increase or decrease in equilibrium species richness, the differential rates in which immigrations and extinctions occur can create biased estimates of short- and long-term trends of species richness. For example, colonising species increase species richness as soon as the first individual is recorded, while species loss is often slower because it involves population dynamics leading to local extinction, a phenomenon described as extinction debt (Ewers & Didham, 2006; Jackson & Sax, 2010; Tilman, May, Lehman, & Nowak, 1994). Alternatively, there can also be a lag in immigration in isolated habitats or when colonising taxa have low dispersal ability (Isbell, Tilman, Polasky, Binder, & Hawthorne, 2013; Seabloom et al., 2006), known as immigration credit (Jackson & Sax, 2010).

These considerations are highly relevant for monitoring biodiversity change, which often is explicitly motivated by a need to assess the impact of human actions on biodiversity or the success of ecosystem management and restoration. In cases with extinction debt or immigration credit, short-term changes in species richness (stasis, increase or decrease) can be uncorrelated with the long-term expected changes in equilibrium species richness in the system. We provide a simple simulation describing three relevant biodiversity scenarios: an environmental change that eventually decreases richness (e.g. fragmentation, exploitation), an environmental change that eventually increases richness (e.g. restoration, protection), and a neutral change (Appendix S2). The model shows that the trajectory towards a new equilibrium richness can be highly nonlinear as soon as time-lags between immigration and extinction prevail. Monitoring richness over time will reflect temporal delays in immigration and extinction rates rather than a new equilibrium state of biodiversity if the assessment period is short in relation to the time-lag. But even if the monitoring continues over time, the nonlinear trajectory will by itself lead to inconspicuous slopes when regressing richness linearly (Vellend et al., 2013) or monotonically (Elahi et al., 2015) over time. Analysing species richness over time is therefore not sufficient to monitor biodiversity trends, because the observed positive or negative trends do not allow for making inferences on the quality of environmental change. Although this point has frequently been made (Buckland et al., 2005; Magurran et al., 2010), the current discussion on richness trends shows that these warnings have not been acknowledged in practice.

1.2 | Establishing a framework for measuring and interpreting biodiversity trends

To be effective, a biodiversity monitoring strategy has to overcome the limitations of comparing patterns of species richness through time, while recognising that assessment programmes will have limited resources and must make decisions within reasonable time horizons. One useful approach to understanding biodiversity change is through estimates of biodiversity turnover reflecting both immigration and extinction, often in a closed range of values (e.g. between 0 and 1 for no to complete exchange of species) and—depending on metrics—reflecting shifts in relative dominance (Chao et al., 2005; Collins, Micheli, & Hartt, 2000; Magurran et al., 2010; Shimadzu, Dornelas, & Magurran, 2015). For example, while the meta-analysis by Dornelas, Gotelli, et al. (2014) showed that there was little signal in the directional change in species richness through time, they found high levels of turnover that appeared to occur more rapidly than could be explained by a simple random drift (neutral) model, implying that community turnover was likely directional (e.g. due to anthropogenic factors). Here, we integrate existing metrics of compositional change into an easily interpretable framework of biodiversity change for monitoring programmes.

The framework provides an interpretation guideline for assessing temporal dynamics of biodiversity within local habitats. We start by introducing two measures of temporal turnover out of a wide range of established metrics of dissimilarity (Magurran & McGill, 2011). As these and related measures are used to quantify different aspects of compositional change in spatial and temporal contexts, we introduce the general term “species exchange ratio” (SER) here to clarify its purpose in the context of monitoring as measuring the proportional exchange of species between an earlier and later sample in a time series.

The simplest way to quantify the overall change in species composition is to measure the sum of immigrations and extinctions as a fraction of the total number of species, which is the complement of Jaccard’s similarity index (Jaccard, 1912), a commonly used metric in biodiversity change studies (Dornelas, Gotelli, et al., 2014; Hallett et al., 2016; Korhonen, Soininen, & Hillebrand, 2010). This richness-based species-exchange ratio, SER_r, is quantified as

$$\mathrm{SER}_r = \frac{S_{\mathrm{imm}} + S_{\mathrm{ext}}}{S_{\mathrm{tot}}} \tag{1}$$

where S_{imm} is the number of species immigrating (newly recorded in the later sample), S_{ext} is the number of species extinct (lost from the previous sample) and S_{tot} is the total number of species across both samples. Such a presence-absence based SER quantifies the gross change in species composition ($S_{\mathrm{imm}} + S_{\mathrm{ext}}$) rather than the net change (Δrichness = $S_{\mathrm{imm}} - S_{\mathrm{ext}}$) on a closed scale between 0 and 1, where 0 means all species persist and 1 all species are exchanged.

Nevertheless, the SER based on species presence-absence suffers from some of the limitations that hamper the assessment of species richness as well: it is particularly sensitive to sample size, changes in rare species and species pool size, limiting the utility of such measures used in isolation (Chao et al., 2005; Chase, Kraft, Smith, Vellend, & Inouye, 2011; Magurran & McGill, 2011). A more robust approach for detecting compositional change through time, therefore, should focus on the differences between species proportional abundances, p_i and p_i', in the first (time 1) and second (time 2) community, respectively. Again, multiple formulations for such abundance-weighted dissimilarities exist (Magurran & McGill, 2011). Here, we use a complement to Wishart’s similarity ratio (Jongman, Ter Braak, & van Tongeren, 1995; Wishart, 1969), as it is closely related to Simpson’s diversity index and the concept of “effective” species numbers (Chase & Knight, 2013; Tuomisto, 2010). Simpson’s diversity is less sensitive to rare species, and more sensitive to changes in evenness of common species. Thus, using a Simpson-based turnover index captures the changes of relative abundances and identity of the most dominant species in the community. Substituting the effective species numbers into Equation 1, we obtain SER_a as a measure of turnover by changes in species proportional abundances (for the math, see Appendix S3).

$$\mathrm{SER}_a = \frac{\sum_i (p_i - p_i')^2}{\sum p_i^2 + \sum p_i'^2 - \sum p_i p_i'} \qquad (2)$$

Like the presence-absence based SER_r, SER_a approaches 0 if the species identity and dominance structure does not change and 1 if all species are replaced. Furthermore, it reduces to the SER_r when species in each sample are equally common.

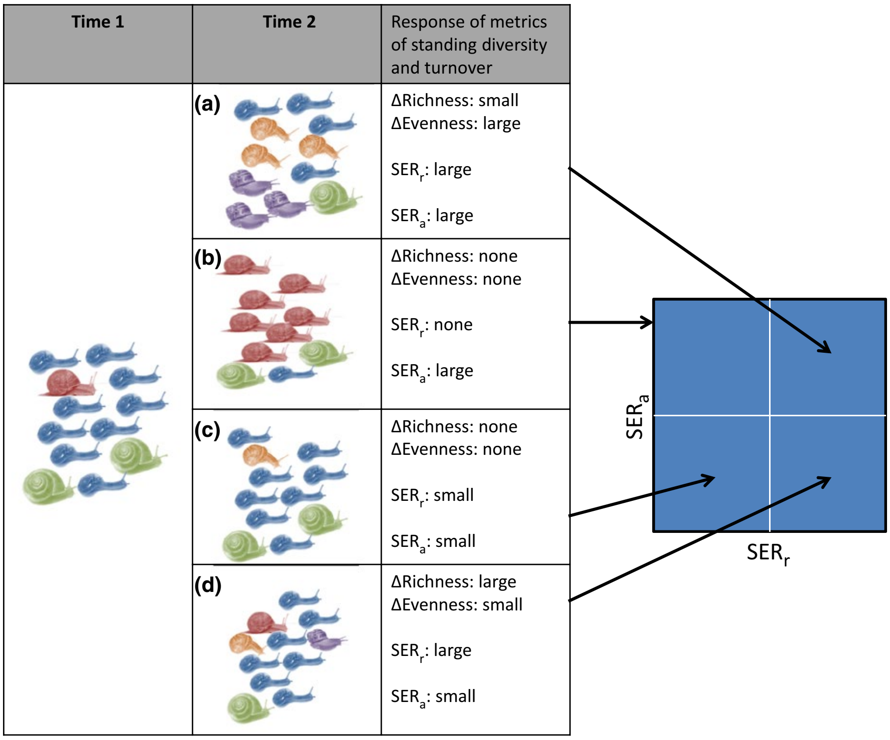
The utility of turnover approaches resides in the quantification of gross changes in biological composition. The interpretation of the turnover estimates is especially useful if compared to a null model (see Dornelas, Gotelli, et al., 2014), as this allows explicit tests of turnover rates that differ from a null expectation based on random population fluctuations. Thus, null model analyses allow directional shifts to be disentangled from stochastic change. However, such null model analyses often go beyond the analytical tools regularly established in monitoring programmes as well as the time and personnel that can be allocated to such analyses. Another advantage of turnover approaches is that the rate of change in composition can be related to the rate of change in environmental variables, reinforcing the need to incorporate environmental context data into monitoring programmes.

Even without a null model, however, the direct comparison of SER_a and SER_r has a strong indicator value for biodiversity changes, which we exemplify in different scenarios of temporal changes (Figure 1). Large values of both SER_a and SER_r (scenario a) indicate that species immigrated or were replaced (SER_r) and at the same time the dominance structure of the community changed (SER_a). By contrast, a shift in dominance structure without immigration or extinction (scenario b) results in large abundance-based turnover but no richness-based turnover, whereas the opposite scenario (c: replacement of a rare species) will lead to zero to low SER_a and—depending on the number of species present—low to medium values of SER_r. Immigration of several new, initially rare species (cf. Appendix S2) leads to large SER_r but small SER_a values (scenario d). The complementary information provided by the SER metrics is loosely similar to the decomposition of the Bray–Curtis index into balanced variation in abundance and abundance gradients (Baselga, 2013), except that both SER focus specifically on the dynamic of species immigration and extinction and are therefore insensitive to variation in absolute species abundance. Thus, the quadrants of the correlation of both SER can be interpreted as combinations of identity and dominance shifts, which all are poorly linked to any changes detected in richness or other diversity indices.

2 | MATERIALS AND METHODS

2.1 | Cases studies: Approach, analyses and data

To illustrate our suggested approach, we analysed three observational datasets as test cases. All three datasets have been established to uncover changes in species composition over time and are characterised by internally consistent standards regarding sampling, analysis and taxonomic resolution. The datasets report on the presence and abundance of autotrophs representing primary producers in marine, freshwater and terrestrial ecosystem types. This cross-system approach was



Time 1	Time 2	Response of metrics of standing diversity and turnover
	(a)	ΔRichness: small ΔEvenness: large SER_r: large SER_a: large
	(b)	ΔRichness: none ΔEvenness: none SER_r: none SER_a: large
	(c)	ΔRichness: none ΔEvenness: none SER_r: small SER_a: small
	(d)	ΔRichness: large ΔEvenness: small SER_r: large SER_a: small

FIGURE 1 Guideline to interpretation of biodiversity change. Starting from an initial community (Time 1), we envision four pathways of changing community composition (Time 2): (a) Simultaneous shift in species identity and dominance structure. (b) Change in dominance structure without species replacements. (c) Replacement of a rare species without changes in the dominance structure. (d) Immigration of multiple rare species without extinction (cf. Appendix S2). For each scenario, we qualitatively describe the response of different metrics of biodiversity change and visualise the expected association of SER_a and SER_r. [Colour figure can be viewed at wileyonlinelibrary.com]

intended to show the versatility of the framework for management of organisms of different generation times. For both phytoplankton datasets, we collapsed the multiple values from 1 year into yearly averages to avoid blurring temporal trends by seasonal dynamics. Moreover, we avoided changes in SER being driven by species blinking in and out at the detection limit of a single sampling event, as small species often have a low predictability of occurrence (Soininen & Luoto, 2014). Consequently, the annual $\mathrm{SER_r}$ measured here is a highly conservative estimate of species turnover, as it was sufficient for a species to be observed in a single sample to be considered present in that year. The terrestrial dataset included annual samples, an appropriate time-scale for the life histories of grassland species. Comparing the absolute values of change in richness or SER between datasets, it should be kept in mind that the same time period means orders of magnitude more generations in the aquatic datasets than in the terrestrial one (see Discussion).

All analyses were performed in R (R Development Core Team, 2015). We first plotted annual richness over time and compared these datasets to the outcome of meta-analyses done on temporal trends of richness (Dornelas, Gotelli, et al., 2014; Elahi et al., 2015; Vellend et al., 2013). We amended the richness trends by analysing the temporal dynamics of annual Simpson diversity ($1 - \Sigma p_i^2$, with p_i = annual proportion of each taxon to total abundance summed across all species in that given year). Simpson indices were calculated in R using the vegan package (Oksanen et al., 2015). We calculated the slopes of richness (raw or log-transfomed as done by the mentioned meta-analyses) and Simpson over time and characterised the temporal dynamics by the median and the 5% and 95% quantiles across sites within a monitoring dataset.

Second, for each year in the monitoring dataset, we recorded the change in richness to all following years and compared this to the quantification of the number of newly recorded species (immigrations) and lost species (local extinctions). This analysis allowed a visualisation of the gross (immigrations, extinctions) and net change (richness) in species composition.

Third, we calculated both turnover metrics ($\mathrm{SER_a}$ and $\mathrm{SER_r}$) from each year to all following years and compared these to the corresponding changes in richness as well as to each other. This assessment allowed explicit tests of the magnitude of changes in composition that can occur in ecological communities without consequently changing species richness. Moreover, the association between turnover metrics differentiated contrasting scenarios of change (Figure 1) in real monitoring datasets. Furthermore, we compared the short-term change in both SER over time to simultaneous changes in richness.

Finally, we asked how biodiversity change accumulates over time by analysing the difference in richness for both forms of SER against the temporal distance between two samples. Thus, each pair-wise comparison between time points within a location was analysed against the temporal distance between the time points (Collins et al., 2000; Dornelas, Gotelli, et al., 2014; McGill et al., 2015). These analyses correspond to the analyses of distance-decay of similarity in spatial and temporal biodiversity analyses (Dornelas, Gotelli, et al., 2014; Korhonen et al., 2010; Soininen, McDonald, & Hillebrand, 2007). The association between community turnover and temporal distance allows disentangling cases in which composition changes directionally or fluctuates without directional shifts. If biodiversity change accumulates over time, we expect a monotonic increase in the average SER with time and the loss of low SER values, because the continuous change does not allow the initial species composition to reappear.

2.2 | Data

2.2.1 | Marine phytoplankton

Samples for marine phytoplankton were taken monthly-bimonthly in Dutch coastal waters at various monitoring stations by the Dutch General Directorate for Public Works and Water Management. We analysed data from the following locations: Rottumerplaat 50 km (53°57′14″N, 6°18′36″E), Noordwijk 70 km (52°34′10″N, 3°31′53″E), Walcheren 70 km (51°57′25″N, 2°40′45″E) and 20 km (51°39′31″N, 3°13′14″E), and Hansweert Geul (51°26′10″N, 4°00′51″E), over the period 2000–2010. Integrated water column samples were taken from the upper mixed layer, fixed with 0.5% Lugol's Iodine solution, and stored and transported in the dark at 4 ± 2°C prior to cell counts. The final dataset includes information on genera or species abundances (534 taxa in total).

All phytoplankton cell counts and identifications were performed by the same laboratory (Koeman & Bijkerk B.V., The Netherlands), following a modified Utermöhl technique based on NEN-EN 15204 (NEN, 2006) using an Olympus IMT-2 inverted microscope. First, smaller phytoplankton cells were identified and counted in five fields of view (FOV) at a magnification of 600×, after which the counting chamber was turned 90° and another 40 FOV were counted. Subsequently, 20 FOV at a 200× magnification were counted after the chamber was turned another 90°. Last, the entire chamber was inspected. The lowest size diameter of cells at each subsample comprised >1, >3, >10 and >20 μm respectively. A minimum of 200 counts were performed per sample, distributed over at least three subsampled size classes.

2.2.2 | Freshwater phytoplankton

Samples for phytoplankton were collected from 131 lakes located within the state of Iowa in the Midwestern United States. Each lake was sampled three times per year, representing early summer, midsummer and late summer growth conditions, from 2001 to 2010, excluding a sampling hiatus in 2008. Phytoplankton samples were collected as integrated water column samples from the surface mixed layer. Phytoplankton samples were preserved in the field following standard techniques (American Public Health Association, 1998) and were stored on ice until arrival at the laboratory.

All phytoplankton cell counts and identifications were performed by the same laboratory (Iowa State University Limnology Laboratory, Ames, IA, USA) following the inverted microscope technique (American Public Health Association, 1998; Lund, Kipling, & Le Cren, 1958). Phytoplankton cells were identified to genus. Biovolume was calculated using standard geometric formulae (Hillebrand, Duerselen, Kirschtel, Pollingher, & Zohary, 1999), with cell dimensions being measured on the first 50 cells or colonies of each genus encountered in each sample. Species proportions were calculated based on biovolume proportions. Phytoplankton cells were counted until 150 individuals of the most abundant genera were counted in each sample. This yielded a total of 158 genera in the dataset.

2.2.3 | Grassland vegetation

This dataset covers 56 herbaceous-dominated terrestrial ecosystems (referred to as "grasslands" for simplicity) spanning 14 countries on six continents sampled for a maximum of 8 years (2007–2015). The dataset thus differs from the others in the spatial extent of the sampling, reflecting different species pools and trajectories of environmental change. Although the data used in this study are observational, all sites are participating in the Nutrient Network global collaborative study (Borer et al., 2014). The per cent cover of all species was visually estimated each year at peak biomass in three 1 m^2 quadrats per site. Only control (unmanipulated) plots for each site were used. There were a total of 361 plot-year combinations in the study, and these data comprised 1,713 unique species. To ensure comparable taxonomy among years and sites, all taxon names were compared to The Plant List (http://www.theplantlist.org/) and corrected for synonymy and spelling prior to inclusion in the dataset (Lind, 2016). Further details on these data are available (Borer et al., 2014).

3 | RESULTS

None of the three monitoring datasets revealed strong temporal changes in annual species richness (Figure 2a–c). From a total of 187 sites across all datasets, the majority (113 sites) showed no significant trend in either richness or log richness. Only for the Iowa lakes, a substantial proportion of the sites showed weak positive trends of richness, the median slopes being <+1 species per year (Appendix Figure S1). Temporal changes in the Simpson diversity index were inconspicuous (Figure 2d–f, Figure S1). 165 sites showed no significant trends across datasets, and those 22 with significant trends were partly negative (eight sites) and partly positive (14 sites).

The number of extinctions and immigrations between years did not vary substantially with time (Figure 2g–i, red and blue bands) either. The absolute magnitude of immigration and extinction was large compared to the standing richness, though. On average, 27.1% of the annual richness was replaced by immigration and 30.7% by extinction in the grassland data (mean across sites, interquartiles 18.1%–36.7% for immigration, 21.3%–38.4% for extinction). In the Iowa lake dataset, mean local extinction corresponded to 39.8% (interquartiles 25.4%–43.2%) of standing richness across lakes and immigrations to 63.5% (interquartiles 58.8%–67.1%). In the taxonomically richest dataset, Dutch coastal phytoplankton, immigration on average was 30.3% (interquartiles 28.3%–32.4%) and local extinction 35.2% (interquartiles 34.2%–35.8%) of annual richness. Given these huge dynamics in species presence, the net change in richness was small (Figure 2g–i, grey bands, means across sites per dataset: −4.3 species per comparison for Dutch phytoplankton, −0.36 for grasslands and +4.6 for Iowa lakes).

Across the datasets, complete or almost complete changes in species inventory were observed without being visible in changing species numbers (Figure 3). The relationship between the absolute change in richness and SER_r was mostly triangle-shaped (Figure 3a–c), with large changes in richness always leading to high SER_r, whereas low (or even no) richness change still corresponded to changes in SER_r between 0.2 and 1. In other words, an almost complete exchange of the species inventory could be observed without a detectable change in richness in all three datasets. Across all sites and temporal comparison, average SER_r ranged from 0.42 (grasslands) to over 0.50 (Dutch phytoplankton) and 0.67 (Iowa lakes), i.e. on average a 42%–67% exchange of species occurred in these ecosystems. The same variance in turnover was observed for SER_a (grand means = 0.39, 0.48 and 0.54 for grassland, Dutch and Iowa datasets, respectively). The variation in SER_a was not related to the absolute change in richness (Figure 3d–f): Across the entire range from zero to intermediate net changes in richness, the SER_a varied across the entire possible range from minimal (0) to maximal (1) values. Consequently, the compositional shifts were not restricted to rare species, but affected the dominance structure at the same time. Comparing richness- and abundance-based SERs suggested that a majority of the temporal comparisons were characterised by large changes in species identity (SER_r) as well as large shifts among the dominant species (SER_a) (Figure 3g–i). In the Dutch phytoplankton and the global grassland data, we observed a positive correlation between both SERs, but in the Iowa phytoplankton data, richness-based and abundance-based assessments were uncorrelated.

Calculating moving averages across time, we found little temporal change in the Δ richness per year in any of the datasets (Figure S2). Turnover estimates, by contrast, showed temporal dynamics, including an initial decline in the abundance-based SER_a in the Iowa lakes and a systematic increase for both SER_r and SER_a in the second half of the observation period (2005–2010) in the Dutch phytoplankton dataset. The latter was caused by a more rapid change in species identity and relative abundance of the dominant species, compared to an inconspicuous trend in species richness.

With increasing temporal distance, species richness showed either increasing (Iowa lakes) or neutral trends (Dutch phytoplankton, global grasslands) (Figure 4a–c). Thus, species richness data indicated a temporal trend of increasing richness in the Iowa dataset, but no accumulated loss or gain of species in the other datasets. By contrast, both SER_a and SER_r increased with increasing temporal distance (Figure 4d–i). The increase in median dissimilarity with time was observed for both measures in all three datasets, but there were differences in the trajectory. For terrestrial plants, median SER_r increased with distance in time, whereas median SER_a increased slowly and levelled off after 4 years (Figure 4f,i). For both phytoplankton datasets, an ongoing accumulation of compositional shifts over time could be observed, which affected the identity of species being present (increasing median SER_r with temporal distance, Figure 4d,e) as well as the identity and dominance structure of the most abundant species (increasing SER_a with temporal distance, Figure 4g,h). For SER_r, a strong increase in the lower (5%) quantile was visible as well; thus, at longer time intervals, species composition was directionally shifted away from the starting composition.

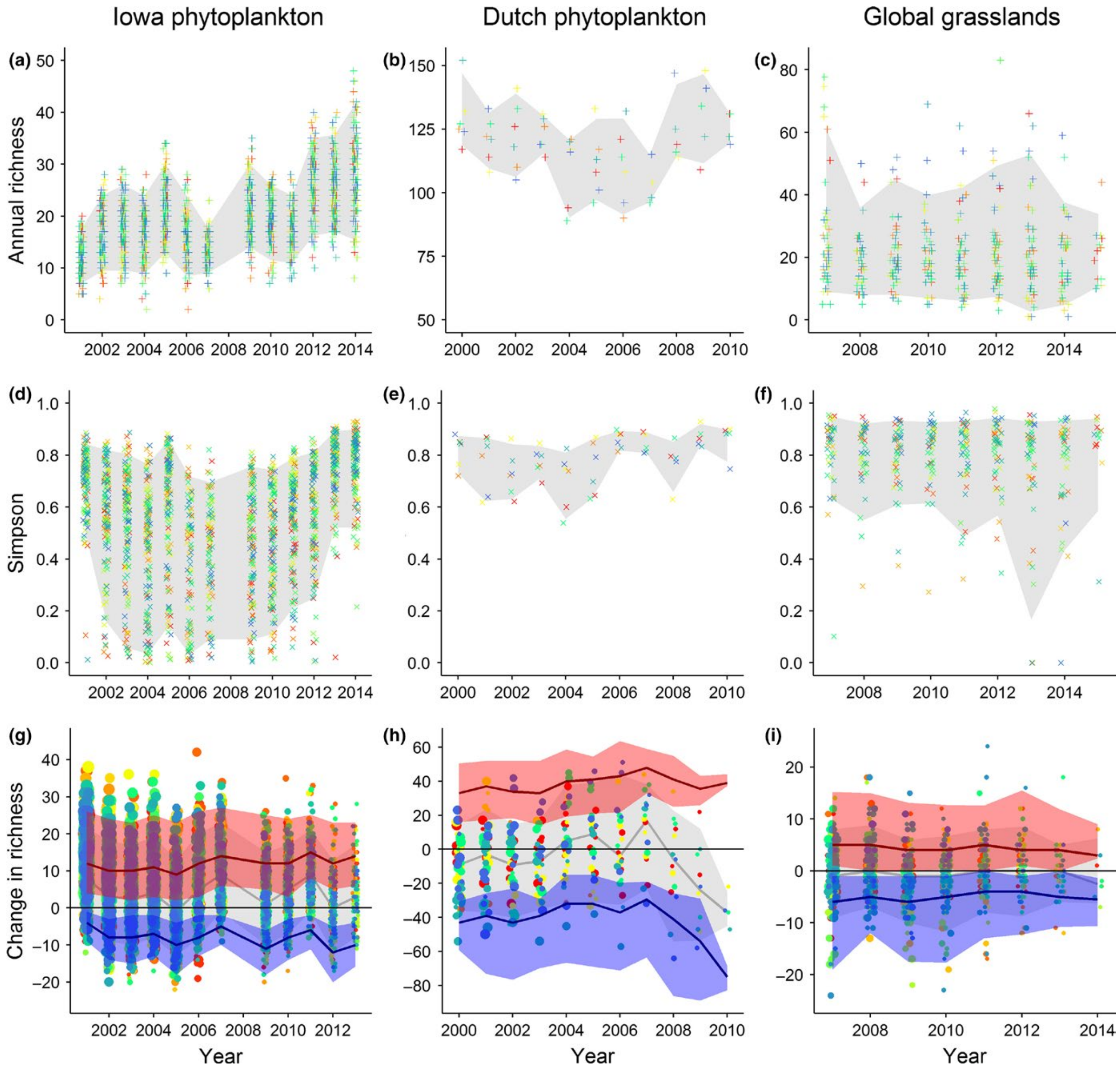


FIGURE 2 Temporal trends in biodiversity for three monitoring datasets from freshwater (Iowa phytoplankton), marine (Dutch coastal phytoplankton) and terrestrial systems (grasslands in the global Nutrient Network). Species richness (a–c) and Simpson diversity index (d–f) as annual values against time. Points are coloured by site or station within each dataset, points are jittered to enhance clarity. Grey shading is the range between the 5% and 95% quantiles of the data. (g–i) Changes in species richness for each dataset, calculated from each starting year onwards. Points are scaled to the temporal distance, with the smallest point size for 1 year difference, and the largest point size for maximum temporal distance. Points show the change in annual richness between years within each site. Grey shading represent 5%–95% quantiles, the dark grey lines represents the median. Net richness change is composed of immigrations (species newly recorded) and extinctions, which are represented by the shaded areas for 5% and 95% quantiles and lines for the median, respectively. Immigrations are shown in red, extinctions as negative values in blue. [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

The known limitations of species richness as a measure of biodiversity, which have been frequently discussed in the scientific literature (Chase & Knight, 2013; Gotelli & Colwell, 2001; Magurran, 2004), are magnified if temporal trends in richness are used to quantify biodiversity change. Empirically, we showed that the relative magnitude of richness change was orders of magnitude smaller than the actual occurrences of extinctions and immigrations (see Figure 2), leading to substantial turnover not only of rare species, but also in identity and relative abundance of dominant species (SER_a, see Figure 3d–f). Thus, major aspects of biodiversity change are not (and cannot be) reflected

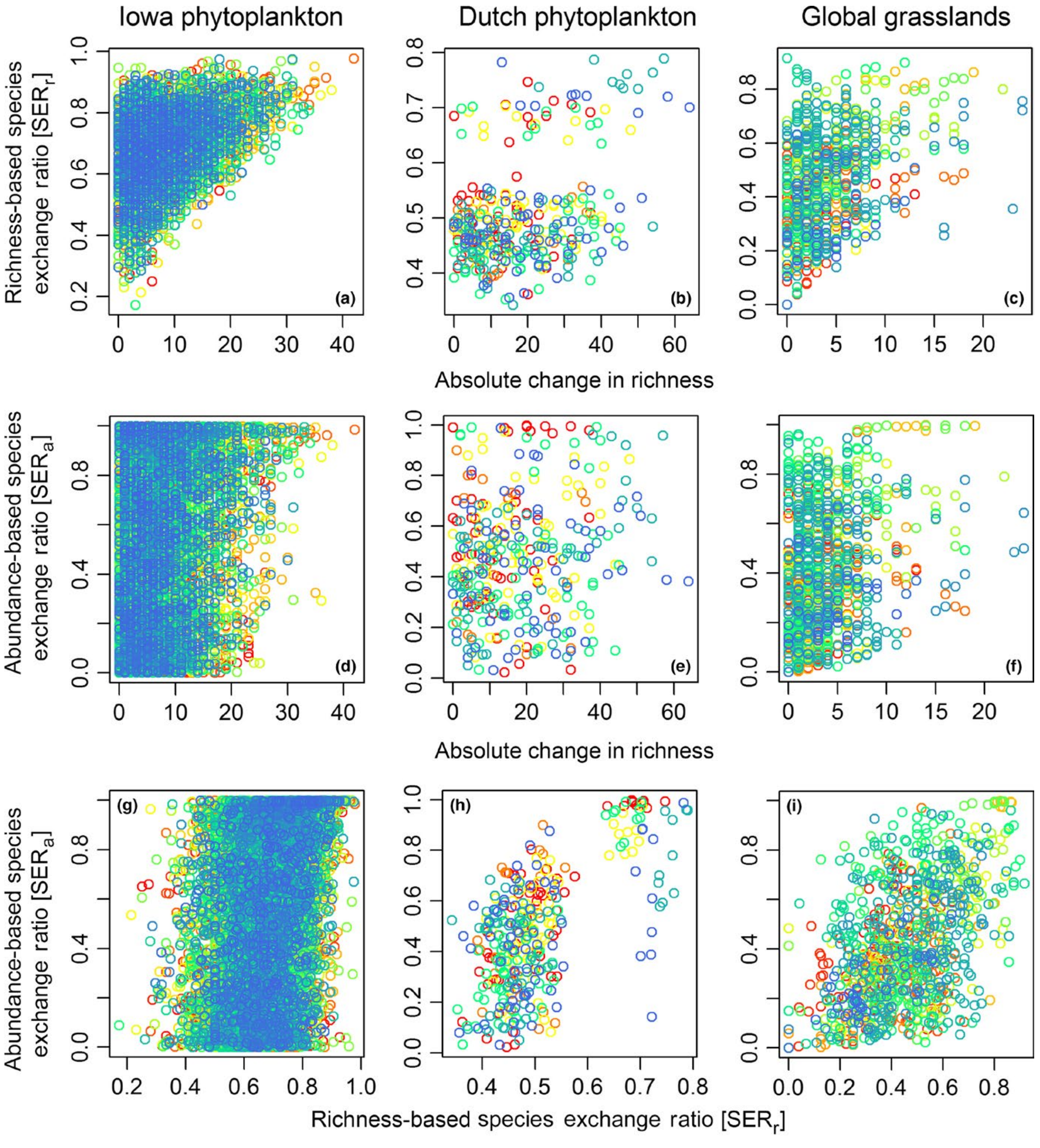


FIGURE 3 Bivariate plots between the absolute change in richness and (a–c) the richness-based as well as the (d–f) abundance-based species exchange ratio (SER$_r$ and SER$_a$), based on annual mean presence and abundance. Bottom panels are bivariate plots between both turnover metrics (g–i). Different colours represent different sites within each of the datasets. [Colour figure can be viewed at wileyonlinelibrary.com]

by changes in species richness—consistent with previous studies showing larger changes in composition than richness across temporal and spatial environmental gradients (Hillebrand, Soininen, & Snoeijs, 2010; Teittinen, Kallajoki, Meier, Stigzelius, & Soininen, 2016). In addition, our analyses showed that richness trends in and of themselves do not allow conclusions on the effect of a management practice, be it a negative impact or a positive conservation effort, on biodiversity.

Therefore, we strongly recommend rethinking the question of measuring "biodiversity loss" in science and monitoring programmes. Global extinctions of species represent true biodiversity loss (Barnosky et al., 2012), whereas what is observed in local ecosystems is biodiversity change, that is, the loss and gain of species identities and abundances. The transformation of a community through anthropogenic pressures does not by itself reduce (or increase) the number of species, but mainly

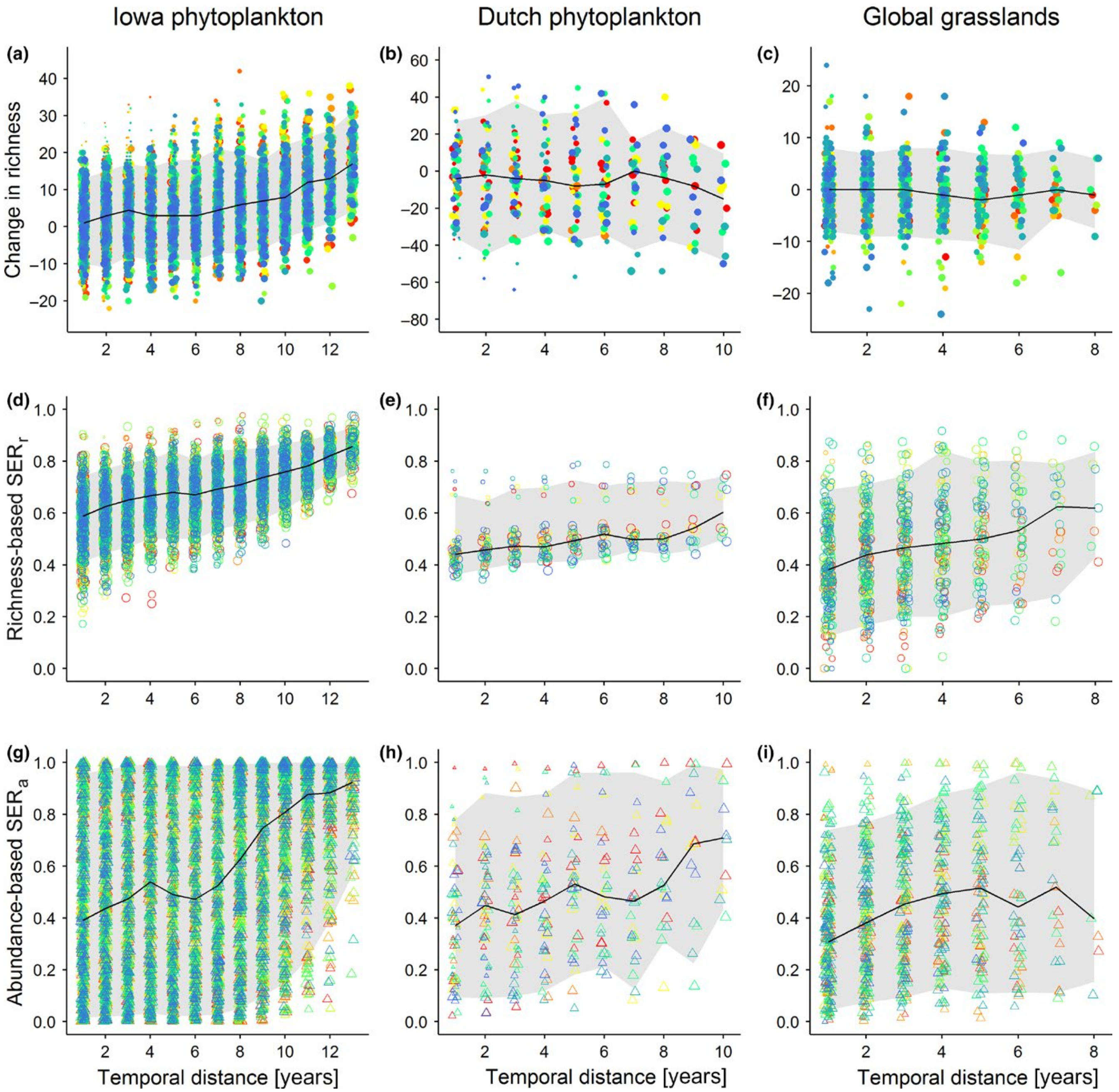


FIGURE 4 Change in species richness (a–c), richness-based (SER_r) (d–f), and abundance-based species exchange ratio (SER_a) (g–i), with increasing temporal distance between years, based on annual mean presence and abundance. Different colours represent different sites within each of the datasets. Grey shading represent 5%–95% quantiles, the darkgrey lines represents the median. [Colour figure can be viewed at wileyonlinelibrary.com]

changes their identity, for example, from long-lived foundation species to weedy ones (Lotze et al., 2006), or from specialist species to generalists (Clavel, Julliard, & Devictor, 2011). The net change in number of species can be zero, but a valid conservation target can be to halt such a shift in species identity. Monitoring local biodiversity trends thus requires information on the rate of compositional shifts rather than addressing trends in univariate measures of diversity (e.g. richness, Simpson), which by themselves are emergent properties of underlying compositional shifts.

We explicitly would like to stress that this conclusion is not new per se. Seabloom et al. (2013) made similar arguments showing that species richness is not a good predictor for biotic resistance to invasions. Dornelas, Gotelli, et al. (2014) emphasised the compositional biodiversity change hidden behind neutral richness trends in their meta-analysis of time series, and they presented temporal turnover analyses. Despite this awareness, however, richness trends remain a standard tool for biodiversity assessments and continue to be debated (Appendix S1). Consequently, it was the absence of a net decline in local richness documented by the recent suite of meta-analyses (Dornelas, Gotelli, et al., 2014; Elahi et al., 2015; Vellend et al., 2013) that has received strong scientific attention and stirred discussions (Cardinale, 2014; Dornelas, Gotelli, McGill, & Magurran, 2014; Gonzalez et al., 2016; Vellend et al., 2017). This discussion focused mainly on issues of data quality, completeness and interpretation, whereas here we emphasise that more fundamentally, analysing trends in species richness can only provide limited knowledge about changes in biodiversity.

Although species turnover is a much more sensitive measure of biodiversity change (Dornelas, Gotelli, et al., 2014), presence-absence turnover indices alone are insufficient, as they—like richness itself—depend on species pool size and detection probability of rare species. Instead, we propose that combining a presence-based and a dominance-based measure of turnover (SER_r and SER_a) allows conclusions on the magnitude of co-occurring shifts in species identity and relative abundance from time series data (cf. Figure 1). For the two phytoplankton datasets, this turnover was derived at the aggregated level of annual occurrences, that is, phenological shifts in seasonal appearance would not be reflected in our SER calculations. Sample-based turnover within years would potentially lead to much larger biodiversity change. On the basis of this conservative approach, we observed a striking disconnection between compositional change, even among the dominant species (cf. SER_a), and changes in richness.

At the same time, our results were congruent with the predominantly neutral trends in richness revealed by other meta-analyses (Dornelas, Gotelli, et al., 2014; Elahi et al., 2015; Supp & Ernest, 2014; Vellend et al., 2013). Our datasets comprised time frames roughly similar to those used in these previous meta-analyses. However, in terms of generation times, the terrestrial dataset was shorter than the aquatic ones and also differs in terms of spatial dimension, covering all continents and different species pools. Consequently, grasslands likely had more localised immigration (as time for long-distance dispersal was lacking) and needed much longer time for competitive shifts. This most probably led to the lower median of species turnover as well as its levelling off with increasing temporal distance, especially for SER_a. With longer observation time, more shifts in the identity and structure of the dominant species could be expected. The plankton communities obviously diverged faster, which also includes shifts among the dominant species, leading to continuous shifts in both SER_r and SER_a.

In addition to the empirical evidence, we offered a simple simulation that does not include the mechanisms regulating immigration and extinction in any natural system, but highlights the fact that richness trends, even if they are found, do not allow a direct conclusion about the quality of biodiversity change. Species richness might increase in a given ecosystem because conditions are improving due to, for example, less exploitation, as has been showcased in some of the studies synthesised by Elahi et al. (2015). Alternatively, richness might increase because the environment has changed in any qualitative direction, but extinction responses are delayed compared to immigration (Appendix S2). This transient increase can be prolonged despite declining environmental quality when environmental changes continue. The magnitude of this transient increase depends on the magnitude and continuation of the change as well as of the time-lag between immigration and extinction. More generally speaking, richness trends will likely be nonlinear and appear neutral over time when analysed by linear or monotonic trends.

The abundant literature on extinction debt has considered the consequences of delayed extinctions when environments change, especially with regard to landscape fragmentation (Ewers & Didham, 2006; Isbell, Tilman, Polasky, & Loreau, 2015; Tilman et al., 1994). These studies have focused on a delay in the reduction in species richness, as fragmentation is considered to increase extinction rates without necessarily altering immigration rates. This is analogous to MacArthur and Wilson's (1967) Theory of Island Biogeography, which associated habitat size with extinction and distance with immigration. Even in the case of fragmentation, this focus on extinction is questionable as smaller fragments have different proportions of (atypical) edge habitats, which might be open for immigration by species with different habitat requirements (Davies, Melbourne, & Margules, 2001; Ibanez, Katz, Peltier, Wolf, & Barrie, 2014). However, when considering environmental change more generally as affecting immigration and extinction rates (e.g. warming climate, changing nutrient concentrations, acidification), our simple simulations suggest that the consequences of extinction debt (or immigration credit) go beyond a delay in the richness response, and can even involve a transient reversal leading to species accumulation.

Our results emphasise that the discussion of whether the biodiversity on our planet is in a state of decline simply cannot be answered by assessing trends of local species richness. Previous criticisms (Cardinale, 2014; Gonzalez et al., 2016) of the meta-analyses mentioned above (Dornelas, Gotelli, et al., 2014; Elahi et al., 2015; Vellend et al., 2013) asked whether the right datasets, locations or metrics of richness change were addressed. However, we argue that the real issue is that the richness trends have limited value for assessing the quality and quantity of biodiversity change. This has to be kept in mind especially if the results of such richness trend analyses are converted into management or scientific advice (Hill et al., 2016). Below, we discuss the implications of our results for the scientific assessment of consequences of biodiversity change and the appropriate spatial scale for biodiversity analysis, as well as for monitoring programmes.

4.1 | Functional consequences of biodiversity change

Vellend et al. (2013, see also Vellend, 2017) concluded that the way biodiversity has been manipulated in the research on biodiversity effects on ecosystem functioning (BEF) lacks a scientific basis as most studies in this area test for the effects of declining richness, which according to their analysis does not occur frequently in nature. Species richness is indeed the biodiversity aspect most frequently addressed in empirical BEF studies (Hillebrand & Matthiessen, 2009), because (1) it can be experimentally controlled more easily than many of the other facets of biodiversity; and (2) alternative ways of manipulating biodiversity (Tilman & Downing, 1994) have been criticised for bearing potential hidden treatments (Huston, 1997). Thus, richness became the main proxy for biodiversity change in BEF experiments. This one-dimensional focus on richness in the BEF literature has been criticised repeatedly (Hillebrand & Matthiessen, 2009; Leibold, Chase, & Ernest, 2017). However, the lack of temporal trends in richness does not invalidate the conclusions taken from BEF experiments (Cardinale et al., 2012; Hooper et al., 2012), because biodiversity effects in BEF experiments are explicitly discussed in the context of species identities (selection effects) and species differences (complementarity effects). When Cardinale et al. (2012) summarised that "[d]iverse communities are more productive because they contain key species that have a large influence on productivity, and differences in functional traits among organisms increase total resource capture," they convey that identity and composition are drivers of ecosystem functioning, both reflecting the presence and combination of traits. Meanwhile, the importance of functional trait diversity is explicitly addressed in a posteriori analyses of richness-based BEF experiments (Petchey, Hector, & Gaston, 2004) and by novel approaches to manipulate functional diversity directly in the field (Ebeling et al., 2014; Liu et al., 2015).

4.2 | Spatial aspects of biodiversity change

In a commentary alongside Vellend's article, Thomas (2013) suggested that stable local richness is the consequence of declining global and increasing regional species richness (see also Sax & Gaines, 2003). Numerous indicators of global biodiversity (e.g. number of extinct or endangered species, relative abundance of species compared to pre-human conditions) indeed show a continuous deterioration (Butchart et al., 2010; Tittensor et al., 2014), but the suggested increase in regional species richness reflects complex distributional shifts beyond simple poleward spatial and earlier temporal occurrence of species in a warming climate (Burrows et al., 2011). As in our simulation (Appendix S2), a changing environment can lead to initial increases in regional species richness, if immigration into the region is fast, but extinctions are delayed. The vast literature on range expansion under climate change points at such different rates of range expansion compared to range contraction leading to broadened latitudinal (Poloczanska et al., 2013) or altitudinal ranges (Morueta-Holme et al., 2015). The regional dimension of biodiversity change thus motivates increased scientific attention on the trailing (or rear) edge of the range (Hampe & Petit, 2005), to uncover signs of delayed regional extinctions.

A second spatial consequence of concomitant changes in global, regional and local biodiversity is a reduction in spatial biodiversity (beta-diversity), that is, biotic homogenisation (Karp et al., 2012; McKinney & Lockwood, 1999; Olden & Rooney, 2006; Van der Plas et al., 2016). In our analysis, we addressed temporal turnover using plot-level data, but did not consider simultaneous changes in spatial turnover, although these two aspects are tightly linked both statistically and ecologically. Statistically, the rate of turnover in time will decrease with increasing spatial scale of sampling, reflecting a common species-time-area relationship, STAR (Adler & Lauenroth, 2003; Adler et al., 2005). This coupling of spatial and temporal sampling effort will affect SER_r more than the abundance-based SER_a. Ecologically, immigration and extinction dynamics in a local habitat will be tightly coupled to the size of the regional species pool and the spatial processes in metacommunities. The relative role of immigration—extinction dynamics vs dominance shifts of persisting species may thus depend on the availability of additional species in the surrounding region: In a completely homogenised landscape, dispersal into a habitat with changing quality is low and the adaptation of species composition to new conditions will be impaired.

4.3 | Species richness trends in a monitoring context

While it is clear that documenting and understanding biodiversity change is critical for global and regional assessments, there is little agreement on how to monitor and quantify such change (Buckland et al., 2005; Hill et al., 2016; Proença et al., 2016; Vačkář et al., 2012). The limited usefulness of species richness for monitoring the status and trends of biodiversity is already reflected by the many calls for development of multiple indicators of biodiversity status (Pereira et al., 2013). For example, the 2002 CBD agreed to monitor biodiversity trends to meet CBD targets by developing indicators to capture changes in biodiversity spanning genes, populations, species and ecosystems (Butchart et al., 2010; Convention on Biological Diversity, 2006). The chosen indicators are a mix of data types compiled to maximise many factors including relevance, breadth of geographical and biodiversity coverage, and cost-effectiveness (Mace & Baillie, 2007), yet in spite of this, considerable gaps remain (Butchart et al., 2010; Mace & Baillie, 2007; McOwen et al., 2016). Furthermore, most of these metrics fail to capture the rates of immigration and extinction, which are critically important for characterising the rate and effects of ecosystem change on community composition and function (Shimadzu et al., 2015).

On the basis of our analyses, we offer a few suggestions for developing new monitoring programmes and to analyse existing data. The first recommendation is to base assessments of biodiversity change on multiple aspects, including changes in identity and dominance, which can be achieved by explicitly addressing the extent of extinctions and immigrations via SER_r and dominance shifts via SER_a. The analysis of both turnover metrics requires abundance data and a consistent nomenclature, but benefits the assessment by providing key insights into the role of environmental change in identity and dominance shifts of entire ecological communities, thus more closely mapping the indicator onto targeted outcomes (Collen & Nicholson, 2014). It should be noted though, that the actual turnover values are system-specific, depending, for example, on species pool size and sampling frequency, and cannot be interpreted as absolute values, that is, $SER_r = 0.5$ is not per se a "high" or "low" turnover. For such an analysis, a null model on random drift in composition has to be constructed (as e.g. implemented by Dornelas, Gotelli, et al., 2014) as a baseline for the realised values. Still, the comparative analysis of SER_r and SER_a allow systematic assessment of co-occurring dominance and identity shifts (Figure 1), which informs more integrated assessments of biodiversity that incorporate functional trait information or scale-transitive analyses (Angeler & Allen, 2016; Hill et al., 2016; Pereira et al., 2013; Scholes & Biggs, 2005). It also provides a first step towards the understanding of mechanisms driving biodiversity change in monitoring (Truchy, Angeler, Sponseller, Johnson, & McKie, 2015; Urban et al., 2016) and thus the type of information needed to make management decisions (Tittensor et al., 2014).

The second recommendation is to monitor temporal biodiversity change in an explicit spatial context, as temporal turnover is affected by spatial aspects of immigration and extinction. Temporal species turnover is conceptually closely linked to spatial dissimilarity (beta-diversity), and combining these metrics of difference in biodiversity assessments is a mandatory link to biodiversity conservation (McKnight et al., 2007; Socolar, Gilroy, Kunin, & Edwards, 2016). Still, existing monitoring programmes, often constrained by funding issues and policy requirements, tend to focus on infrequent (down to single) assessments in an extended spatial grid or frequent assessments on few (down to single) locations. The empirical evidence for massive compositional turnover and the theoretical indication of the importance of spatial dynamics for this temporal turnover (and vice versa) mandate the establishment of monitoring assessments over time and space, exemplified by some national biodiversity monitoring programmes (BDM Coordination Office, 2014; Fölster, Johnson, Futter, & Wilander, 2014).

A third recommendation, although not easily met in the face of budget constraints, is the focus on long-term consistency. Temporal (and spatial) turnover accumulates over time (Figure 4) and transient dynamics are likely to occur (Appendix S2). Therefore, biodiversity assessments need a long memory to disentangle long-term from short-term changes and to reveal the full extent of biodiversity change (see Gonzalez et al., 2016 for similar argumentation). Moreover, changing the number of sites during the programme shifts the frequency distribution of time intervals considered to more short-term comparisons (cf. Figure 4). Because biodiversity monitoring requires specialised knowledge and is often time-intensive, such a long-term memory is less easily achieved in biodiversity monitoring than in other monitoring programmes focusing on abiotic parameters. While we have abiotic time series spanning tens to hundreds of years, for example, ocean turbidity through Secchi depth (Boyce, Lewis, & Worm, 2010), global temperature (Smith, Reynolds, Peterson, & Lawrimore, 2008) or atmospheric CO_2 concentrations (Keeling, Whorf, Wahlen, & Vanderplicht, 1995), most biodiversity time series are much shorter. In addition, these biological data series suffer from issues of changing sampling effort, taxonomic resolution and expertise, which require backtracking and harmonising species names. Consequently, our information on the degree of environmental change, as observed in the past and predicted for the future, is much more compelling than the knowledge on biodiversity change. In spite of these challenges, biodiversity monitoring programmes that quantify species turnover will generate a far more reliable understanding of the biotic response to changing environments than programmes solely tracking species richness.

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AUTHORS' CONTRIBUTIONS

H.H. designed the paper and laid out the analyses. H.H., E.T.B., J.M.C., W.S.H., D.H., S.L., A.M.L., A.B.R., E.W.S. and D.B.V. developed the framework for monitoring biodiversity change during a series of workshops. A.B.R. (together with H.H. and B.B.) developed the temporal turnover metrics based on Simpson diversity. H.H. and J.M.C. conceived the discussion on limitations of richness. B.B. provided the simulations of richness change. E.T.B., J.D., C.T.F., W.S.H., A.M.L., E.W.S., D.B.V. provided the data for the case studies. H.H. and A.B.R. conducted the analyses. H.H. wrote the manuscript with substantial input from all co-authors.

DATA ACCESSIBILITY

Data are available via the Dryad Digital Repository https://doi.org/10.5061/dryad.1sd59 (Hillebrand et al., 2017).

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