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Local biodiversity change reflects interactions among changing abundance, evenness, and richness

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Abstract

Biodiversity metrics often integrate data on the presence and abundance of multiple species. Yet our understanding of covariation between changes to the numbers of individuals, the evenness of species relative abundances, and the total number of species remains limited. Using individual-based rarefaction curves, we show how expected positive relationships among changes in abundance, evenness and richness arise, and how they can break down. We then examined interdependencies between changes in abundance, evenness and richness in more than 1100 assemblages sampled either through time or across space. As predicted, richness changes were greatest when abundance and evenness changed in the same direction, and countervailing changes in abundance and evenness acted to constrain the magnitude of changes in species richness. Site-to-site differences in abundance, evenness, and richness were often decoupled, and pairwise relationships between these components across assemblages were weak. In contrast, changes in species richness and relative abundance were strongly correlated for assemblages varying through time. Temporal changes in local biodiversity showed greater inertia and stronger relationships between the component changes when compared to site-to-site variation. Overall, local variation in assemblage diversity was rarely due to repeated passive samples from an approximately static species abundance distribution. Instead, changing species relative abundances often dominated local variation in diversity. Moreover, how changing relative abundances combined with changes to total abundance frequently determined the magnitude of richness changes. Embracing the interdependencies between changing abundance, evenness and richness can provide new information to better understand biodiversity change in the Anthropocene.

KEYWORDS
abundance, biodiversity change, evenness, rarefaction, species richness

INTRODUCTION

Measures of biodiversity are used to describe patterns and understand ecological and evolutionary processes. Species origination (speciation plus colonization) and extinction are the most fundamental processes for biodiversity dynamics (MacArthur & Wilson, 1967; Storch et al., 2022). These processes combine with productivity (Currie, 1991; Mittelbach et al., 2001), disturbance frequency and intensity (Connell, 1978; Miller et al., 2011), historical (Latham & Ricklefs, 1993) and biogeographic factors (e.g., Kreft et al., 2008), land use modifications (Newbold et al., 2015), and climate change (Antão, Bates, et al., 2020; Scheffers et al., 2016) to drive variation in biodiversity. Mathematically, these processes and drivers alter the total abundance of individuals, the evenness of species relative abundances, and the species richness of assemblages, and changes in all these components contribute to variation in biodiversity. Yet little is known about how components are changing in combination within assemblages, and whether certain combinations act to constrain variation in biodiversity.

Measures of biodiversity estimated from a given (local) sample depend largely on two components (see, e.g., He & Legendre, 2002; McGill, 2011a). First, the total number of individuals (Fisher et al., 1943; Preston, 1962), whereby fewer individuals are expected to (nonlinearly) lead to fewer species. Second, the total number of species and their relative abundances within the regional species pool (i.e., the set of all potential colonizing species in a region), which we refer to as the Species Abundance Distribution (SAD; McGill et al., 2007). Whenever two or more samples across space or time differ in the total number of individuals, the shape of the SAD, or both, there will be changes in most metrics of biodiversity. However, changes in abundance and the SAD are not always correlated, and, when decoupled, the magnitude and direction of change in derived biodiversity metrics can differ considerably.

Variation in the total number of individuals is a long-standing, first-order explanation of variation in species richness (Coleman et al., 1982; Fisher et al., 1943; Gaston, 2000; Scheiner & Willig, 2005; Srivastava & Lawton, 1998; Storch et al., 2018). In the context of species–area relationships, this has been termed the "passive sampling hypothesis" (Coleman et al., 1982), and as local assemblages increase in size they are expected to include more species from the regional pool due to sampling processes alone. Larger (Connor & McCoy, 1979) or more productive areas (Wright, 1983) are also predicted to have more species driven by an increased number of individuals. In these cases, processes other than sampling are considered important, such as decreased extinction likelihood due to increased population sizes (Preston, 1962; Srivastava & Lawton, 1998; Wright, 1983), and commonly referred to as the "more individuals hypothesis" (Srivastava & Lawton, 1998). Anthropogenic drivers can also influence the number of individuals in assemblages (e.g., via eutrophication, exploitation, harvesting, or land clearing), potentially impacting biodiversity due to changes to the total number of individuals (Blowes et al., 2020; Newbold et al., 2015). If biodiversity varies primarily via changes in the numbers of individuals, positive relationships between altered numbers of individuals and altered species richness are expected. In such cases, other metrics of species diversity that control for variation in numbers of individuals, such as species richness expected for a given number of individuals, known as rarefied richness, should be relatively unchanged.

Changes to the shape of the SAD can drive variation in biodiversity through time or space. For example, co-occurrence and coexistence of species can be altered by changes to resource diversity (MacArthur, 1965), environmental or habitat heterogeneity (Shmida & Wilson, 1985; Tilman, 1982), interspecific interactions (e.g., keystone predation; Menge et al., 1994; Paine, 1974), biological invasions (Vilà et al., 2011), and external perturbations (Hughes et al., 2007). Alterations to any of these features can change biodiversity by changing species relative abundances and the size of the species pool (via species additions or subtractions). Anthropogenic factors can also favor some species and disfavor others, potentially altering the relative abundance of species (e.g., due to selective exploitation; Blowes et al., 2020), or the size of the species pool (e.g., species with large ranges replacing those with small ranges, Newbold et al., 2018). In these cases, biodiversity change will be characterized by positive relationships between species richness change and changes in metrics sensitive to relative abundance, such as rarefied richness, evenness and diversity metrics that incorporate species relative abundances.

Changing components of biodiversity can covary in different and informative ways. Yet, to date, there has been little exploration of this covariation in time or space, nor of the theoretical linkages. For example, whether total abundances and the evenness of species relative abundances change in similar or decoupled ways, and how this influences biodiversity change is largely unknown. However, syntheses of relationships between different biodiversity metrics, which can reflect different combinations of component changes, have typically found relationships to be weak. For example, Stirling and Wilsey (2001) showed that although strong positive correlations between species richness, diversity, and evenness metrics were expected from a neutral model (Caswell, 1976), there was considerable variation in the strength, and even the sign of the relationships in 323 empirical comparisons. Similarly, Soininen et al. (2012) examined temporal ($n = 212$) and spatial variation ($n = 17$) in aquatic data sets, and again found considerable heterogeneity in the relationship between richness and evenness. Using data from 91 assemblages, McGill (2011b) concluded that most biodiversity metrics align with three axes of empirical variation (total abundance, evenness, and richness); components subsequently shown to be relatively uncorrelated across space for a subset of 37 of the 91 assemblages (Chase et al., 2018a). Collectively, these studies suggest that static biodiversity estimates are multidimensional and that different metrics can covary or be unrelated.

Where ecologists have quantified variation in multiple components of local diversity, the focus has typically been on averages across assemblages, with each component treated as a separate, independent response. For example, analyses of the local assemblages documented by the BioTIME database (Dornelas et al., 2018) show that numbers of individuals, species richness, and dominance (quantified as the relative abundance of the most numerically dominant species, and conceptually the complement of evenness) are highly variable among data sets, but on average, have no directional trend (Blowes et al., 2019; Dornelas et al., 2014; Jones & Magurran, 2018). On the other hand, analyses of the PREDICTS database (Hudson et al., 2017) documenting spatial contrasts between assemblages in more pristine habitats with those in different land use categories, show that human-altered habitats frequently have fewer species and often fewer individuals (Newbold et al., 2015, 2020). However, these results describe average changes across assemblages estimated independently, whereas, as we describe in more detail below, component changes are unlikely to be completely independent.

Here, we first provide a conceptual overview of how changes in the main components underlying local biodiversity (total abundance, evenness, and species richness) can combine using individual-based rarefaction curves. Using simplified scenarios with contrasting component changes, we show that the sign (or direction) of changes in total abundance and evenness can combine to determine the magnitude of expected richness changes, and whether positive pairwise relationships prevail. We then empirically assess interdependencies between abundance, evenness, and richness changes using compilations of ecological assemblage data. In the face of natural and anthropogenically driven environmental variation in time or space, we ask whether changes in the components of local biodiversity show positive relationships (i.e., change in the same direction). Or, alternatively, are component changes sufficiently heterogeneous that variation in biodiversity depends on which of the underlying components (numbers of individuals or the SAD) are changing, and how the different component changes combine?

METHODS

Conceptual relationships between changes in total abundance, evenness and richness

Individual-Based Rarefaction (IBR) curves (Gotelli & Colwell, 2001; Hurlbert, 1971) are well suited for visualizing relationships among changes in total abundance, evenness, and species richness (Figure 1; Cayuela et al., 2015; Chase et al., 2018a; McGlinn et al., 2019). The end point of the IBR curve depicts the total number of individuals of all

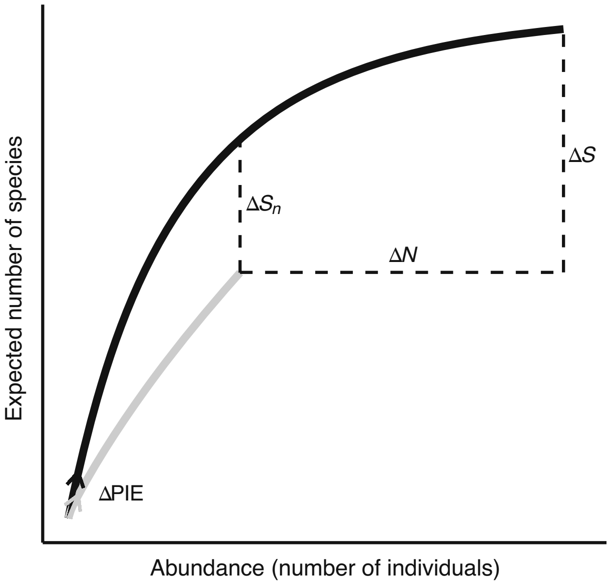


FIGURE 1 (a) Individual-based rarefaction (IBR) curves for two hypothetical assemblages, showing the four components we use to quantify change (number of individuals [N], species richness [S], rarified richness [S_n], probability of interspecific encounter [PIE]). We show ΔPIE on the figure to illustrate how changes of the PIE (it is equivalent to the slope at the base of the curve) alters the IBR, but use the numbers equivalent transformation (ΔS_{PIE}) in all analyses.

species combined, and variation between assemblages in where the curve terminates quantifies changes to the number of individuals (ΔN, Figure 1) and species richness (ΔS, Figure 1). The shape (or curvature) of the IBR curve reflects species relative abundances and the size of the species pool (i.e., the SAD). We use two parts of the curve to characterize changes in the SAD between assemblages. First, because it is standardized to an equal number of individuals (n), changes in rarefied richness, ΔS_n (Figure 1), reflects changes to species relative abundances only. Second, we use the numbers equivalent (or effective number of species) transformation of the Probability of Interspecific Encounter (PIE; Hurlbert, 1971). The PIE is equal to the slope at the base of the rarefaction curve (Olszewski, 2004) and represents a metric of evenness that is relatively insensitive to sample effort (more even communities have a higher PIE, Figure 1). Transformation of the PIE to the numbers equivalent (S_{PIE}) aids comparisons to species richness (i.e., ΔS and ΔS_{PIE} have the same units; Jost, 2006). S_{PIE} is equal to the inverse of Simpson concentration (Jost, 2006), and diversity of order $q = 2$ (Hill, 1973; Jost, 2007), $D = \left(\sum_{i=1}^{S} p_i^q\right)^{1/(1-q)} = 1/\sum_{i=1}^{S} p_i^2$, where S is the number of species and p_i is the proportion of the assemblage represented by species i. As a consequence, changes in S_{PIE} (ΔS_{PIE}) are most strongly influenced by the number of abundant or common species in assemblages.

Altered numbers of individuals, but no change to the SAD, can underpin differences in diversity between assemblages. Changes only to the number of individuals being passively sampled from the same underlying SAD (Figure 2a) result in ΔS and ΔN being positively related with the same sign (Figure 2g), whereas ΔS_n (Figure 2h) and ΔS_{PIE} (Figure 2i) will be approximately zero (and have a weak or no relationship with ΔS). This has been variously referred to in the literature as a sampling effect, the rarefaction effect, and the passive sampling hypothesis (Coleman et al., 1982; Gotelli & Colwell, 2001; Palmer et al., 2000).

Changes in species richness (ΔS) can also be solely associated with changes to relative abundance (i.e., $\Delta N \approx 0$), which weakens or removes the expectation for a positive relationship between changes in richness and total abundance. For example, changes in species richness can be associated with SAD changes due, e.g., to increased numbers of common species, increased evenness (He & Legendre, 2002), or additions to the species pool (Figure 2b), which results in a positive relationship between ΔS and ΔS_{PIE} (Figure 2i). Finally, if total abundance and relative abundance change in the same direction (e.g., more individuals and increased evenness, Figure 2c), then positive pairwise relationships are expected between changes in abundance, evenness, and richness (Figure 2g–i).

In contrast, even if numbers of individuals increase ($\Delta N > 0$), expected gains in species richness can be constrained by decreased evenness. For example, opposing changes in total abundance and evenness can potentially result in no change to species richness (Figure 2d), and no relationship between ΔS and ΔN (Figure 2g). Or, if changes to the SAD are sufficiently strong, they can offset any expected gains due to more individuals (Figure 2e), and result in a negative relationship between ΔS and ΔN (Figure 2g). Alternatively, opposing changes to total numbers of individuals and evenness could result in a positive relationship between ΔS and ΔN if, for example, the effects of more individuals on species richness outweighs that of decreased evenness (Figure 2f).

These simplified scenarios illustrate the potential for interdependencies between component changes. In particular, they show that the signs of changes in total abundance and evenness (i.e., ΔN and ΔS_{PIE}) can strongly influence the magnitude of richness changes, and whether expected positive relationships between changes in abundance, evenness and richness are found. ΔN is associated with the IBR curve stretching or

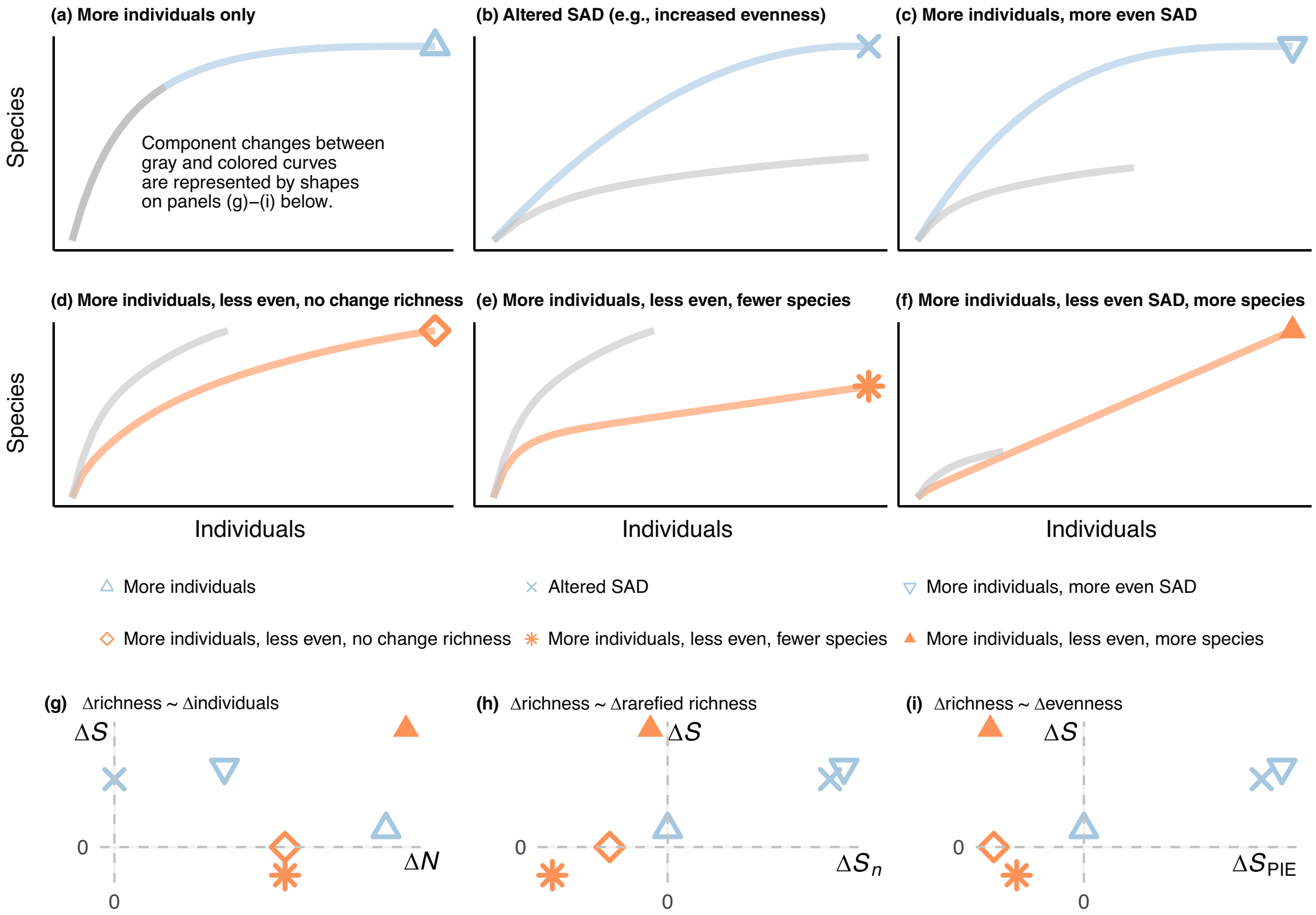


FIGURE 2 Conceptual illustrations of potential pathways of assemblage diversity change and corresponding relationships between component changes. Starting from a reference assemblage (depicted with gray rarefaction curves), diversity change can be due to (a) more individuals only, (b) changes to the species abundance distribution only (e.g., increased species pool size or increased evenness), or (c) changes in total abundance and the SAD that result in positive pairwise relationships between ΔN, ΔS_n, ΔS_{PIE}, and ΔS. However, if the signs of ΔN and ΔS_{PIE} differ, their relationships with ΔS weaken and species richness can (d) remain static, (e) decrease, or (f) increase. We visualize pairwise relationships between component changes for each scenario (i.e., the different shaped symbols) using: (g) changes in species richness as a function of changes to the number of individuals, (h) changes in species richness as a function of changes in rarefied richness, and (i) changes in species richness as a function of changes in evenness.

contracting along the *x*-axis, and ΔS_{PIE} characterizes changes that flex the curve up or down from the base along the *y*-axis (Olszewski, 2004). When ΔN and ΔS_{PIE} have the same sign, assemblages are expected to fall into the lower left and upper right quadrants of Figure 2g–i (i.e., component changes with the same sign and positive pairwise relationships). In contrast, when ΔN and ΔS_{PIE} have different signs, they can have countervailing effects that constrain richness changes, the strength of their pairwise relationships with ΔS will be diminished and potentially reversed, and the likelihood of assemblages falling into the upper left and lower right quadrants of Figure 2g–i increases (i.e., opposing signs and negative pairwise relationships).

Empirical relationships among total abundance, evenness, and richness

Next, we evaluate empirical relationships by fitting models that allow for correlations between component changes to data from 1125 assemblages. Our goal for the empirical analyses was to examine relationships between changing components in temporal and spatial contexts across a broad range of environmental conditions. We compiled data documenting either temporal or spatial variation of assemblage composition in one of either naturally varying or perturbed environmental conditions. Temporal variation quantified rates of change (per year) for each component for an assemblage at a single location through time. Analyses of spatial variation quantified component differences between sites in different land use categories in perturbed environments, or between random pairs of sites in naturally varying environments.

Based on our conceptual overview, we expect pairwise relationships between abundance, evenness, and richness changes to be generally positive. Changes in species richness are also expected to be largest for assemblages where all pairwise relationships are positive. In contrast, opposing changes in total abundance and evenness (i.e., ΔN and ΔS_{PIE} have different signs) are expected to constrain changes in species richness. Additionally, if variation in local diversity is dominated by altered total abundances and species richness, strong positive relationships between ΔS and ΔN, but weaker relationships between ΔS and ΔS_n and ΔS and ΔS_{PIE} should emerge across assemblages. Alternatively, strong relationships between either ΔS and ΔS_n and/or ΔS and ΔS_{PIE}, accompanied by a weaker relationship between ΔS and ΔN, would indicate that changes to the SAD are the dominant component of local variation in biodiversity.

Temporal changes: Natural environmental variation

Temporal changes in natural assemblages were quantified using the BioTIME database (Dornelas et al., 2018). Annual rates of change (i.e., change per year) for each metric were estimated with models fit to data that documents over 45,000 species in time series with an average duration of 13 years. Taxonomic groups in our analysis came from surveys in marine, freshwater, and terrestrial ecosystems, and included plants (and other producers), invertebrates, fish, amphibians, reptiles, birds, and mammals, as well as several surveys that collected data from multiple taxa. Here, we only used time series that had numerical abundance data available (i.e., studies that recorded counts of the number of individuals for each species in an assemblage), and our analysis included 288 studies. Locations sampled in the BioTIME database document places with varying degrees of anthropogenic environmental change, but do not include manipulated assemblages or before-after-control-impact studies (Dornelas et al., 2018). Accordingly, we contrast the environmental variation sampled by BioTIME with assemblage time series that experienced documented perturbations (*Temporal changes: Experimental or natural perturbations*).

To quantify changes at the local scale within BioTIME, studies with large extents were broken up into smaller cell-level time series, while still maintaining the integrity of individual studies (i.e., different studies were not combined, even when samples were collected in the same grid cell). We used sample-based rarefaction (Gotelli & Colwell, 2001) to standardize the number of samples per year for each time series (see Blowes et al., 2019 for details). For the calculation of rarefied richness (S_n), the minimum total number of individuals was determined for each time series and set as the target n for which expected richness was calculated; cell-level time series where $n < 5$ were discarded. This process resulted in 42,604 cell-level time series from the 288 studies, and we focus on the study-level estimates of change in our results and discussion.

Temporal changes: Experimental or natural perturbations

To complement the environmental variation sampled by the BioTIME database, we searched for time series data with either experimental or natural perturbations. Specifically, we queried the U.S. LTER network using the Data Portal of the Environmental Data Initiative (https://portal.edirepository.org/nis/home.jsp) with the search terms “experiment” and “time” and “abundance.” Records returned were checked to confirm that samples documented assemblages of similar species collected with the same methodology, and following data standardization (i.e., minimum of five individuals per sample, and standardization of sample effort through time), our analysis included 11 studies (see Appendix S1: Section S2 for references), and annual rates of change (per year) were estimated for 63 study–treatment combinations; rates of change for all treatments (including controls) were quantified in our analyses. Natural and experimental treatments included changes due to warming, eutrophication, fire, grazing, restoration, severe storms or other disturbances, and kelp removal. Taxonomic groups included algae, plants, invertebrates, fish, birds, and mammals.

Spatial comparisons: Natural environmental variation

We combined two existing compilations of data to examine spatial variation of biodiversity in relatively natural environmental contexts. The CESTES database (Jeliazkov et al., 2020; Jeliazkov & The CESTES Consortium, 2019) contains assemblage data from studies that sampled species at multiple sites (it also includes information on traits and environment that we do not use here); we removed studies with explicit human impacts identified as an environmental feature, and our analysis included 19 studies that sampled terrestrial, freshwater, and marine assemblages from a number of taxonomic groups (birds, plants, insects, macroinvertebrates, fishes, and mammals). McGill (2011b) compiled data sets with two or more local assemblages containing species abundance data; we removed studies documenting disturbances and other perturbations, resulting in 32 studies being retained. From the combined 51 studies, those with many sites were randomly subsampled down to 10 sites so that they did not dominate the results. Within each study, an arbitrary site was assigned as the "reference" site, and differences were quantified between every site and the reference within studies; our analysis included a total of 356 spatial comparisons.

Spatial comparisons: Anthropogenic perturbations

To quantify spatial differences in biodiversity associated with anthropogenic land use, we used the PREDICTS database (Hudson et al., 2017). We used the 2016 release of the database (downloaded from https://data.nhm.ac.uk/dataset/the-2016-release-of-the-predicts-database on 10 July 2020). We limited our analyses to studies with abundance data for individuals, and those with known land use categories (primary vegetation, mature secondary vegetation, intermediate secondary vegetation, plantation forest, cropland, pasture, and urban); studies where land use was not recorded were omitted. This resulted in 237 combinations of source ID and study (some sources had multiple studies, denoted SS in the database), and 418 estimates of difference relative to the reference land use (primary vegetation) category.

Statistical models

To estimate changes in the different metrics while accounting for expected correlations between them, we fit multivariate multilevel models to the data. Similar to the way univariate multilevel (also called hierarchical or mixed-effects) models fit to a single response can allow varying (also called random) intercepts and slopes to be correlated, this approach estimates changes in all components simultaneously while allowing for (and estimating) correlations between them. Response distributions for all metrics were chosen to ensure changes were estimated on similar measurement scales, and because all metrics take only positive values, log response scales were used for all components.

For the *Temporal changes: Natural environmental variation* data, total abundance (*N*) was fit with a model that assumed a lognormal distribution and identity link function, and Poisson distributions with log link functions were fit to S_n, S_{PIE}, and S; Poisson distributions were chosen for S_n and S_{PIE} values rounded to integers based on visual assessments that showed lognormal models fit to raw S_n and S_{PIE} values greatly underpredicted the density of ones in the data. For the *Temporal changes: Experimental or natural perturbations* data, *S* was no longer an integer value after standardizing sampling effort and all metrics were fit with models that assumed lognormal distributions and identity link functions. Both spatial data sets were fit with models that assumed lognormal distributions and identity link functions for total abundance (*N*), rarefied richness (S_n), and evenness (S_{PIE}) and a Poisson distribution and log-link function for species richness (*S*).

The *Temporal changes: Natural environmental variation* model included non-varying intercepts and slopes for year and varying intercepts and slopes for studies and cells for all responses. To allow for correlations between changes in the different responses, varying study- and cell-level parameters for all responses were drawn from a single multivariate normal distribution for each level (i.e., one for studies, one for cells; see Appendix S1: Section S1 for equations). The model fit to the *Temporal changes: Experimental or natural perturbations* data similarly included non-varying intercepts and slopes for year, and had varying intercepts for study, site, and block fitted separately for each response. For these data, correlations between changes in the different responses were modeled by drawing varying intercepts and slopes for each combination of treatment and study for all responses from a single multivariate normal distribution (see Appendix S1: Section S2 for equations).

The model fit to the *Spatial comparisons: Natural environmental variation* data included non-varying intercepts for data source (i.e., CESTES and McGill). Correlations between the different responses were modeled by assuming varying intercepts and slopes (representing the reference site and departures for all other sites from the reference, respectively) for each study and response came from a single multivariate normal distribution; over-dispersion in the richness response was modeled using an observation-level varying intercept (see Appendix S1: Section S3 for equations). The model fit to the *Spatial comparisons: Anthropogenic perturbations* data included non-varying intercepts and slopes (representing the reference [primary vegetation] category and departures from the reference for each land use category, respectively), and varying intercepts for sites and blocks were modeled separately for each response. Correlations between changes in the different responses were modeled by assuming that varying intercepts and slopes (as per the non-varying intercepts and slopes) for each combination of source and study and each response came from a single multivariate normal distribution (see Appendix S1: Section S4 for equations).

All statistical models were estimated using the Hamiltonian Monte Carlo (HMC) sampler Stan (Carpenter et al., 2017), and coded using the *brms* package (Bürkner, 2017). Details of all model specifications and the iterations and warmup periods are provided in Appendix S1, as are the priors (which were weakly regularizing). Visual inspection of the HMC chains and model diagnostics (Rhat < 1.05) showed good mixing of chains and convergence, and model adequacy assessed visually using posterior predictive checks showed that the models were able to make predictions similar to the empirical data (see Appendix S1: Figures S1–S4). Code for all analyses is archived (Blowes et al., 2022).

RESULTS

Temporal changes in perturbed environments had the highest percentage of assemblages with at least one component trend (ΔN, ΔS_n, ΔS_{PIE}, or ΔS) that differed from zero (44%), followed by spatial comparisons across land use categories (29%), and then temporal changes (21%) and spatial comparisons in naturally varying environments (12%). Component changes that differed from zero showed broadly similar patterns across data sets, with one exception: trends differing from zero for multiple components were less common for spatial comparisons between assemblages in naturally varying environments (Appendix S1: Figure S5).

Pairwise relationships between changing components were typically positive (i.e., had the same sign), though exceptions to this general pattern were found for all data sources (Figure 3). For assemblages where ΔN and ΔS_{PIE} had the same sign (though not necessarily differing statistically from zero), richness changes were typically larger in magnitude (Figure 3). In contrast, assemblages where ΔN and ΔS_{PIE} had opposing signs typically exhibited changes in richness that were smaller in magnitude (Figure 3). This tendency for countervailing changes in abundance and evenness to constrain richness changes was most apparent for spatial differences between different land use categories (Figure 3j–l), and there was a high proportion of assemblages that were growing in size ($\Delta N > 0$) where decreasing species richness ($\Delta S < 0$; Figure 3j) was accompanied by declining evenness ($\Delta S_{\mathrm{PIE}} < 0$).

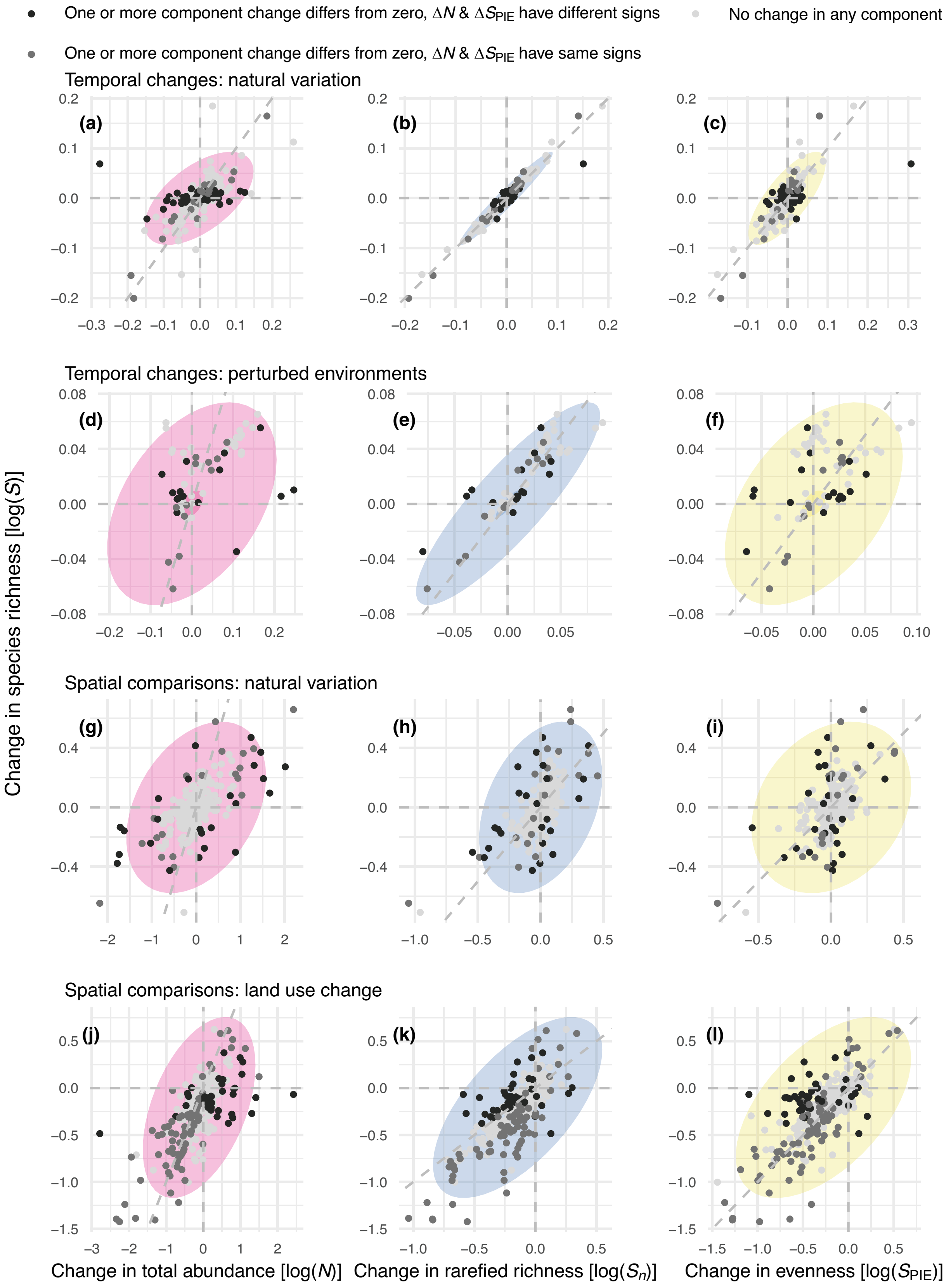
The strongest relationships were found for components changing through time, and relationships between richness and changes in the SAD, rarefied richness (Figure 3b,e) and evenness (Figures 3c,f and 4a,b), were stronger than those between changes in richness and total abundance (Figures 3a,c and 4a,b). Spatial comparisons had generally weak relationships overall. No strong relationships between changing components emerged for comparisons in natural environments (Figures 3g–i and 4c), and only weakly positive relationships between changes in abundance, evenness and richness were found for comparisons between primary vegetation and different land use categories (Figures 3j–l and 4d).

Temporal changes in naturally varying assemblages were roughly centered on zero for all metrics (Figure 3a–c). Across assemblages, altered numbers of individuals and species richness changes had a moderately positive relationship (Figure 4a), weakened predominantly by assemblages that had opposing abundance and evenness relationships (Figure 3a). In contrast, relationships between changes in species richness and rarefied richness, and between richness changes and evenness changes were strong (Figure 4a). Assemblages in perturbed environments had slightly positive temporal trends on average in all components (Figure 3d–f). Across assemblages, ΔS and ΔN (Figures 3d and 4b) and ΔS and ΔS_{PIE} (Figures 3f and 4b) had relatively weak positive relationships, whereas ΔS and ΔS_n (Figures 3e and 4b) showed a strong positive relationship.

Spatial comparisons in naturally varying environments exhibited highly heterogeneous patterns of change centered around zero for all metrics (Figure 3g–i). Decoupled component changes meant that relationships between them were generally absent or weak across assemblages (Figure 4c). Spatial comparisons between assemblages in primary vegetation and those in different land use categories were also highly heterogeneous, though there were typically fewer individuals, less even assemblages and fewer species relative to primary vegetation (Figure 3j–l). Across assemblages, land use change was typically associated with relatively weak positive relationships between changes in the components of local diversity (Figure 4d).

DISCUSSION

Our conceptual overview using individual-based rarefaction curves clearly shows how the expectation of positive pairwise relationships between changes in abundance, evenness and richness arises. If curves stretch or contract, we expect positive relationships between changes in total abundance and richness. Similarly, if curves flex upwards or downwards, positive relationships between changes in evenness and richness are expected. Rarefaction curves also show how contrasting signs of changes in abundance and evenness can strongly determine the magnitude of richness



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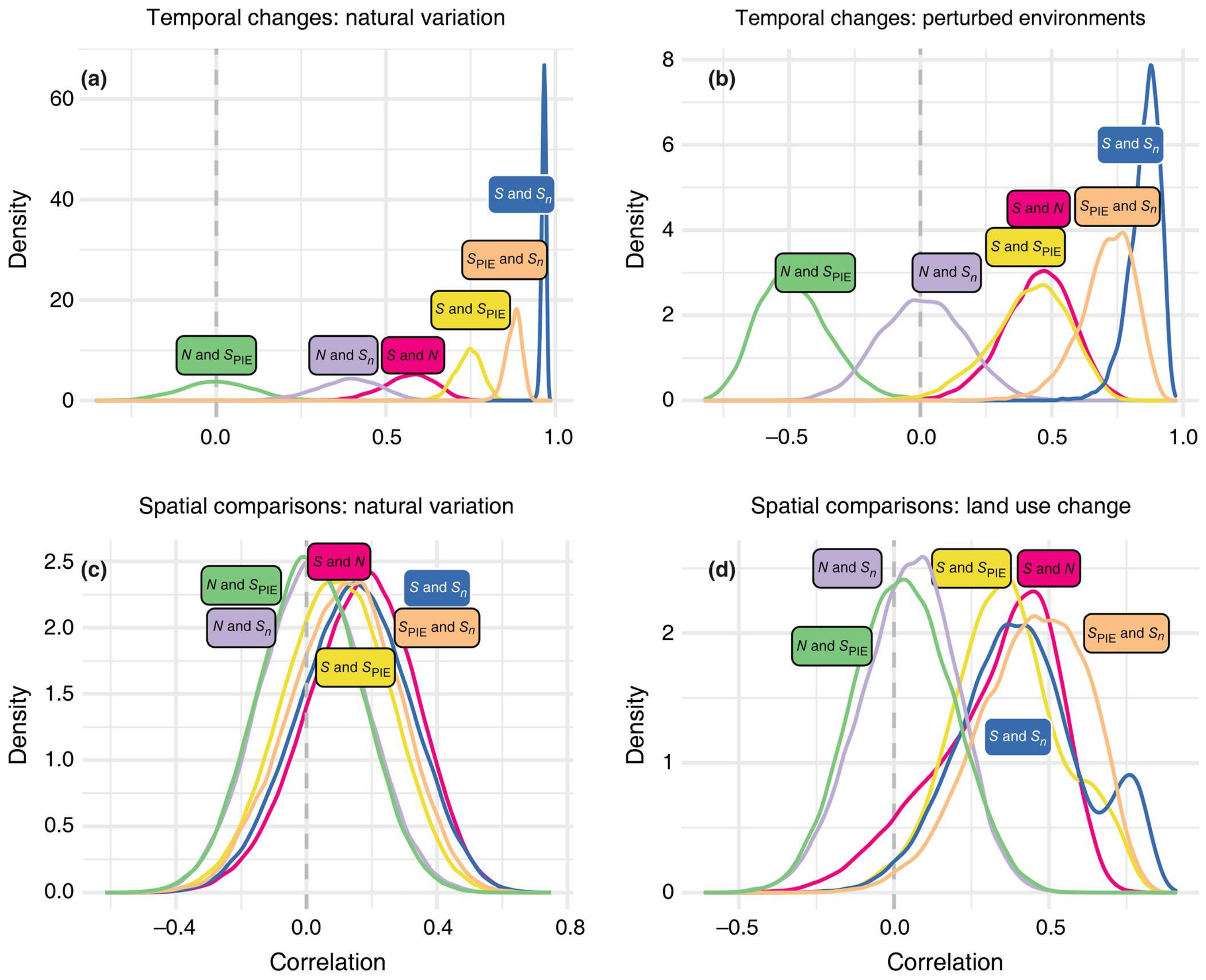

FIGURE 4 Component correlations among studies within each data source. Density plots for the posterior distribution of pairwise correlations between component changes for (a) temporal changes in naturally varying environments, (b) temporal changes in perturbed environments, (c) spatial comparisons along natural gradients, and (d) spatial comparisons between different land use categories. Correlations estimated separately for sites and land use categories relative to the references were combined on panels (c) and (d).

changes and control whether positive relationships between changes in richness and the other components (abundance and evenness) are likely. Both these predictions were generally well supported by our empirical analyses. Relationships between changes in abundance, evenness, and richness were generally positive, and richness changes were typically greater for assemblages with strictly positive pairwise relationships. Countervailing changes in total abundance and evenness, where found, often constrained the magnitude of changes in species

FIGURE 3 Empirical relationships between four components of local diversity change. Change in species richness as a function of changes in the numbers of individuals (left column), rarefied richness (middle column), and evenness (right column) for (a–c) study-level estimates of temporal changes in naturally varying environments; (d–f) estimates of temporal change for combinations of study and treatment in perturbed environments; (g–i) spatial comparisons within studies to an arbitrary reference site in naturally varying environments; and (j–l) spatial comparisons within studies of diversity in primary vegetation to that in different land use categories. Colored concentration ellipses show the confidence interval (5% and 95%) of the posterior distributions. Dotted gray lines are x and $y = 0$, and $x = y$. See Appendix S1: Figure S6 for remaining pairwise relationships. Scale of x- and y-axes vary between panels; one estimate with $\Delta\log(N) = -1.79$, $\Delta\log(S) = -3.77$, $\Delta\log(S_n) = -3.23$, $\Delta\log(S_{\mathrm{PIE}}) = -3.21$, removed from (j–l) for clarity.

richness and acted to weaken relationships between ΔN and ΔS and ΔS_{PIE} and ΔS. Spatial comparisons had the most heterogeneous relationships between changes in abundance, evenness, and richness, and in relatively natural environments changes were sufficiently decoupled that no strong relationships emerged across assemblages. In contrast, strong positive correlations between temporal changes in species richness (ΔS) and changes in metrics associated with altered SADs (ΔS_n, ΔS_{PIE}) emerged across assemblages. These temporal results show strong support for the prediction that variation in relative abundances can dominate local variation in biodiversity (Chapin et al., 2000), even when human impacts are less direct.

Variation in assemblage size does not dominate local diversity change

Overall, only ~2% of assemblages in this study (22 of 1125) had changes consistent with a strong "sampling" effect on changes in species richness (i.e., ΔN and ΔS having the same sign and being the only changes different from zero). This finding complements existing evidence showing that, despite many tests, empirical evidence for the more-individuals hypothesis (Srivastava & Lawton, 1998) remains equivocal (Storch et al., 2018; Vagle & McCain, 2020). While both (species-level) population variability and variation associated with sampling (Vagle & McCain, 2020) likely contribute to the weak response of species richness to variation in the total number of individuals, our results are broadly consistent with previous syntheses showing that broad-scale spatial variation in richness was rarely driven simply by variation in the numbers of individuals (Currie et al., 2004; Storch et al., 2018). Our results indicate that variation in local diversity, through time or from site to site, is not due to changes in assemblage size passively sampling more or less from a static SAD. Instead, we show that variation in local biodiversity can be strongly influenced by changes to species relative abundances. These changes can be occurring at multiple scales (Blowes et al., 2020; Hillebrand et al., 2008), and could reflect altered local environmental conditions (e.g., altered resource or habitat availability and diversity, eutrophication, local harvest, or exploitation), or changes at broader scales that alter the species pool (via species additions or subtractions).

Our general result showing that variation in the total abundance of an assemblage through time or space is often decoupled from changes in metrics of biodiversity such as species richness also cautions against making "apples to oranges" comparisons in the context of quantifying biodiversity change. For example, some estimates of change are based on either population-level abundance (e.g., Living Planet Index; WWF, 2020), or assemblage-level abundance (e.g., insect declines; Van Klink et al., 2020; Wagner, 2020), whereas other change estimates are based on patterns of the number or identity of species present (e.g., Dornelas et al., 2014; Newbold et al., 2015). Our results show that assuming abundance and richness changes are strongly correlated will often be an oversimplification. Moreover, the importance of altered relative abundances for local biodiversity variation means that biodiversity change estimates will frequently depend on whether changes in species relative abundances influence the metrics used (see e.g., Antão et al. 2020b).

Contrasting component relationships between temporal changes versus spatial comparisons of biodiversity

Relationships between changing components of biodiversity showed strikingly different patterns between temporal changes and spatial comparisons. Moreover, these differences were generally greater than those found between naturally varying and perturbed assemblages, for either temporal changes or spatial comparisons.

Pairwise relationships between changes in abundance, evenness, and richness were typically weak for spatial comparisons. Decoupling was greatest, and pairwise relationships weakest, for changes between sites experiencing relatively natural environmental variation. However, given our simple conceptual framework shows that some degree of interdependence cannot be avoided, we caution against overinterpreting the relative independence of these component changes, and further analyses examining component change relationships along continuous spatial gradients are warranted. Indeed, evenness and richness are never numerically independent (Jost, 2010), and the weak overall relationship between changes in richness and evenness for these data was in part due to assemblages with countervailing changes in abundance and evenness. Most importantly, these highly variable component changes further emphasize the need for a holistic approach to quantifying biodiversity change (Avolio et al., 2021; Chase et al., 2018a).

Our prediction that the signs of changes in abundance and evenness can strongly determine the magnitude of richness changes was most evident for spatial contrasts between primary vegetation and other land use categories (Newbold et al., 2015, 2020). Assemblages with the greatest declines in abundance and evenness had the greatest richness declines. In contrast, when abundance and evenness changes had opposing signs, richness changes were tempered. Indeed, countervailing abundance and evenness changes were frequently associated with components other than species richness (i.e., ΔN, ΔS_n, and/or ΔS_{PIE}) having a trend that differed from zero across all data sources (Appendix S1: Table S1). This highlights that even apparently decoupled or weakly correlated component changes have interdependencies that can remain important determinants of variation in biodiversity.

In contrast to assemblage differences between sites, there was strong coupling between species richness and SAD changes through time. In particular, the strength of the relationship between ΔS_{n} and ΔS resulted in estimates of change being similar for most assemblage time series in relatively natural environments (Figure 3b). In some cases, this occurred despite countervailing changes in total abundance and evenness (Figure 3a,b). For assemblages where abundance and evenness changed in the same direction, similar estimates of ΔS_n and ΔS indicate that abundance changes were occurring along a relatively flat region of the individual-based rarefaction curve. This shows that changes to the total number of individuals need not strongly influence species richness, even where signs are the same and they have a positive relationship. The strong association between richness changes and altered relative abundances has important implications for examining causes and/or consequences of biodiversity change (Crowder et al., 2010; Hillebrand et al., 2008). Even where the expected positive relationships between abundance, evenness and richness are found, we can more fully understand assemblage changes when all component changes are examined simultaneously.

While both approaches, time series and spatial comparisons (or space-for-time substitutions), have contributed to our understanding of biodiversity change, the relative merits of each for our understanding of ecological dynamics has not been discussed much (Adler et al., 2020). The largely decoupled component changes found here for spatial comparisons suggest that too much focus on average changes across assemblages, such as those in total abundance or in species richness, risks masking highly heterogeneous changes occurring within assemblages in multiple components. Moreover, decoupled, heterogeneous component changes complicate using spatial comparisons to infer temporal changes. The smaller effect sizes found here for time series indicates greater inertia compared to site-to-site variation. More generally, the strong role of changes to the SAD for variation in local biodiversity suggests that deepening our understanding of altered patterns of relative abundance across scales represents an important direction for future theoretical and empirical work. Here our focus has been on numerical relationships between component changes, and using process-based models (e.g., Thompson et al., 2020) to examine how altered metacommunity dynamics impact patterns of relative abundance across scales could help our understanding of how different processes impact component relationships. Similarly, empirical studies could ask whether local environmental changes are affecting evenness, or if changes occurring at broader spatial scales are impacting the size of species pool and the regional SAD?

CONCLUSIONS

We found strong correlations between changes in the SAD and species richness changes through time, whereas relationships between abundance and richness changes for both temporal and spatial diversity variation were generally weak. Our findings confirm that altered species relative abundances, and/or changes to the size of the species pool, often strongly influence local diversity change (Chapin et al., 2000), even where human impacts are less direct. However, our results also reinforce cautions against examining changes to any one component of biodiversity change in isolation (e.g., Avolio et al., 2021; Chase et al., 2018a; Wilsey et al., 2005).

To be most useful, quantifying (co)variation in the different components of biodiversity needs to be done coherently. Individual-based rarefaction curves and associated metrics can provide a visually intuitive characterization of relationships among changing components of biodiversity. While ecologists are increasingly looking beyond species richness to quantify biodiversity change (e.g., Dornelas et al., 2014; Hillebrand et al., 2018), different components of biodiversity and its change within assemblages are most often analyzed independently and frequently with metrics lacking conceptual unity. Conceptually and empirically, our results emphasize that changes to the most frequently quantified aspects of biodiversity, including changes to the numbers of individuals, and the relative abundance and total number of species are highly interdependent. Examining how within-assemblage component changes covary with potential drivers could reveal insights masked by independent estimates of aggregate change across assemblages, and provide new information for understanding variation in biodiversity in the Anthropocene.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data used in the manuscript are already in the public domain. BioTIME (BioTIME Consortium, 2018; Dornelas et al., 2018) is accessible through the BioTIME website (http://biotime.st-andrews.ac.uk) and archived at https://zenodo.org/record/1095627. Perturbed time series were compiled using the data portal of the Environmental Data Initiative (https://portal.edirepository.org/nis/home.jsp), with query details described in the *Methods* section; code for compilation and standardization is archived in combination with code for all analyses (Blowes et al., 2022). The 2016 release of the PREDICTS database (Hudson et al., 2016) as used here is available at https://doi.org/10.5519/0066354. McGill's SAD data were previously archived (Chase et al., 2018b): https://doi.org/10.6084/m9.figshare.6945704. CESTES database (Jeliazkov & the CESTES consortium, 2019) is available at https://doi.org/10.25829/idiv.286-21-2695. Code for all analyses archived (with code for accessing and cleaning the EDI data; Blowes et al., 2022) at https://doi.org/10.5281/zenodo.6651628.

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REFERENCES

Adler, P. B., E. P. White, and M. H. Cortez. 2020. "Matching the Forecast Horizon with the Relevant Spatial and Temporal Processes and Data Sources." *Ecography* 43: 1–11.

Antão, L. H., A. E. Bates, S. A. Blowes, C. Waldock, S. R. Supp, A. E. Magurran, M. Dornelas, and A. M. Schipper. 2020. "Temperature-Related Biodiversity Change across Temperate Marine and Terrestrial Systems." *Nature Ecology & Evolution* 4: 927–33.

Antão, L. H., J. Pöyry, R. Leinonen, and T. Roslin. 2020. "Contrasting Latitudinal Patterns in Diversity and Stability in a High-Latitude Species-Rich Moth Community." *Global Ecology and Biogeography* 29: 896–907.

Avolio, M. L., K. J. Komatsu, S. L. Collins, E. Grman, S. E. Koerner, A. T. Tredennick, K. R. Wilcox, S. Baer, E. H. Boughton, and A. J. Britton. 2021. "Determinants of Community Compositional Change Are Equally Affected by Global Change." *Ecology Letters* 24: 1892–904.

BioTIME Consortium. 2018. "BioTIME." Zenodo. https://doi.org/10.5281/zenodo.5026943.

Blowes, S. A., J. M. Chase, A. Di Franco, O. Frid, N. J. Gotelli, P. Guidetti, T. M. Knight, F. May, D. J. McGlinn, and F. Micheli. 2020. "Mediterranean Marine Protected Areas Have Higher Biodiversity Via Increased Evenness, Not Abundance." *Journal of Applied Ecology* 57: 578–89.

Blowes, S. A., S. R. Supp, L. H. Antão, A. Bates, H. Bruelheide, J. M. Chase, F. Moyes, et al. 2019. "The Geography of Biodiversity Change in Marine and Terrestrial Assemblages." *Science* 366: 339–45.

Blowes, S., G. Daskalova, M. Dornelas, T. Engel, N. Gotelli, A. Magurran, I. Martins, et al. 2022. "sablowes/MulticomponentBioChange: MulticomponentBioChange v1." Zenodo. https://doi.org/10.5281/zenodo.6651628.

Bürkner, P.-C. 2017. "brms: An R Package for Bayesian Multilevel Models Using Stan." *Journal of Statistical Software* 80: 1–28.

Carpenter, B., A. Gelman, M. D. Hoffman, D. Lee, B. Goodrich, M. Betancourt, M. Brubaker, J. Guo, P. Li, and A. Riddell. 2017. "Stan: A Probabilistic Programming Language." *Journal of Statistical Software* 76: 1–32. https://doi.org/10.18637/jss.v076.i01.

Caswell, H. 1976. "Community Structure: A Neutral Model Analysis." *Ecological Monographs* 46: 327–54.

Cayuela, L., N. J. Gotelli, and R. K. Colwell. 2015. "Ecological and Biogeographic Null Hypotheses for Comparing Rarefaction Curves." *Ecological Monographs* 85: 437–55.

Chapin, F. S., III, E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, and S. E. Hobbie. 2000. "Consequences of Changing Biodiversity." *Nature* 405: 234–42.

Chase, J. M., B. J. McGill, D. J. McGlinn, F. May, S. A. Blowes, X. Xiao, T. M. Knight, O. Purschke, and N. J. Gotelli. 2018a. "Embracing Scale-Dependence to Achieve a Deeper Understanding of Biodiversity and its Change across Communities." *Ecology Letters* 21: 1737–51.

Chase, J. M., B. J. McGill, D. J. McGlinn, F. May, S. A. Blowes, X. Xiao, T. M. Knight, O. Purschke, and N. J. Gotelli. 2018b. "Appendix 1 from Chase et al. Embracing Scale-Dependence to Achieve a Deeper Understanding of Biodiversity and its Change across Communities. Contains Raw Data and References for Rarefaction Curves and Analyses Presented in Figures 2 and 3." Figshare. Dataset. https://doi.org/10.6084/m9.figshare.6945704.v3.

Coleman, B. D., M. A. Mares, M. R. Willig, and Y.-H. Hsieh. 1982. "Randomness, Area, and Species Richness." *Ecology* 63: 1121–33.

Connell, J. H. 1978. "Diversity in Tropical Rain Forests and Coral Reefs." *Science* 199: 1302–10.

Connor, E. F., and E. D. McCoy. 1979. "The Statistics and Biology of the Species-Area Relationship." *The American Naturalist* 113: 791–833.

Crowder, D. W., T. D. Northfield, M. R. Strand, and W. E. Snyder. 2010. “Organic Agriculture Promotes Evenness and Natural Pest Control.” *Nature* 466: 109–12.

Currie, D. J. 1991. “Energy and Large-Scale Patterns of Animal-and Plant-Species Richness.” *The American Naturalist* 137(1): 27–49.

Currie, D. J., G. G. Mittelbach, H. V. Cornell, R. Field, J.-F. Guégan, B. A. Hawkins, D. M. Kaufman, J. T. Kerr, T. Oberdorff, and E. O’Brien. 2004. “Predictions and Tests of Climate-Based Hypotheses of Broad-Scale Variation in Taxonomic Richness.” *Ecology Letters* 7: 1121–34.

Dornelas, M., L. H. Antao, F. Moyes, A. E. Bates, A. E. Magurran, D. Adam, A. A. Akhmetzhanova, et al. 2018. “BioTIME: A Database of Biodiversity Time Series for the Anthropocene.” *Global Ecology and Biogeography* 27: 760–86.

Dornelas, M., N. J. Gotelli, B. McGill, H. Shimadzu, F. Moyes, C. Sievers, and A. E. Magurran. 2014. “Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss.” *Science* 344: 296–9.

Fisher, R. A., A. S. Corbet, and C. B. Williams. 1943. “The Relation between the Number of Species and the Number of Individuals in a Random Sample of an Animal Population.” *The Journal of Animal Ecology* 12(1): 42–58.

Gaston, K. J. 2000. “Global Patterns in Biodiversity.” *Nature* 405: 220–7.

Gotelli, N. J., and R. K. Colwell. 2001. “Quantifying Biodiversity: Procedures and Pitfalls in the Measurement and Comparison of Species Richness.” *Ecology Letters* 4: 379–91.

He, F., and P. Legendre. 2002. “Species Diversity Patterns Derived from Species–Area Models.” *Ecology* 83: 1185–98.

Hill, M. O. 1973. “Diversity and Evenness: A Unifying Notation and its Consequences.” *Ecology* 54: 427–32.

Hillebrand, H., D. M. Bennett, and M. W. Cadotte. 2008. “Consequences of Dominance: A Review of Evenness Effects on Local and Regional Ecosystem Processes.” *Ecology* 89: 1510–20.

Hillebrand, H., B. Blasius, E. T. Borer, J. M. Chase, J. A. Downing, B. K. Eriksson, C. T. Filstrup, W. S. Harpole, D. Hodapp, and S. Larsen. 2018. “Biodiversity Change Is Uncoupled from Species Richness Trends: Consequences for Conservation and Monitoring.” *Journal of Applied Ecology* 55: 169–84.

Hudson, L. N., T. Newbold, S. Contu, S. L. Hill, I. Lysenko, A. De Palma, H. R. Phillips, T. I. Alhusseini, F. E. Bedford, and D. J. Bennett. 2017. “The Database of the Predicts (Projecting Responses of Ecological Diversity in Changing Terrestrial Systems) Project.” *Ecology and Evolution* 7: 145–88.

Hudson, L., T. Newbold, S. Contu, S. L. Hill, I. Lysenko, A. De Palma, H. Phillips, et al., 2016. “The 2016 Release of the PREDICTS Database [Data Set].” Natural History Museum. https://doi.org/10.5519/0066354.

Hughes, A. R., J. E. Byrnes, D. L. Kimbro, and J. J. Stachowicz. 2007. “Reciprocal Relationships and Potential Feedbacks between Biodiversity and Disturbance.” *Ecology Letters* 10: 849–64.

Hurlbert, S. H. 1971. “The Nonconcept of Species Diversity: A Critique and Alternative Parameters.” *Ecology* 52: 577–86.

Jeliazkov, A., and The CESTES Consortium. 2019. “A Global Database for Metacommunity Ecology: Species, Traits, Environment and Space—version 1.0 (CESTES v1.0).” https://doi.org/10.25829/idiv.286-21-2695.

Jeliazkov, A., D. Mijatovic, S. Chantepie, N. Andrew, R. Arlettaz, L. Barbaro, N. Barsoum, et al. 2020. “A Global Database for Metacommunity Ecology, Integrating Species, Traits, Environment and Space.” *Scientific Data* 7: 1–15.

Jones, F. A., and A. E. Magurran. 2018. “Dominance Structure of Assemblages Is Regulated over a Period of Rapid Environmental Change.” *Biology Letters* 14: 20180187.

Jost, L. 2006. “Entropy and Diversity.” *Oikos* 113: 363–75.

Jost, L. 2007. “Partitioning Diversity into Independent Alpha and Beta Components.” *Ecology* 88: 2427–39.

Jost, L. 2010. “The Relation between Evenness and Diversity.” *Diversity* 2: 207–32.

Kreft, H., W. Jetz, J. Mutke, G. Kier, and W. Barthlott. 2008. “Global Diversity of Island Floras from a Macroecological Perspective.” *Ecology Letters* 11: 116–27.

Latham, R. E., and R. E. Ricklefs. 1993. “Global Patterns of Tree Species Richness in Moist Forests: Energy-Diversity Theory Does Not Account for Variation in Species Richness.” *Oikos* 67(2): 325–33.

MacArthur, R. H. 1965. “Patterns of Species Diversity.” *Biological Reviews* 40: 510–33.

MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.

McGill, B. J. 2011a. “Linking Biodiversity Patterns by Autocorrelated Random Sampling.” *American Journal of Botany* 98: 481–502.

McGill, B. J. 2011b. In *Species Abundance Distributions. In Biological Diversity: Frontiers in Measurement & Assessment*, edited by A. Magurran and B. McGill, 105–22. Oxford: Oxford University Press.

McGill, B. J., R. S. Etienne, J. S. Gray, D. Alonso, M. J. Anderson, H. K. Benecha, M. Dornelas, et al. 2007. “Species Abundance Distributions: Moving beyond Single Prediction Theories to Integration within an Ecological Framework.” *Ecology Letters* 10: 995–1015.

McGlinn, D. J., X. Xiao, F. May, N. J. Gotelli, T. Engel, S. A. Blowes, T. M. Knight, O. Purschke, J. M. Chase, and B. J. McGill. 2019. “Measurement of Biodiversity (MoB): A Method to Separate the Scale-Dependent Effects of Species Abundance Distribution, Density, and Aggregation on Diversity Change.” *Methods in Ecology and Evolution* 10: 258–69.

Menge, B. A., E. L. Berlow, C. A. Blanchette, S. A. Navarrete, and S. B. Yamada. 1994. “The Keystone Species Concept: Variation in Interaction Strength in a Rocky Intertidal Habitat.” *Ecological Monographs* 64: 249–86.

Miller, A. D., S. H. Roxburgh, and K. Shea. 2011. “How Frequency and Intensity Shape Diversity–Disturbance Relationships.” *Proceedings of the National Academy of Sciences USA* 108: 5643–8.

Mittelbach, G. G., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, S. I. Dodson, and L. Gough. 2001. “What Is the Observed Relationship between Species Richness and Productivity?” *Ecology* 82: 2381–96.

Newbold, T., L. N. Hudson, S. L. Hill, S. Contu, I. Lysenko, R. A. Senior, L. Börger, D. J. Bennett, A. Choimes, and B. Collen. 2015. “Global Effects of Land Use on Local Terrestrial Biodiversity.” *Nature* 520: 45–50.

Newbold, T., L. N. Hudson, S. Contu, S. L. Hill, J. Beck, Y. Liu, C. Meyer, H. R. Phillips, J. P. Scharlemann, and A. Purvis. 2018. “Widespread Winners and Narrow-Ranged Losers: Land

Use Homogenizes Biodiversity in Local Assemblages Worldwide.” *PLoS Biology* 16: e2006841.

Newbold, T., P. Oppenheimer, A. Etard, and J. J. Williams. 2020. “Tropical and Mediterranean Biodiversity Is Disproportionately Sensitive to Land-Use and Climate Change.” *Nature Ecology & Evolution* 4: 1630–8.

Olszewski, T. D. 2004. “A Unified Mathematical Framework for the Measurement of Richness and Evenness within and among Multiple Communities.” *Oikos* 104: 377–87.

Paine, R. T. 1974. “Intertidal Community Structure.” *Oecologia* 15: 93–120.

Palmer, M. W., D. B. Clark, and D. A. Clark. 2000. “Is the Number of Tree Species in Small Tropical Forest Plots Nonrandom?” *Community Ecology* 1: 95–101.

Preston, F. W. 1962. “The Canonical Distribution of Commonness and Rarity: Part I.” *Ecology* 43: 185–215.

Scheffers, B. R., L. De Meester, T. C. Bridge, A. A. Hoffmann, J. M. Pandolfi, R. T. Corlett, S. H. Butchart, P. Pearce-Kelly, K. M. Kovacs, and D. Dudgeon. 2016. “The Broad Footprint of Climate Change from Genes to Biomes to People.” *Science* 354: aaf7671.

Scheiner, S. M., and M. R. Willig. 2005. “Developing Unified Theories in Ecology as Exemplified with Diversity Gradients.” *The American Naturalist* 166: 458–69.

Shmida, A. V. I., and M. V. Wilson. 1985. “Biological Determinants of Species Diversity.” *Journal of Biogeography* 12(1): 1–20.

Soininen, J., S. Passy, and H. Hillebrand. 2012. “The Relationship between Species Richness and Evenness: A Meta-Analysis of Studies across Aquatic Ecosystems.” *Oecologia* 169: 803–9.

Srivastava, D. S., and J. H. Lawton. 1998. “Why more Productive Sites Have More Species: An Experimental Test of Theory Using Tree-Hole Communities.” *The American Naturalist* 152: 510–29.

Stirling, G., and B. Wilsey. 2001. “Empirical Relationships between Species Richness, Evenness, and Proportional Diversity.” *The American Naturalist* 158: 286–99.

Storch, D., E. Bohdalková, and J. Okie. 2018. “The More-Individuals Hypothesis Revisited: The Role of Community Abundance in Species Richness Regulation and the Productivity–Diversity Relationship.” *Ecology Letters* 21: 920–37.

Storch, D., I. Šímová, J. Smyčka, E. Bohdalková, A. Toszogyova, and J. G. Okie. 2022. “Biodiversity Dynamics in the Anthropocene: How Human Activities Change Equilibria of Species Richness.” *Ecography* 2022. https://doi.org/10.1111/ecog.05778.

Thompson, P. L., L. M. Guzman, L. De Meester, Z. Horváth, R. Ptacnik, B. Vanschoenwinkel, D. S. Viana, and J. M. Chase. 2020. “A Process-Based Metacommunity Framework Linking Local and Regional Scale Community Ecology.” *Ecology Letters* 23: 1314–29.

Tilman, D. 1982. *Resource Competition and Community Structure*. Princeton: Princeton University Press.

Vagle, G. L., and C. M. McCain. 2020. “Natural Population Variability May Be Masking the More-Individuals Hypothesis.” *Ecology* 101: e03035.

Van Klink, R., D. E. Bowler, K. B. Gongalsky, A. B. Swengel, A. Gentile, and J. M. Chase. 2020. “Meta-Analysis Reveals Declines in Terrestrial but Increases in Freshwater Insect Abundances.” *Science* 368: 417–20.

Vilà, M., J. L. Espinar, M. Hejda, P. E. Hulme, V. Jarošík, J. L. Maron, J. Pergl, U. Schaffner, Y. Sun, and P. Pyšek. 2011. “Ecological Impacts of Invasive Alien Plants: A Meta-Analysis of their Effects on Species, Communities and Ecosystems.” *Ecology Letters* 14: 702–8.

Wagner, D. L. 2020. “Insect Declines in the Anthropocene.” *Annual Review of Entomology* 65: 457–80.

Wilsey, B. J., D. R. Chalcraft, C. M. Bowles, and M. R. Willig. 2005. “Relationships among Indices Suggest that Richness Is an Incomplete Surrogate for Grassland Biodiversity.” *Ecology* 86: 1178–84.

Wright, D. H. 1983. “Species-Energy Theory: An Extension of Species-Area Theory.” *Oikos* 41: 496–506.

WWF. 2020. *Living Planet Report 2020-Bending the Curve of Biodiversity Loss*. Gland: World Wildlife Fund.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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