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 how changes to the numbers of individuals, the evenness of species' relative abundances, and the total number of species covary remains limited, both theoretically and empirically. Using individual-based rarefaction curves, we first show how expected positive relationships among changes in abundance, evenness and richness arise, and how they can break down. We then examined the interdependency between changes in abundance, evenness and richness more than 1100 assemblages sampled either through time or across space. As expected, richness changes were greatest when abundance and evenness changed in the same direction, whereas countervailing changes in abundance and evenness acted to constrain the magnitude of changes in species richness. Site-to-site variation in diversity was greater than rates of change through time. Moreover, changes in abundance, evenness, and richness were often spatially decoupled, and pairwise relationships between changes in these components were weak between sites. In contrast, changes in species richness and relative abundance were strongly correlated for assemblages sampled through time, meaning temporal changes in local biodiversity showed greater inertia and stronger relationships between the components changes when compared to site-to-site variation. Both temporal and spatial variation in local assemblage diversity were rarely attributable solely to changes in assemblage size sampling more or less of a static species abundance distribution. Instead, changing species' relative abundances often dominate local variation in diversity. Moreover, how these altered patterns of relative abundance combine with changes to total abundance strongly determine the magnitude of richness changes. Interdependencies found here suggest looking beyond changes in abundance, evenness and

richness as separate responses offering unique insights into diversity change can increase our understanding of biodiversity change.

Introduction

Measures of biodiversity and its change are frequently used to determine the magnitude, direction and pace of ecosystem modifications (Diaz et al. 2019). Descriptions of the distribution and abundance of organisms are central to basic ecological research (Krebs 1972, Andrewartha & Birch 1984), and biodiversity itself is a multifaceted concept that combines information on the distribution and abundance of multiple species. There have been numerous metrics proposed to quantify different aspects of biodiversity (e.g., Hill 1973, Gotelli and Colwell 2001, Magurran & McGill 2011, Chao and Jost 2012), most of which depend on sample effort and scale (Rosenzweig 1995, Whittaker et al. 2001, McGill 2011a, Chase & Knight 2013). This inherent complexity in the quantification of biodiversity poses significant challenges for syntheses of its temporal and spatial variation.

Here, we argue that in order to understand biodiversity change, it is critical to look beyond aggregate metrics of biodiversity. Specifically, we need to examine how changes in the key components that lead to these aggregate metrics interact and combine with each other. Currently, different components that underlie biodiversity represent important, but largely independent lines of evidence for biodiversity change. For example, one body of work on biodiversity change is focused on quantifying total abundances of all species within assemblages, such as recent work documenting declines of birds (e.g., Rosenberg et al. 2019) and insects (Wagner 2020). A related body of work focuses instead on population-level ‘winners’ and ‘losers’ within assemblages (McKinney & Lockwood 2000), species with increasing and decreasing trends in occupancy or abundance (e.g., WWF 2020). However, changes in the means of these metrics do not capture the variability and nuance in either the assemblage- and population-level abundance trends across space and among taxa (e.g., van Klink et al. 2020, Daskalova et al. 2020a, Leung et al. 2020). Moreover, trends in total assemblage abundance provide only one window into potentially complex changes that could be occurring in other components of biodiversity, and while changes to species' relative abundances do influence biodiversity metrics, population-level trends themselves cannot be used to calculate assemblage-level (i.e., biodiversity) metrics (e.g., Dornelas et al. 2019). Even when quantifying similar response metrics (i.e., species richness), syntheses of biodiversity change in space due to differential land use conditions have found declines of species richness (e.g., Newbold et al. 2015, 2018), whereas analyses of time series have shown that, on average, species richness increases roughly offset decreases (Dornelas et al. 2014, Blowes et al. 2019), despite often significant modifications to climate and habitat (Antão et al. 2020a, Daskalova et al. 2020b). Finally, the prediction that human activities likely impact species relative abundances more frequently than they do species occurrences (Chapin et al. 2000), has not resulted in a strong focus on assemblage-level evenness in existing syntheses (but see, e.g., Crowder et al. 2010, Zhang et al. 2012, Jones & Magurran 2018). Importantly, changes in all these components, abundance, evenness and richness, 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 observed biodiversity change.

The biodiversity estimated from a given (local) sample depends largely on two factors (see e.g., He and Legendre 2002, McGill 2011a). First, the total number of individuals (Fisher et al. 1943, Preston 1962), whereby fewer individuals are expected to (non-linearly) lead to fewer species in a given sample. Second, the total number of species and their relative abundances within the species pool, which we refer to as the Species Abundance Distribution (SAD; McGill et al.

2007). Samples will have lower species richness when the species pool has relatively few highly abundant species and many rare species (i.e., less even SADs), compared to samples from a species pool of the equivalent size with more equitable species abundances. 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 could differ considerably.

Variation in the total number of individuals is a long-standing, first-order explanation of variation in richness (Fisher et al. 1943, Coleman et al. 1982, Srivastava & Lawton 1998, Gaston 2000, Scheiner & Willig 2005, Storch et al. 2018). A positive relationship between numbers of individuals and species richness can be derived via multiple mechanisms (Scheiner & Willig 2005), and is sometimes termed the ‘more-individuals hypothesis’ (Srivastava & Lawton 1998), or, in the context of species-area relationships, the ‘passive sampling hypothesis’ (Coleman et al. 1982). Species richness has been posited to increase in places that are larger (Connor & McCoy 1979) or more productive (Wright 1983), simply because of increased numbers of individuals. Likewise, some anthropogenic drivers can 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 (Newbold et al. 2015, Blowes et al. 2020, Jones et al. 2020). If biodiversity varies primarily via changes in the numbers of individuals, positive relationships between altered numbers of individuals and species richness changes are expected. In such cases, however, other metrics of species diversity that control for variation in numbers of individuals, such as the richness expected for a given number of individuals—known as rarefied richness—should be relatively unchanged.

Changes to the shape of the SAD can also drive biodiversity change 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 (Tilman 1982, Shmida & Wilson 1985), interspecific interactions (e.g., keystone predation; Paine 1974, Menge et al. 2020), 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 favour some species and disfavour 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 such cases, biodiversity change will be characterised by positive relationships between species richness change and changes in metrics sensitive to relative abundance, such as rarefied richness, evenness and diversity metrics sensitive to species' relative abundances.

The 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 datasets, 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. 2018). Collectively, these studies suggest that static biodiversity estimates are multidimensional, and that different metrics can covary or be unrelated.

Where ecologists have quantified changes in multiple components of local diversity, the focus has typically been on averages across assemblages, where each component is 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 (the complement of evenness) are highly variable among datasets, but on average, have no directional trend (Dornelas et al. 2014, Jones & Magurran 2018, Blowes et al. 2019). 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 overview the theoretical context for how the main components underlying local biodiversity (total abundance, evenness and species richness) can change in time or space using individual-based rarefaction curves. We focus on six simplified scenarios of change with contrasting patterns of covariation among component changes, showing that the signs of changes in total abundance and evenness strongly determine whether all components can be expected to have positive pairwise relationships. We then empirically assess the relationships between abundance, evenness and richness changes using compilations of ecological assemblage data. This includes data from 351 assemblages varying through time and 774 assemblages monitored across space. In the face of natural and anthropogenically-driven environmental variation in time and space, we ask whether changes in the components of local biodiversity show positive relationships (i.e., change in the same direction). Or, 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?

Quantifying the multicomponent nature of biodiversity change

Individual-based rarefaction curves (Hurlbert 1971, Gotelli & Colwell 2001) are well suited for visualising and characterising empirical variation in total abundance, evenness and species richness (Appendix 1; Figure 1; Cayuela et al. 2015, Chase et al. 2018, McGlinn et al. 2019).

We use four metrics associated with the IBR (Figure 1) to show how changes in the different components are related to each other. Plotting pairwise relationships between changes in species richness (ΔS) and total abundance (ΔN; Fig. 2a), and two metrics sensitive to changes in relative abundance (ΔS_n, Fig. 2b; and, ΔS_{PIE}, Fig. 2c; see Chase et al. 2018, and Appendix 1 for further details on metrics and interpretation) show whether changing components have positive relationships (i.e., the same sign) or otherwise, and how altered patterns of total and relative abundance combine in terms of changes in species richness. We next outline how expectations of positive relationships between changing components arise and break down using six simplified scenarios of change.

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 2d) result in ΔS and ΔN being positively related with the same sign (Figure 2a), whereas ΔS_n and ΔS_{PIE} will be approximately zero (and have a weak or no relationship with ΔS, Figure 2b, c, respectively). This has been variously referred to in the literature as a sampling effect, the rarefaction effect, the more-individuals hypothesis, and the passive sampling hypothesis (Coleman et al. 1982, Gotelli & Cowell 2001, Palmer et al. 2000, Srivastava & Lawton 1998).

The expected positive relationship between changes in richness (ΔS) and abundance (ΔN) weakens when altered numbers of species are associated only with changes to relative abundance (i.e., $\Delta N \sim 0$). Changes in species richness associated with relatively rare species would be seen in a positive relationship between ΔS and ΔS_n (Figure 2e), whereas SAD changes due, for e.g., to increased numbers of common species, increased evenness, or increases to the size of the species pool result in a positive relationship between ΔS and ΔS_{PIE} (Figure 2f). Even where numbers of individuals increase ($\Delta N > 0$), expected gains in species richness can be constrained by decreased evenness, resulting in no changes to species richness (Figure 2g), or possibly, a negative relationship between ΔS and ΔN, when changes to the SAD are sufficiently strong (Figure 2h). Alternately, 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 2i).

A positive relationship between ΔS and ΔS_{n} (Figure 2b) can occur due to altered numbers of rare species (Figure 2e), or changes to the species pool size or the evenness of relative abundances (Figure 2f). However, changes in species richness associated only with altered numbers of individuals (Figure 2d), or changes in total abundance and evenness with opposing signs (Figure 2g-i) can weaken or reverse the expectation of a positive relationship between ΔS and ΔS_{n}.

As assemblages become more or less even, numbers of species are expected to change in a similar direction (He & Legendre 2002), resulting in an expected positive relationship between ΔS and ΔS_{PIE} (Figure 2c). However, again, the expectation of positive relationship between changes in richness (ΔS) and evenness (ΔS_{PIE}) can be weakened if richness changes are associated only with altered numbers of individuals (Figure 2d), or where only the number of rare species are changing (Figure 2e). Finally, changes in total abundance (ΔN) and evenness (ΔS_{PIE}) with opposing signs (Figure 2g-i) will tend to weaken and possibly reverse the expected positive relationship between ΔS and ΔS_{PIE}. Such changes could occur, for example, if altered environmental conditions strongly favour some species and disfavour others, resulting in higher abundances of one or only a few dominant species.

Our rarefaction-based framework shows that the key to understanding any breakdown of the expected positive relationships between changing abundance, evenness and richness are in the signs of changes in total abundance and evenness (i.e., ΔN and ΔS_{PIE}). ΔN is associated with the curve stretching or contracting along the x-axis, and ΔS_{PIE} characterises changes that flex the curve up or down from the base along the y-axis (Olszewski 2004). If ΔN and ΔS_{PIE} have different signs, the strength of their relationships with ΔS will be diminished, and the likelihood of patterns of assemblage change moving from the lower left and upper right quadrants (component changes with the same sign and positive relationships) towards, and possibly into, the upper left and lower right quadrants (opposing signs and negative pairwise relationships) of Figure 2a-c increases.

Overall, we expect to see positive relationships between abundance, evenness and richness changes. However, more complex interdependencies are possible, and the assumption that these components represent independent response variables (e.g., Dornelas et al. 2014, Newbold et al. 2015) is questionable. To evaluate empirical relationships among component changes we use data from 587 studies and 1125 assemblages and models that allow for correlations between component changes; 299 of these studies examined changes through time, and 288 document comparisons across spatial locations. We expect to find larger changes in species richness for assemblages where total abundance and evenness move in the same direction (i.e., ΔN and ΔS_{PIE} have the same sign, and all pairwise relationships between changes in abundance, evenness and richness are positive). If observed local diversity changes are dominated by altered total abundances and species richness, the strong positive relationships between ΔS and ΔN, but weaker relationships between ΔS and ΔS_n, as well as between ΔS and ΔS_{PIE} should emerge. 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 assemblage change.

Methods

Overview

We took a comparative approach to examine relationships between changes in total abundance, evenness and species richness. Specifically, we sought data documenting assemblages varying either through time or space, in one of either predominantly naturally-varying or perturbed environments. The saturating, asymptotic nature of the IBR means that many common functions used in ecology, such as the Michaelis-Menten or the type-II functional response offer multiple parameterisations for inferences regarding different parts of the curve (see Bolker 2008 for examples of different parameterisations). However, for consistency with the conceptual framework introduced above, and because ecologists are more familiar with direct examinations of diversity measures, we estimated four metrics: total numbers of individuals (N), the expected number of species for n individuals (S_n), the numbers equivalent conversion of the Probability of Interspecific Encounter (S_{PIE}, which hereafter, we refer to as evenness due to its sensitivity to the relative abundance of species), and total species richness (S). The number of individuals, n, used in the calculation of rarefied richness (S_n) was the minimum abundance observed for a given comparison (i.e., within a time series or for a particular spatial comparison); observations where

$n < 5$ were discarded before analysis. We took this approach to rarefaction rather than first extrapolating to two times the observed number of individuals (as advocated, e.g., by Chao et al. 2014) for consistency with the conceptual framework, and to simplify the interpretation of relationships between changes in abundance, evenness and richness.

To estimate changes in the different metrics that account for the expected correlations between them, we fit multivariate multilevel models. Similar to the way multilevel (also called hierarchical or mixed-effects) models fit to a single (univariate) response allow varying (random) intercepts and slopes to be correlated, this approach estimates changes in all components whilst allowing for correlations between them.

Temporal comparisons: natural environmental variation

To quantify temporal change among natural assemblages at the local scale, we used the BioTIME database (Dornelas et al. 2018), which documents over 45 thousand 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 (see *Temporal comparisons: 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 standardise 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 comparisons: 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 from the U.S. LTER network (including terrestrial, freshwater and marine systems of multiple taxa) using the Data Portal of the Environmental Data Initiative (https://portal.edirepository.org/nis/home.jsp). Following data standardisation (i.e., minimum of five individuals per sample, and standardisation of sample effort through time), our analysis included 11 studies (see supplementary material) and temporal change was estimated in 63 study-treatment combinations. 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

To examine spatial patterns of biodiversity change across relatively natural environmental contexts (and without obvious human impacts), we combined two existing compilations of data. The CESTES database (Jeliazkov et al. 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), and a compilation of datasets with two or more local assemblages containing species abundance data (McGill 2011b). From CESTES, we excluded 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). Similarly, studies documenting disturbances and other perturbations were removed from the McGill (2011b) compilation, resulting in 32 studies being retained. From the combined 51 studies, those with many sites were randomly subsampled down to ten sites so that they did not dominate the results. Within each study, an arbitrary site was assigned as the ‘reference’ site, and change was 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 due to anthropogenic land use, we used the PREDICTS database, which is a collation of studies comparing reference to impacted sites

(Hudson et al. 2017). Here we used the 2016 release of the database (downloaded from https://data.nhm.ac.uk/ on 10th 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 change relative to the reference land use category, primary vegetation.

Statistical models

Similar models were fit to each data source. For the *Temporal comparisons: 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 comparisons: experimental or natural perturbations* data, S was no longer an integer value after standardising 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 Possion distribution and log-link function for species richness (S).

The *Temporal comparisons: natural environmental variation* models 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 supplement for equations). The models fit to the *Temporal comparisons: 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 modelled by drawing varying intercepts and slopes for each combination of treatment and study for all responses from a single multivariate normal distribution (see supplement for equations).

The models 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 modelled 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 modelled using an observation-level varying intercept (see supplement for equations). Models 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 modelled separately for each response. Correlations between changes in the different responses were modelled 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 supplement for equations).

All statistical models were fit using the Hamiltonian Monte Carlo (HMC) sampler Stan (Carpenter et al. 2017), and coded using the 'brms' package (Burkner 2017). Details of all model specifications, and the iterations and warmup periods are provided in the supplement, as are the priors (which were weakly regularising). 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 Supplement Figures S1-4). Code for all analyses is available at https://github.com/sablowes/MulticomponentBioChange, and will be archived following publication.

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%), temporal changes (21%) and spatial comparisons in naturally varying environments (12%). Component changes that differed from zero showed broadly similar patterns across datasets, with one exception: trends differing from zero for multiple components were less common for spatial comparisons between assemblages in naturally varying environments (Figure 3).

Temporal changes were typically smaller in magnitude (Figure 4a-f) and exhibited generally stronger relationships across assemblages (Figure 5a, b) compared to spatial changes (Figure 4g-l, Figure 5c, d). Within assemblages, changes of abundance and richness (ΔN, ΔS, Figure 4a, d, g, j), changes in rarefied richness and species richness (ΔS_n and ΔS, Figure 4b, e, h, k) and evenness and richness changes (ΔS_{PIE} and ΔS, Figure 4c, f, i, l) typically had the same sign, though there were exceptions to this general pattern. For assemblages where ΔN and ΔS_{PIE} had the same sign (though not necessarily differing from zero), the magnitude of richness changes was typically larger (Figure 4). In contrast, if ΔN and ΔS_{PIE} had opposing signs, richness changes were often of a smaller magnitude (Figure 4). This tendency for countervailing changes in abundance and evenness to reduce the magnitude of richness changes was most apparent for spatial changes associated with different land use categories (Figure 4j-l), and among these assemblages having opposing abundance and evenness changes, there was a high proportion that were growing in size ($\Delta N > 0$) but with declining species richness ($\Delta S < 0$; Figure 4j).

Temporal changes in naturally varying assemblages were roughly centred on zero for all metrics (Figure 4a-c). Across assemblages, altered numbers of individuals and species richness changes had a moderately positive relationship (Figure 5a), weakened by assemblages that had opposing abundance and evenness relationships (Figure 4a). In contrast, relationships between changes in species richness and rarefied richness, and between richness changes and evenness changes were strong (Figure 5a). Assemblages in perturbed environments had slightly positive temporal trends on average in all components (Figure 4d-f). Across assemblages, ΔS and ΔN (Figure 4d, 5b) and ΔS and ΔS_{PIE} (Figure 4f, 5b) had relatively weak positive relationships, whereas ΔS and ΔS_n (Figure 4e, 5b) showed a strong positive relationship.

Spatial comparisons in naturally varying environments exhibited highly heterogeneous patterns of change centred around zero for all metrics (Figure 4g-i), and decoupled component changes meant that relationships between them were generally absent or weak across assemblages (Figure 5c). Spatial comparisons between assemblages in primary vegetation versus 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 4j-l). Across assemblages, land use change was typically associated with relatively weak positive relationships between changes in the components of local diversity (Figure 5d).

Discussion

Our conceptual framework showed how the expectation for positive relationships between changes in abundance, evenness and richness arises, and that the signs of changes in abundance and evenness hold the key to this expectation breaking down. Our empirical analyses generally found support for positive relationships between abundance, richness and evenness, and within assemblages, changes in multiple components were common. However, component changes were also frequently highly heterogeneous within assemblages, and countervailing changes in total abundance and evenness often constrained the magnitude of changes in species richness.

Relationships between changes in abundance, evenness, and richness were most heterogeneous for spatial comparisons, and sufficiently decoupled that no strong relationships emerged across assemblages. In contrast to the frequent decoupling of component changes for spatial comparisons, 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. This strong relationship between changes in species richness and altered SADs runs counter to the common expectation that changes in the numbers of individuals underpin diversity gradients (e.g., Gaston 2000, Scheiner & Willig 2005), and shows that variation in relative abundances can dominate local variation in biodiversity.

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 ‘more-individuals’ effect on changes in species richness (i.e., ΔN & ΔS having the same sign, and being the only changes different from zero). 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 local assemblages changing in size are not simply passively sampling more or less from a static SAD. Instead, we show that local biodiversity change can be strongly influenced by changes to species’ relative abundances. Changes to species’ relative abundances can be occurring at multiple scales (Hillebrand et al. 2008, Blowes et al. 2020), and can reflect altered local environmental conditions (e.g., altered resource or habitat diversity, eutrophication, local harvest or exploitation), or changes at broader scales that alter the species pool.

Our general result that changes in the total abundance of an assemblage through time or space are 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, Wagner 2000, van Klink et al. 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 variation in relative abundances for local biodiversity change means that biodiversity trends may often depend on whether altered relative abundances influence the metrics used (see e.g., Antão et al. 2020b).

Patterns of temporal versus spatial biodiversity change

Differences between patterns of temporal versus spatial change emerged from our analyses. Moreover, these differences were generally greater than those found between naturally-varying and perturbed assemblages, for either the temporal or spatial comparisons. In general, the magnitude of changes of all components across space were larger than rates of change through time. Multiple factors likely contributed to the larger effect sizes found for spatial changes. For example, patterns of autocorrelation likely differ between the dimensions, with temporal data more likely to resample individuals than the spatial comparisons, limiting the magnitude of changes possible. Likewise, the units of change differ between temporal (where change was standardised to an annual rate [change per year]) and spatial comparisons (change between discrete sites). It is also possible that any given site-to-site comparison encompassed a greater range of environmental variation. However, it is important to note that at the local scale on which we have focussed, direct comparisons between the effect sizes are difficult.

Pairwise relationships between changes in abundance, evenness and richness were typically weaker in space compared to time. Decoupling was greatest, and pairwise relationships weakest, for spatial comparisons between sites with relatively natural environmental variation. These highly variable component changes to environmental variation emphasise the need for a wholistic approach to quantifying community changes (Avolio et al. 2021). Our conceptual framework showed that the signs of changes in abundance and evenness can strongly constrain the magnitude of richness changes, a pattern generally supported by our empirical analyses. In particular, we found that the signs of abundance and evenness changes often determined the magnitude of richness losses associated with land use modification (Newbold et al. 2015, 2020). Assemblages with the greatest declines in abundance and evenness had the greatest richness declines. In contrast, when changes in abundance and evenness were in opposite directions, 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 (Supplementary Table 1). This shows that even for apparently decoupled component changes, interdependencies between biodiversity components remain important to overall biodiversity change.

In contrast to assemblage changes 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 4b). In some cases, this occurred despite countervailing changes in total abundance and evenness (Figure 4a, 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. Instead, richness changes were more strongly associated with altered relative abundances, which has important implications for examining causes and/or consequences of biodiversity change (Hillebrand et al. 2008, Crowder et al. 2010). These cases highlight that 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. Our finding of smaller effect sizes for time series indicates greater inertia for assemblage changes occurring through time, compared to site-to-site variation. More generally, the strong role of changes to the SAD for variation in local biodiversity suggests that examining drivers of altered patterns of relative abundance across scales (e.g., are local environmental changes affecting evenness or are changes occurring at broader spatial scales impacting the size of species pool) are an important direction for future empirical work.

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 change 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. 2010), 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., Wilsey et al. 2005, Chase et al. 2018, Avolio et al. 2021).

To be most useful, variation in the different components of biodiversity need to be coherently conceptualised. Individual-based rarefaction curves and associated metrics provide an intuitive and illustrative characterisation of relationships among changing components of local biodiversity. Whilst 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 analysed independently, and with metrics lacking conceptual unification. Our results emphasise that changes to the most frequently quantified aspects of biodiversity, including changes to the numbers of individuals, and the relative abundance and total numbers of species are highly interdependent. Examining how within-assemblage component changes covary with potential drivers could reveal insights masked by independent aggregate estimates of change and provide new information for understanding biodiversity change in the Anthropocene.

Open research statement: All data used in the manuscript are already in the public domain. The BioTIME database is accessible through the BioTIME website (http://biotime.st-andrews.ac.uk) and a Zenodo repository (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); code for compilation and standardisation available at https://github.com/chase-lab/BioTIMEx. PREDICTS is available at https://www.predicts.org.uk/. McGill SAD data were previously archived at: https://doi.org/10.6084/m9.figshare.6945704. CESTES database is available at https://doi.org/10.25829/idiv.286-21-2695. Code for all analyses is available at https://github.com/sablowes/MulticomponentBioChange, which will be archived when accepted.

References

Antão, L.H., Bates, A.E., Blowes, S.A., Waldock, C., Supp, S.R., Magurran, A.E., Dornelas, M., Schipper, A.M., 2020a. Temperature-related biodiversity change across temperate marine and terrestrial systems. Nature Ecology & Evolution 4, 927–933.

Antão, L.H., Pöyry, J., Leinonen, R., Roslin, T., 2020b. 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., Komatsu, K.J., Collins, S.L., Grman, E., Koerner, S.E., Tredennick, A.T., Wilcox, K.R., Baer, S., Boughton, E.H., Britton, A.J., 2021. Determinants of community compositional change are equally affected by global change. Ecology Letters 24, 1892–1904.

Blowes, S.A., Chase, J.M., Di Franco, A., Frid, O., Gotelli, N.J., Guidetti, P., Knight, T.M., May, F., McGlinn, D.J., Micheli, F., 2020. Mediterranean marine protected areas have higher biodiversity via increased evenness, not abundance. Journal of Applied Ecology 57, 578–589.

Blowes, S.A., Supp, S.R., Antão, L.H., Bates, A., Bruelheide, H., Chase, J.M., Moyes, F., Magurran, A., McGill, B., Myers-Smith, I.H., Winter, M., Bjorkman, A.D., Bowler, D.E., Byrnes, J.E., Gonzalez, A., Hines, J., Isbell, F., Jones, H.P., Navarro, L.M., Thompson, P.L., Vellend, M., Waldock, C., Dornelas, M., 2019. The geography of biodiversity change in marine and terrestrial assemblages. Science 366, 339–345.

Bolker, B.M., 2008. Ecological models and data in R. Princeton University Press.

Bürkner, P.-C., 2017. brms: An R package for Bayesian multilevel models using Stan. Journal of Statistical Software 80, 1–28.

Carpenter, B., Gelman, A., Hoffman, M.D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., Riddell, A., 2017. Stan: A probabilistic programming language. Journal of Statistical Software 76.

Caswell, H., 1976. Community structure: a neutral model analysis. Ecological monographs 46, 327–354.

Cayuela, L., Gotelli, N.J., Colwell, R.K., 2015. Ecological and biogeographic null hypotheses for comparing rarefaction curves. Ecological Monographs 85, 437–455.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., n.d. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecology 84, 45–67.

Chao, A., Jost, L., 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93, 2533–2547.

Chase, J.M., Knight, T.M., 2013. Scale-dependent effect sizes of ecological drivers on biodiversity: why standardised sampling is not enough. Ecol Lett 16, 17–26.

Chase, J.M., McGill, B.J., McGlinn, D.J., May, F., Blowes, S.A., Xiao, X., Knight, T.M., Purschke, O., Gotelli, N.J., 2018. Embracing scale-dependence to achieve a deeper understanding of biodiversity and its change across communities. Ecol Lett 21, 1737–1751.

Chase, J.M., McGill, B.J., Thompson, P.L., Antão, L.H., Bates, A.E., Blowes, S.A., Dornelas, M., Gonzalez, A., Magurran, A.E., Supp, S.R., Winter, M., Bjorkman, A.D., Bruelheide, H., Byrnes, J.E., Sarmento Cabral, J., Elahi, R., Gomez, C., Guzman, H.M., Isbell, F., Myers-Smith, I.H., Jones, H.P., Hines, J., Vellend, M., Waldock, C., O'Connor, M., 2019. Species richness change across spatial scales. Oikos 1–13.

Coleman, B.D., Mares, M.A., Willig, M.R., Hsieh, Y.-H. 1982. Randomness, area, and species richness. Ecology 63: 1121-1133.

Connor, E.F., McCoy, E.D., 1979. The statistics and biology of the species-area relationship. The American Naturalist 113, 791–833.

Crowder, D.W., Northfield, T.D., Strand, M.R., Snyder, W.E., 2010. Organic agriculture promotes evenness and natural pest control. Nature 466, 109–112.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J.-F., Hawkins, B.A., Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'Brien, E., 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecology letters 7, 1121–1134.

Daskalova, G.N., Myers-Smith, I.H., Godlee, J.L., 2020a. Rare and common vertebrates span a wide spectrum of population trends. Nature Communications 4394.

Daskalova, G.N., Myers-Smith, I.H., Bjorkman, A.D., Blowes, S.A., Supp, S.R., Magurran, A.E., Dornelas, M., 2020b. Landscape-scale forest loss as a catalyst of population and biodiversity change. Science 368, 1341–1347.

Díaz, S., Settele, J., Brondízio, E.S., Ngo, H.T., Agard, J., Arneth, A., Balvanera, P., Brauman, K.A., Butchart, S.H., Chan, K.M., 2019. Pervasive human-driven decline of life on Earth points to the need for transformative change. Science 366.

Dornelas, M., Antao, L.H., Moyes, F., Bates, A.E., Magurran, A.E., Adam, D., Akhmetzhanova, A.A., Appeltans, W., Arcos, J.M., Arnold, H., 2018. BioTIME: A database of biodiversity time series for the Anthropocene. Glob Ecol Biogeogr 27, 760–786.

Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., Magurran, A.E., 2014. Assemblage time series reveal biodiversity change but not systematic loss. Science 344, 296–299.

Dornelas, M., Gotelli, N.J., Shimadzu, H., Moyes, F., Magurran, A.E., McGill, B.J., 2019. A balance of winners and losers in the Anthropocene. Ecol Lett 22, 847–854.

Fisher, R.A., Corbet, A.S., Williams, C.B., 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 42–58.

Gaston, K.J., 2000. Global patterns in biodiversity. Nature 405, 220–227.

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol Lett 4, 379–391.

He, F., Legendre, P., 2002. Species diversity patterns derived from species–area models. Ecology 83, 1185–1198.

Hill, M.O., 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54, 427–432.

Hillebrand, H., Bennett, D.M., Cadotte, M.W., 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. Ecology 89, 1510–1520.

Hillebrand, H., Blasius, B., Borer, E.T., Chase, J.M., Downing, J.A., Eriksson, B.K., Filstrup, C.T., Harpole, W.S., Hodapp, D., Larsen, S., 2018. Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. Journal of Applied Ecology 55, 169–184.

Hudson, L.N., Newbold, T., Contu, S., Hill, S.L., Lysenko, I., De Palma, A., Phillips, H.R., Alhusseini, T.I., Bedford, F.E., Bennett, D.J., 2017. The database of the Predicts (Projecting responses of ecological diversity in changing terrestrial systems) project. Ecology and Evolution 7, 145–188.

Hughes, A.R., Byrnes, J.E., Kimbro, D.L., Stachowicz, J.J., 2007. Reciprocal relationships and potential feedbacks between biodiversity and disturbance. Ecology letters 10, 849–864.

Hurlbert, S.H., 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52, 577–586.

Jeliazkov, A., Mijatovic, D., Chantepie, S., Andrew, N., Arlettaz, R., Barbaro, L., Barsoum, N., Bartonova, A., Belskaya, E., Bonada, N., 2020. A global database for metacommunity ecology, integrating species, traits, environment and space. Scientific data 7, 1–15.

Jones, F.A., Magurran, A.E., 2018. Dominance structure of assemblages is regulated over a period of rapid environmental change. Biology letters 14, 20180187.

Jones, F.A., Dornelas, M., Magurran, A.E., 2020. Recent increases in assemblage rarity are linked to increasing local immigration. Royal Society open science 7, 192045.

Jost, L., 2006. Entropy and diversity. Oikos 113, 363–375.

Jost, L., 2007. Partitioning diversity into independent alpha and beta components. Ecology 88, 2427–2439.

Leung, B., Hargreaves, A.L., Greenberg, D.A., McGill, B., Dornelas, M., Freeman, R., 2020. Clustered versus catastrophic global vertebrate declines. Nature 588, 267–271.

MacArthur, R.H., 1965. Patterns of species diversity. Biological reviews 40, 510–533.

Magurran, A.E., McGill, B.J., 2011. Biological diversity: frontiers in measurement and assessment. Oxford University Press.

May, F., Gerstner, K., McGlinn, D.J., Xiao, X., Chase, J.M., 2018. mobsim: An R package for the simulation and measurement of biodiversity across spatial scales. Methods in Ecology and Evolution 9, 1401–1408.

McGill, B.J., 2011a. Linking biodiversity patterns by autocorrelated random sampling. Am J Bot 98, 481–502.

McGill, B.J., 2011b. Species abundance distributions, in: Biological Diversity: Frontiers In Measurement & Assessment (Eds Magurran, A. & McGill, B.). Oxford University Press, pp. 105–122.

McGill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J., Benecha, H.K., Dornelas, M., Enquist, B.J., Green, J.L., He, F., Hurlbert, A.H., Magurran, A.E., Marquet, P.A., Maurer, B.A., Ostling, A., Soykan, C.U., Ugland, K.I., White, E.P., 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. Ecol Lett 10, 995–1015.

McGlinn, D.J., Xiao, X., May, F., Gotelli, N.J., Engel, T., Blowes, S.A., Knight, T.M., Purschke, O., Chase, J.M., McGill, B.J., 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, 258–269.

McKinney, M.L., Lockwood, J.L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in ecology & evolution 14, 450–453.

Menge, B.A., Berlow, E.L., Blanchette, C.A., Navarrete, S.A., Yamada, S.B., 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. Ecological monographs 64, 249–286.

Newbold, T., Hudson, L.N., Contu, S., Hill, S.L., Beck, J., Liu, Y., Meyer, C., Phillips, H.R., Scharlemann, J.P., Purvis, A., 2018. Widespread winners and narrow-ranged losers: Land use homogenizes biodiversity in local assemblages worldwide. PLoS biology 16, e2006841.

Newbold, T., Hudson, L.N., Hill, S.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., 2015. Global effects of land use on local terrestrial biodiversity. Nature 520, 45–50.

Newbold, T., Oppenheimer, P., Etard, A., Williams, J.J., 2020. Tropical and Mediterranean biodiversity is disproportionately sensitive to land-use and climate change. Nature Ecology & Evolution 4, 1630–1638.

Olszewski, T.D., 2004. A unified mathematical framework for the measurement of richness and evenness within and among multiple communities. Oikos 104, 377–387.

Paine, R.T., 1974. Intertidal community structure. Oecologia 15, 93–120.

Palmer, M.W., Clark, D.B., Clark, D.A., 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.

Rosenberg, K.V., Dokter, A.M., Blancher, P.J., Sauer, J.R., Smith, A.C., Smith, P.A., Stanton, J.C., Panjabi, A., Helft, L., Parr, M., 2019. Decline of the North American avifauna. Science 366, 120–124.

Rosenzweig, M.L., 1995. Species diversity in space and time. Cambridge University Press.

Scheiner, S.M., Willig, M.R., 2005. Developing unified theories in ecology as exemplified with diversity gradients. The American Naturalist 166, 458–469.

Shmida, A.V.I., Wilson, M.V., 1985. Biological determinants of species diversity. Journal of biogeography 1–20.

Soininen, J., Passy, S., Hillebrand, H., 2012. The relationship between species richness and evenness: a meta-analysis of studies across aquatic ecosystems. Oecologia 169, 803–809.

Srivastava, D.S., Lawton, J.H., 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. The American Naturalist 152, 510–529.

Stirling, G., Wilsey, B., 2001. Empirical relationships between species richness, evenness, and proportional diversity. The American Naturalist 158, 286–299.

Storch, D., Bohdalková, E., Okie, J., 2018. The more-individuals hypothesis revisited: the role of community abundance in species richness regulation and the productivity–diversity relationship. Ecol Lett 21, 920–937.

Tilman, D., 1982. Resource competition and community structure. Princeton University Press.

Vagle, G.L., McCain, C.M., n.d. Natural population variability may be masking the more-individuals hypothesis. Ecology 101, e03035.

Van Klink, R., Bowler, D.E., Gongalsky, K.B., Swengel, A.B., Gentile, A., Chase, J.M., 2020. Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. Science 368, 417–420.

Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y., Pyšek, P., 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology letters 14, 702–708.

Wagner, D.L., 2020. Insect declines in the Anthropocene. Annual review of entomology 65, 457–480.

Whittaker, R.J., Willis, K.J., Field, R., 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. Journal of biogeography 28, 453–470.

Wright, D.H., 1983. Species-energy theory: an extension of species-area theory. Oikos 496–506.

WWF, 2020. Living Planet Report 2020-Bending the curve of biodiversity loss. World Wildlife Fund, Gland, Switzerland.

Zhang, Y., Chen, H.Y., Reich, P.B., 2012. Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. Journal of ecology 100, 742–749.

Figure 1: Individual-based rarefaction (IBR) curves for samples from two hypothetical assemblages. We characterise diversity change using four components of the IBR curve: altered numbers of individuals (ΔN), changes in species richness (ΔS), and two metrics that capture changes to the SAD – changes in rarefied richness (ΔS_n) and changes in the numbers equivalent conversion of the Probability of Interspecific Encounter (ΔS_{PIE}). Note, we show ΔPIE on the figure to illustrate changes of the PIE with the IBR, but use the numbers equivalent transformation (ΔS_{PIE}) in all analyses.

Figure 2: Relationships between component changes and potential pathways of local assemblage diversity change. Different combinations of change in total abundance, evenness and richness can be visualised using three pairwise relationships between metrics associated with the individual-based rarefaction curve: (a) changes in species richness as a function of changes to the number of individuals, (b) changes in species richness as a function of changes to rarefied richness, and (c) changes in species richness as a function of changes in evenness. Dashed diagonal line is x = y. Six simplified pathways of change illustrated with rarefaction curves: starting from a reference assemblage (depicted with grey rarefaction curves), diversity change due to (c) more individuals only, (b) more rare species, or (d) changes to the species abundance distribution (e.g., increased species pool size or increased evenness) result in positive relationships between combinations of 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. Assemblages and rarefaction curves were created using the mobsim package (May et al. 2018).

Figure 3: Summary of assemblage diversity components with a high probability of change (90% credible interval did not overlap zero) for (a) temporal changes in naturally varying environments, (b) temporal changes in perturbed environments, (c) spatial changes relative to an arbitrary reference, (d) spatial changes relative to primary vegetation. Assemblages with no component changes different from zero are reported as insets for clarity. Metric abbreviations: total number of individuals (N), expected number of species for n individuals (S_n), numbers equivalent transformation of the Probability of Interspecific Encounter (S_{PIE}), and total species richness (S). Number following each bar is the count of assemblages for that category.

Figure 4: 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) estimates of spatial changes within studies from an arbitrary reference site along natural environmental gradients; and, (j-l) estimates of spatial change within studies between primary vegetation and different land use categories. Coloured concentration ellipses show 10% increments (5 – 95%) of the posterior distributions. Dotted grey lines are x = y = 0, and x = y for visual reference. See Supplementary Figure 5 for remaining pairwise relationships. NB: Scale of x- and y-axes vary between panels; one estimate with $\Delta\log(N) = -1.79$, $\Delta\log(S) = -3.77$, $\Delta\log(S_n) = -3.23$, $\Delta\log(S_{PIE}) = -3.21$, removed from (j-l) for clarity.

Figure 5: Component correlations among studies within each data source. Density plots for the posterior distribution of pairwise correlations between component changes for (a) temporal comparison in naturally varying environments, (b) temporal comparisons in perturbed environments, (c) spatial comparisons along natural gradients, and (d) spatial comparisons between different land use categories. NB: correlations estimated separately for sites and land use categories relative to the references were combined here for clarity on (c) and (d).

858 **Figure 1**

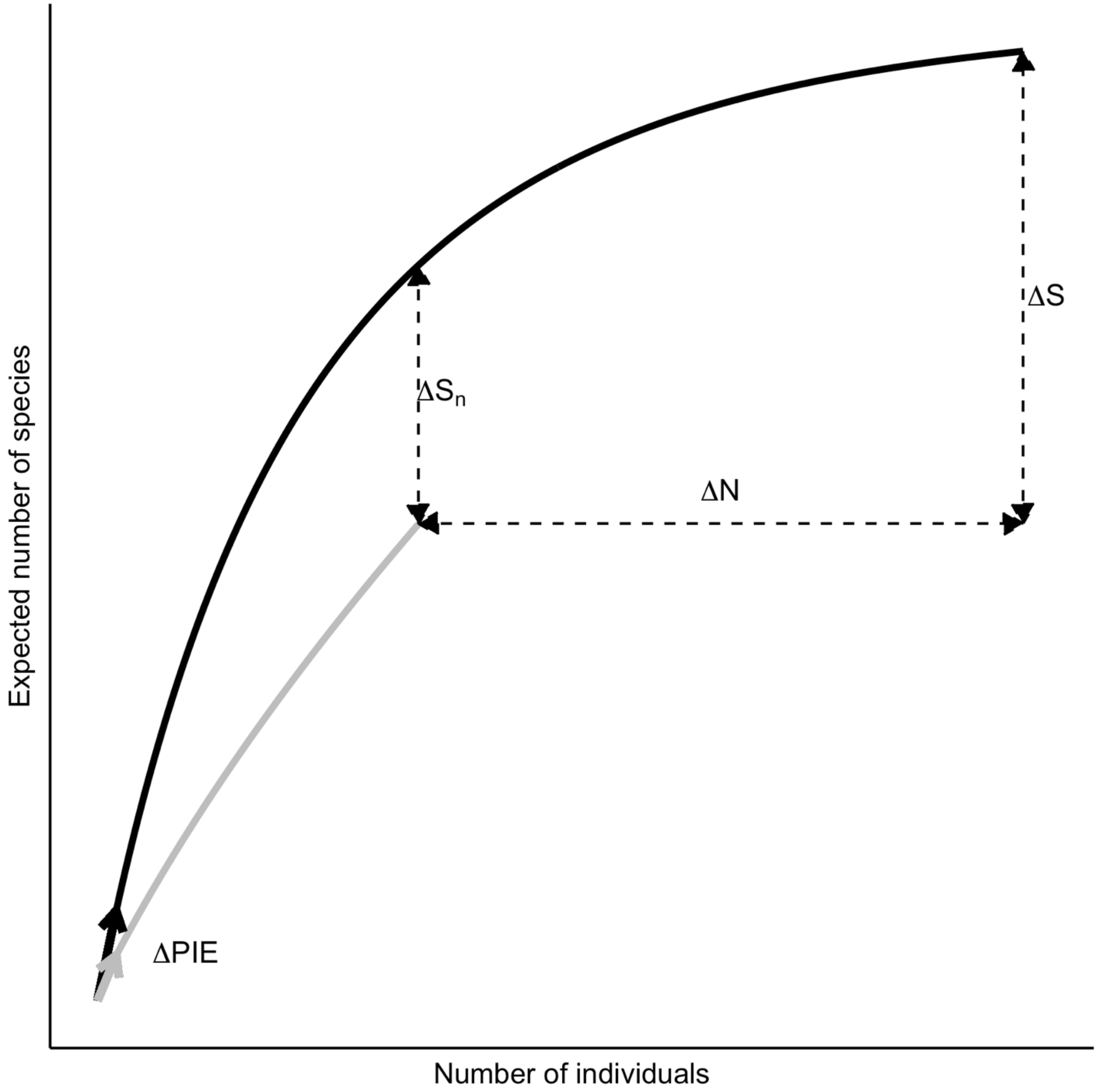

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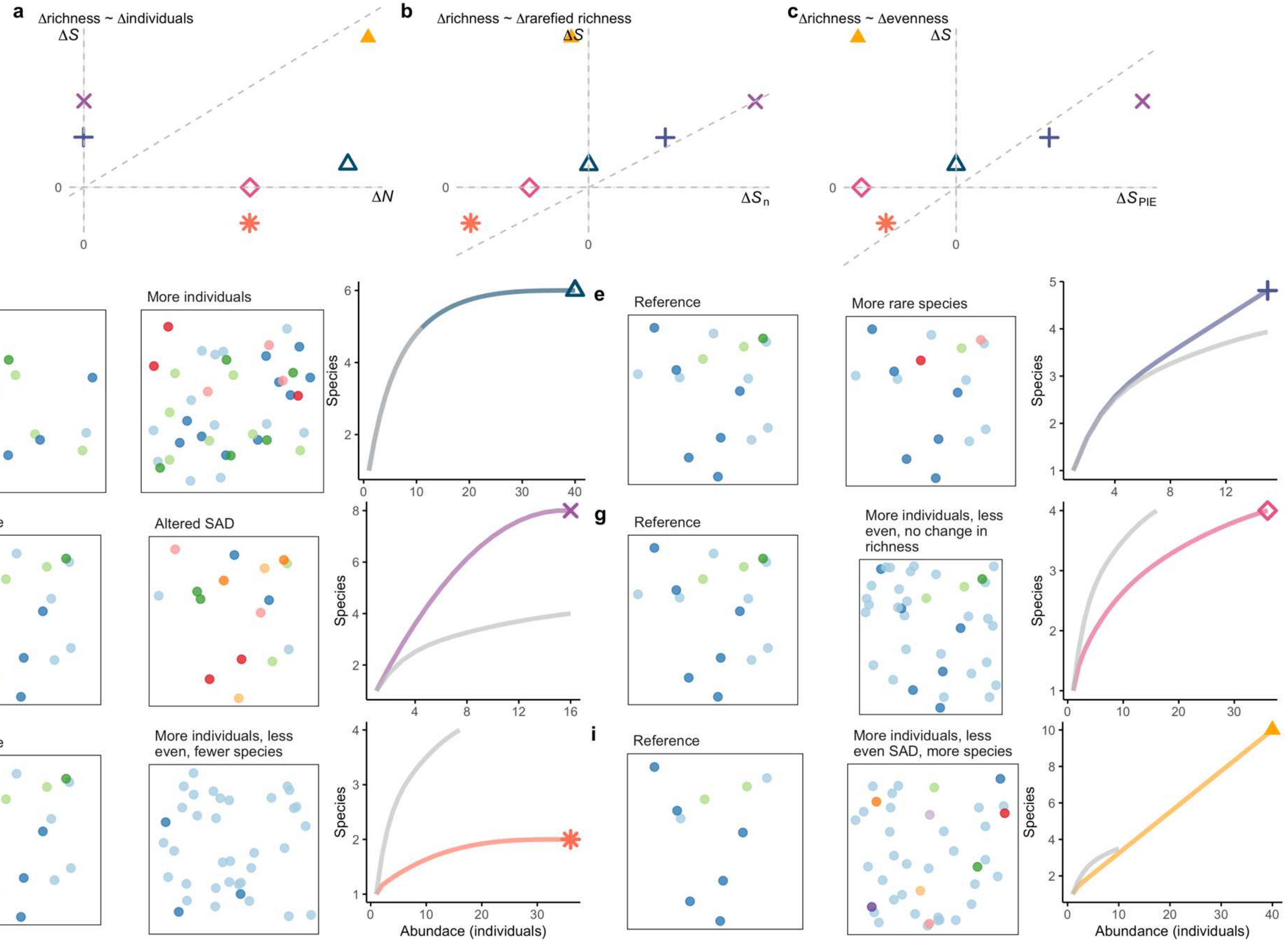
Figure 2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ΔN
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b
Δrichness ~ Δrarefied richness
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ΔS_n
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Δrichness ~ Δevenness
ΔS
0
ΔS_{PIE}
0
d
Reference
More individuals
Species
6
4
2
0
10
20
30
40
e
Reference
More rare species
Species
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Reference
Altered SAD
Species
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Figure 3

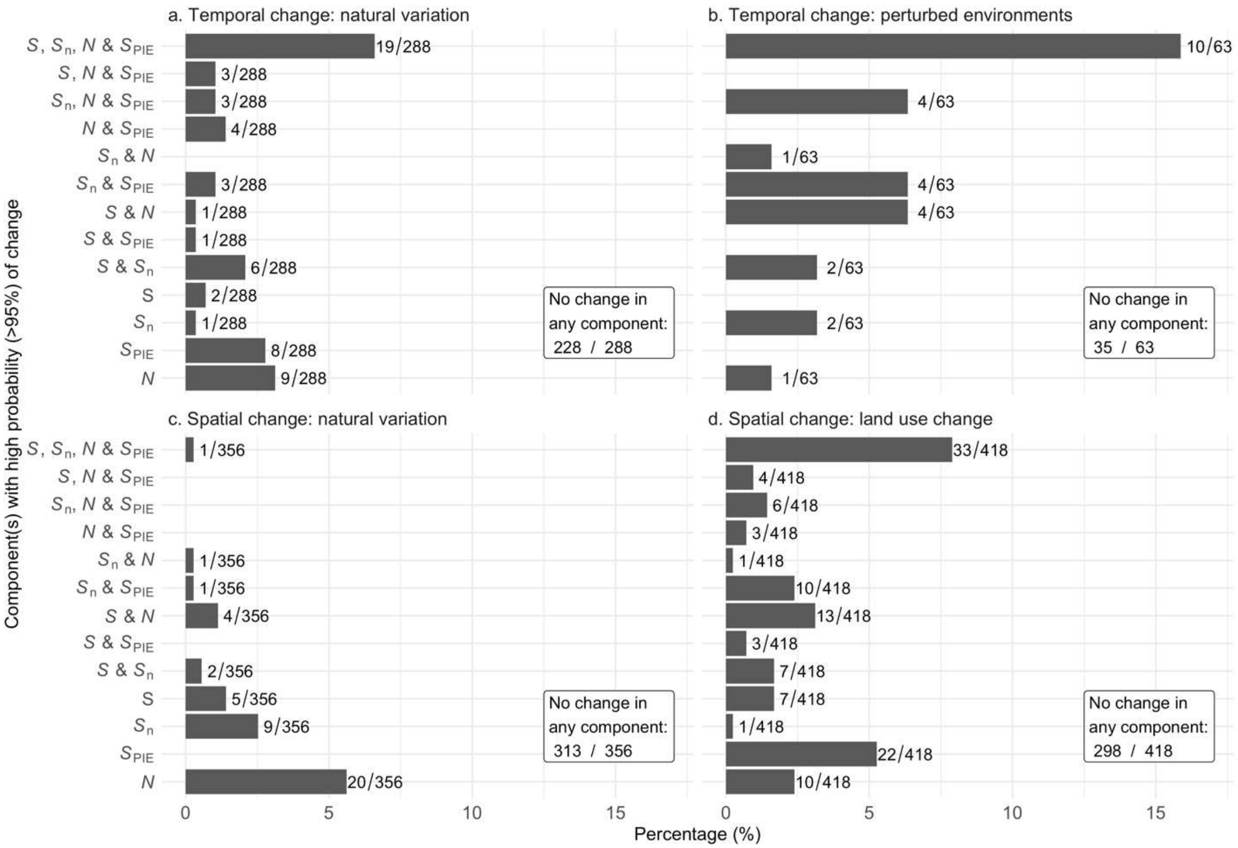

a. Temporal change: natural variation
b. Temporal change: perturbed environments
c. Spatial change: natural variation
d. Spatial change: land use change
Component(s) with high probability (>95%) of change
S, S_n, N & S_{PIE}
S, N & S_{PIE}
S_n, N & S_{PIE}
N & S_{PIE}
S_n & N
S_n & S_{PIE}
S & N
S & S_{PIE}
S & S_n
S
S_n
S_{PIE}
N
19/288
3/288
3/288
4/288
3/288
1/288
1/288
6/288
2/288
1/288
8/288
9/288
No change in any component: 228 / 288
10/63
4/63
1/63
4/63
4/63
2/63
2/63
1/63
No change in any component: 35 / 63
1/356
1/356
1/356
4/356
2/356
5/356
9/356
20/356
No change in any component: 313 / 356
33/418
4/418
6/418
3/418
1/418
10/418
13/418
3/418
7/418
7/418
1/418
22/418
10/418
No change in any component: 298 / 418
0
5
10
15
Percentage (%)

Figure 4

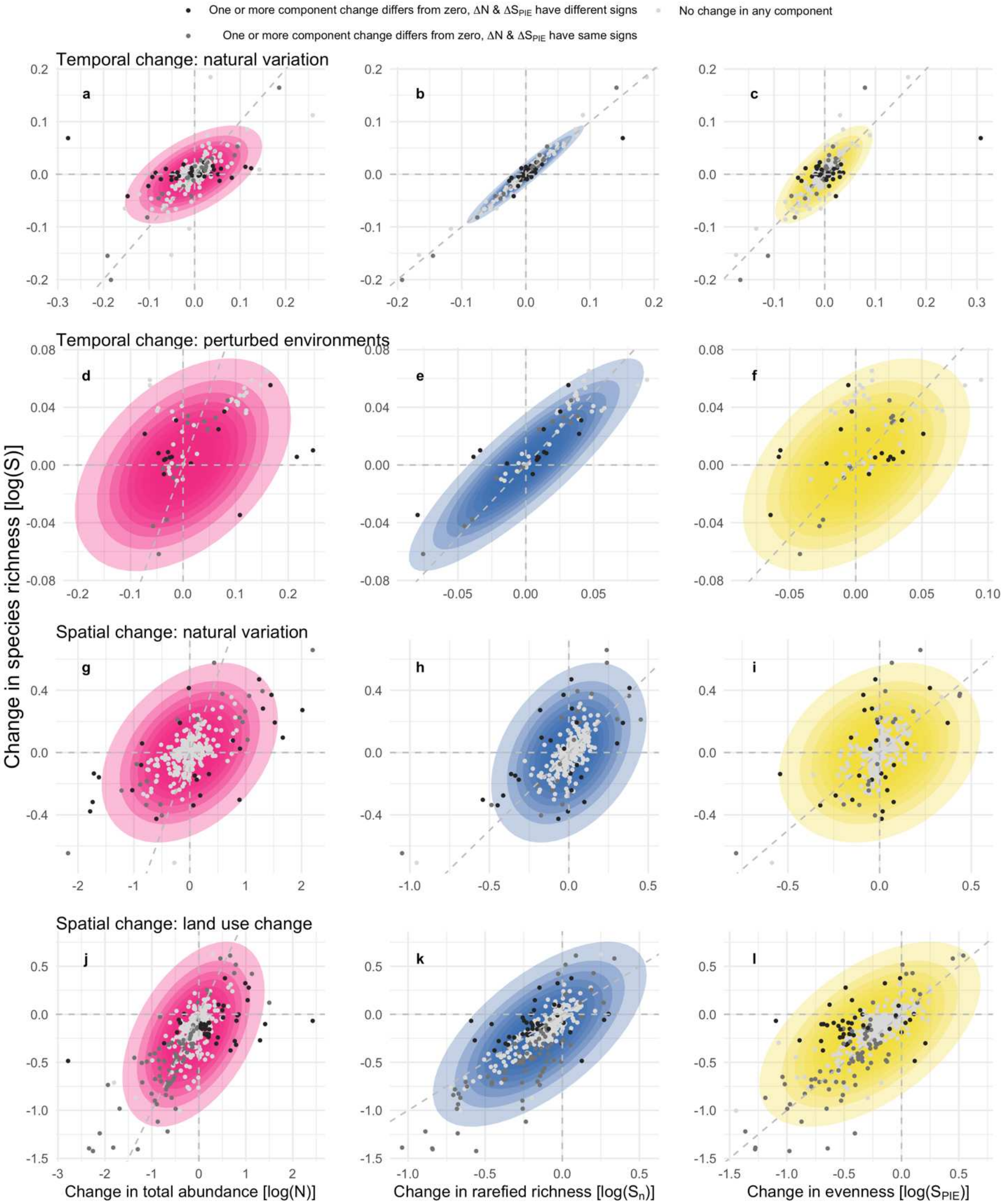
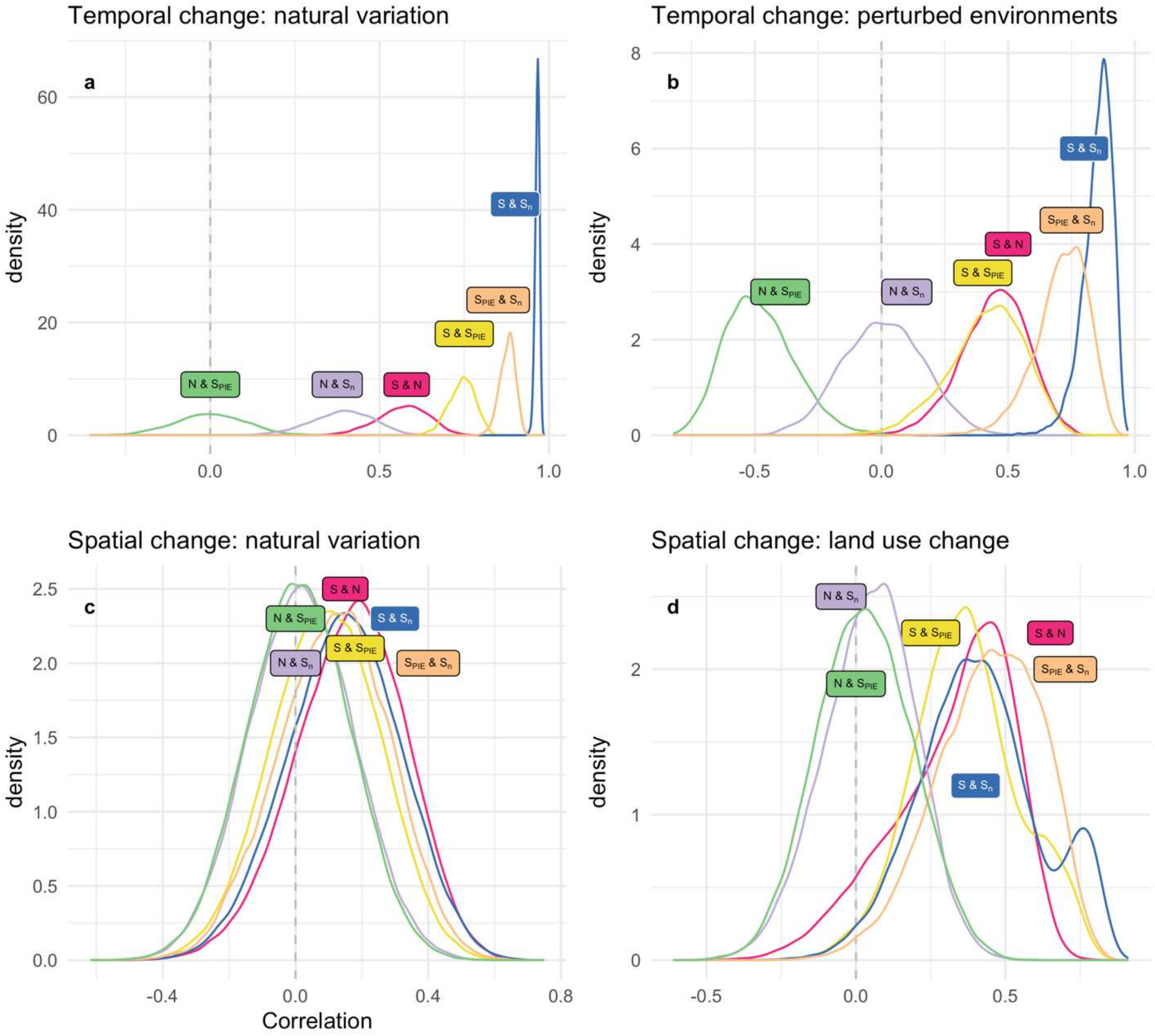

● One or more component change differs from zero, ΔN & ΔS_PIE have different signs
● No change in any component
● One or more component change differs from zero, ΔN & ΔS_PIE have same signs
Temporal change: natural variation
a
b
c
Temporal change: perturbed environments
d
e
f
Spatial change: natural variation
g
h
i
Spatial change: land use change
j
k
l
Change in species richness [log(S)]
Change in total abundance [log(N)]
Change in rarefied richness [log(S_n)]
Change in evenness [log(S_PIE)]

Figure 5


Temporal change: natural variation
a
density
60
40
20
0
0.0
0.5
1.0
S & S_n
S_{PIE} & S_n
S & S_{PIE}
N & S_{PIE}
N & S_n
S & N
Temporal change: perturbed environments
b
density
8
6
4
2
0
-0.5
0.0
0.5
1.0
S & S_n
S_{PIE} & S_n
S & N
S & S_{PIE}
N & S_{PIE}
N & S_n
Spatial change: natural variation
c
density
2.5
2.0
1.5
1.0
0.5
0.0
-0.4
0.0
0.4
0.8
Correlation
S & N
N & S_{PIE}
S & S_n
S & S_{PIE}
N & S_n
S_{PIE} & S_n
Spatial change: land use change
d
density
2
1
0
-0.5
0.0
0.5
N & S_n
S & S_{PIE}
S & N
N & S_{PIE}
S_{PIE} & S_n
S & S_n