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

107 across space and among taxa (e.g., van Klink et al. 2020, Daskalova et al. 2020a, Leung et al.
108 2020). Moreover, trends in total assemblage abundance provide only one window into potentially
109 complex changes that could be occurring in other components of biodiversity, and while changes
110 to species' relative abundances do influence biodiversity metrics, population-level trends
111 themselves cannot be used to calculate assemblage-level (i.e., biodiversity) metrics (e.g.,
112 Dornelas et al. 2019). Even when quantifying similar response metrics (i.e., species richness),
113 syntheses of biodiversity change in space due to differential land use conditions have found
114 declines of species richness (e.g., Newbold et al. 2015, 2018), whereas analyses of time series
115 have shown that, on average, species richness increases roughly offset decreases (Dornelas et al.
116 2014, Blowes et al. 2019), despite often significant modifications to climate and habitat (Antão
117 et al. 2020a, Daskalova et al. 2020b). Finally, the prediction that human activities likely impact
118 species relative abundances more frequently than they do species occurrences (Chapin et al.
119 2000), has not resulted in a strong focus on assemblage-level evenness in existing syntheses (but
120 see, e.g., Crowder et al. 2010, Zhang et al. 2012, Jones & Magurran 2018). Importantly, changes
121 in all these components, abundance, evenness and richness, contribute to variation in
122 biodiversity. Yet little is known about how components are changing in combination within
123 assemblages, and whether certain combinations act to constrain observed biodiversity change.
124
125 The biodiversity estimated from a given (local) sample depends largely on two factors (see e.g.,
126 He and Legendre 2002, McGill 2011a). First, the total number of individuals (Fisher et al. 1943,
127 Preston 1962), whereby fewer individuals are expected to (non-linearly) lead to fewer species in
128 a given sample. Second, the total number of species and their relative abundances within the
129 species pool, which we refer to as the Species Abundance Distribution (SAD; McGill et al.

130 2007). Samples will have lower species richness when the species pool has relatively few highly
131 abundant species and many rare species (i.e., less even SADs), compared to samples from a
132 species pool of the equivalent size with more equitable species abundances. Whenever two or
133 more samples across space or time differ in the total number of individuals, the shape of the
134 SAD, or both, there will be changes in most metrics of biodiversity. However, changes in
135 abundance and the SAD are not always correlated, and, when decoupled, the magnitude and
136 direction of change in derived biodiversity metrics could differ considerably.
137
138 Variation in the total number of individuals is a long-standing, first-order explanation of
139 variation in richness (Fisher et al. 1943, Coleman et al. 1982, Srivastava & Lawton 1998, Gaston
140 2000, Scheiner & Willig 2005, Storch et al. 2018). A positive relationship between numbers of
141 individuals and species richness can be derived via multiple mechanisms (Scheiner & Willig
142 2005), and is sometimes termed the 'more-individuals hypothesis' (Srivastava & Lawton 1998),
143 or, in the context of species-area relationships, the 'passive sampling hypothesis' (Coleman et al.
144 1982). Species richness has been posited to increase in places that are larger (Connor & McCoy
145 1979) or more productive (Wright 1983), simply because of increased numbers of individuals.
146 Likewise, some anthropogenic drivers can influence the number of individuals in assemblages
147 (e.g., via eutrophication, exploitation, harvesting or land clearing), potentially impacting
148 biodiversity due to changes to the total number of individuals (Newbold et al. 2015, Blowes et al.
149 2020, Jones et al. 2020). If biodiversity varies primarily via changes in the numbers of
150 individuals, positive relationships between altered numbers of individuals and species richness
151 changes are expected. In such cases, however, other metrics of species diversity that control for

152 variation in numbers of individuals, such as the richness expected for a given number of
153 individuals—known as rarefied richness—should be relatively unchanged.
154
155 Changes to the shape of the SAD can also drive biodiversity change through time or space. For
156 example, co-occurrence and coexistence of species can be altered by changes to resource
157 diversity (MacArthur 1965), environmental or habitat heterogeneity (Tilman 1982, Shmida &
158 Wilson 1985), interspecific interactions (e.g., keystone predation; Paine 1974, Menge et al.
159 2020), biological invasions (Vilà et al. 2011), and external perturbations (Hughes et al. 2007).
160 Alterations to any of these features can change biodiversity by changing species' relative
161 abundances and the size of the species pool (via species additions or subtractions).
162 Anthropogenic factors can also favour some species and disfavour others, potentially altering the
163 relative abundance of species (e.g., due to selective exploitation; Blowes et al. 2020), or the size
164 of the species pool (e.g., species with large ranges replacing those with small ranges, Newbold et
165 al. 2018). In such cases, biodiversity change will be characterised by positive relationships
166 between species richness change and changes in metrics sensitive to relative abundance, such as
167 rarefied richness, evenness and diversity metrics sensitive to species' relative abundances.
168
169 The changing components of biodiversity can covary in different and informative ways. Yet, to
170 date, there has been little exploration of this covariation in time or space, nor of the theoretical
171 linkages. For example, whether total abundances and the evenness of species' relative
172 abundances change in similar or decoupled ways, and how this influences biodiversity change is
173 largely unknown. However, syntheses of relationships between different biodiversity metrics,
174 which can reflect different combinations of component changes, have typically found

175 relationships to be weak. For example, Stirling and Wilsey (2001) showed that although strong
176 positive correlations between species richness, diversity and evenness metrics were expected
177 from a neutral model (Caswell 1976), there was considerable variation in the strength, and even
178 the sign of the relationships in 323 empirical comparisons. Similarly, Soininen et al. (2012)
179 examined temporal (n = 212) and spatial variation (n = 17) in aquatic datasets, and again found
180 considerable heterogeneity in the relationship between richness and evenness. Using data from
181 91 assemblages, McGill (2011b) concluded that most biodiversity metrics align with three axes
182 of empirical variation (total abundance, evenness and richness); components subsequently shown
183 to be relatively uncorrelated across space for a subset of 37 of the 91 assemblages (Chase et al.
184 2018). Collectively, these studies suggest that static biodiversity estimates are multidimensional,
185 and that different metrics can covary or be unrelated.
186
187 Where ecologists have quantified changes in multiple components of local diversity, the focus
188 has typically been on averages across assemblages, where each component is treated as a
189 separate, independent response. For example, analyses of the local assemblages documented by
190 the BioTIME database (Dornelas et al. 2018) show that numbers of individuals, species richness,
191 and dominance (the complement of evenness) are highly variable among datasets, but on
192 average, have no directional trend (Dornelas et al. 2014, Jones & Magurran 2018, Blowes et al.
193 2019). On the other hand, analyses of the PREDICTS database (Hudson et al. 2017)
194 documenting spatial contrasts between assemblages in more pristine habitats with those in
195 different land use categories, show that human-altered habitats frequently have fewer species and
196 often fewer individuals (Newbold et al. 2015, 2020). However, these results describe average

197 changes across assemblages estimated independently, whereas, as we describe in more detail
198 below, component changes are unlikely to be completely independent.
199
200 Here, we first overview the theoretical context for how the main components underlying local
201 biodiversity (total abundance, evenness and species richness) can change in time or space using
202 individual-based rarefaction curves. We focus on six simplified scenarios of change with
203 contrasting patterns of covariation among component changes, showing that the signs of changes
204 in total abundance and evenness strongly determine whether all components can be expected to
205 have positive pairwise relationships. We then empirically assess the relationships between
206 abundance, evenness and richness changes using compilations of ecological assemblage data.
207 This includes data from 351 assemblages varying through time and 774 assemblages monitored
208 across space. In the face of natural and anthropogenically-driven environmental variation in time
209 and space, we ask whether changes in the components of local biodiversity show positive
210 relationships (i.e., change in the same direction). Or, are component changes sufficiently
211 heterogeneous that variation in biodiversity depends on which of the underlying components
212 (numbers of individuals or the SAD) are changing, and how the different component changes
213 combine?
214
215 **Quantifying the multicomponent nature of biodiversity change**
216
217 Individual-based rarefaction curves (Hurlbert 1971, Gotelli & Colwell 2001) are well suited for
218 visualising and characterising empirical variation in total abundance, evenness and species
219 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

289 richness are positive). If observed local diversity changes are dominated by altered total
290 abundances and species richness, the strong positive relationships between ΔS and ΔN, but
291 weaker relationships between ΔS and ΔS_n, as well as between ΔS and ΔS_{PIE} should emerge.
292 Alternatively, strong relationships between either ΔS and ΔS_n and/or ΔS and ΔS_{PIE}, accompanied
293 by a weaker relationship between ΔS and ΔN, would indicate that changes to the SAD are the
294 dominant component of local assemblage change.
295
296 **Methods**
297 *Overview*
298 We took a comparative approach to examine relationships between changes in total abundance,
299 evenness and species richness. Specifically, we sought data documenting assemblages varying
300 either through time or space, in one of either predominantly naturally-varying or perturbed
301 environments. The saturating, asymptotic nature of the IBR means that many common functions
302 used in ecology, such as the Michaelis-Menten or the type-II functional response offer multiple
303 parameterisations for inferences regarding different parts of the curve (see Bolker 2008 for
304 examples of different parameterisations). However, for consistency with the conceptual
305 framework introduced above, and because ecologists are more familiar with direct examinations
306 of diversity measures, we estimated four metrics: total numbers of individuals (N), the expected
307 number of species for n individuals (S_n), the numbers equivalent conversion of the Probability of
308 Interspecific Encounter (S_{PIE}, which hereafter, we refer to as evenness due to its sensitivity to the
309 relative abundance of species), and total species richness (S). The number of individuals, n, used
310 in the calculation of rarefied richness (S_n) was the minimum abundance observed for a given
311 comparison (i.e., within a time series or for a particular spatial comparison); observations where

312 $n < 5$ were discarded before analysis. We took this approach to rarefaction rather than first
313 extrapolating to two times the observed number of individuals (as advocated, e.g., by Chao et al.
314 2014) for consistency with the conceptual framework, and to simplify the interpretation of
315 relationships between changes in abundance, evenness and richness.
316
317 To estimate changes in the different metrics that account for the expected correlations between
318 them, we fit multivariate multilevel models. Similar to the way multilevel (also called
319 hierarchical or mixed-effects) models fit to a single (univariate) response allow varying (random)
320 intercepts and slopes to be correlated, this approach estimates changes in all components whilst
321 allowing for correlations between them.
322
323 *Temporal comparisons: natural environmental variation*
324 To quantify temporal change among natural assemblages at the local scale, we used the
325 BioTIME database (Dornelas et al. 2018), which documents over 45 thousand species in time
326 series with an average duration of 13 years. Taxonomic groups in our analysis came from
327 surveys in marine, freshwater and terrestrial ecosystems, and included plants (and other
328 producers), invertebrates, fish, amphibians, reptiles, birds, and mammals, as well as several
329 surveys that collected data from multiple taxa. Here, we only used time series that had numerical
330 abundance data available (i.e., studies that recorded counts of the number of individuals for each
331 species in an assemblage), and our analysis included 288 studies. Locations sampled in the
332 BioTIME database document places with varying degrees of anthropogenic environmental
333 change, but do not include manipulated assemblages or before-after-control-impact studies
334 (Dornelas et al. 2018). Accordingly, we contrast the environmental variation sampled by

335 BioTIME with assemblage time series that experienced documented perturbations (see *Temporal*
336 *comparisons: experimental or natural perturbations*).
337
338 To quantify changes at the local scale within BioTIME, studies with large extents were broken
339 up into smaller cell-level time series while still maintaining the integrity of individual studies
340 (i.e., different studies were not combined, even when samples were collected in the same grid
341 cell). We used sample-based rarefaction (Gotelli & Colwell 2001) to standardise the number of
342 samples per year for each time series (see Blowes et al. 2019 for details). For the calculation of
343 rarefied richness (S_n), the minimum total number of individuals was determined for each time
344 series, and set as the target n for which expected richness was calculated; cell-level time series
345 where $n < 5$ were discarded. This process resulted in 42,604 cell-level time series from the 288
346 studies, and we focus on the study-level estimates of change in our results and discussion.
347
348 *Temporal comparisons: experimental or natural perturbations*
349 To complement the environmental variation sampled by the BioTIME database, we searched for
350 time series data with either experimental or natural perturbations from the U.S. LTER network
351 (including terrestrial, freshwater and marine systems of multiple taxa) using the Data Portal of
352 the Environmental Data Initiative (https://portal.edirepository.org/nis/home.jsp). Following data
353 standardisation (i.e., minimum of five individuals per sample, and standardisation of sample
354 effort through time), our analysis included 11 studies (see supplementary material) and temporal
355 change was estimated in 63 study-treatment combinations. Natural and experimental treatments
356 included changes due to warming, eutrophication, fire, grazing, restoration, severe storms or

357 other disturbances, and kelp removal. Taxonomic groups included algae, plants, invertebrates,
358 fish, birds, and mammals.
359
360 *Spatial comparisons: natural environmental variation*
361 To examine spatial patterns of biodiversity change across relatively natural environmental
362 contexts (and without obvious human impacts), we combined two existing compilations of data.
363 The CESTES database (Jeliazkov et al. 2019) contains assemblage data from studies that
364 sampled species at multiple sites (it also includes information on traits and environment that we
365 do not use here), and a compilation of datasets with two or more local assemblages containing
366 species abundance data (McGill 2011b). From CESTES, we excluded studies with explicit
367 human impacts identified as an environmental feature, and our analysis included 19 studies that
368 sampled terrestrial, freshwater and marine assemblages from a number of taxonomic groups
369 (birds, plants, insects, macroinvertebrates, fishes and mammals). Similarly, studies documenting
370 disturbances and other perturbations were removed from the McGill (2011b) compilation,
371 resulting in 32 studies being retained. From the combined 51 studies, those with many sites were
372 randomly subsampled down to ten sites so that they did not dominate the results. Within each
373 study, an arbitrary site was assigned as the 'reference' site, and change was quantified between
374 every site and the reference within studies; our analysis included a total of 356 spatial
375 comparisons.
376
377 *Spatial comparisons: anthropogenic perturbations*
378 To quantify spatial differences in biodiversity due to anthropogenic land use, we used the
379 PREDICTS database, which is a collation of studies comparing reference to impacted sites

380 (Hudson et al. 2017). Here we used the 2016 release of the database (downloaded from
381 https://data.nhm.ac.uk/ on 10th July 2020). We limited our analyses to studies with abundance
382 data for individuals, and those with known land use categories (primary vegetation, mature
383 secondary vegetation, intermediate secondary vegetation, plantation forest, cropland, pasture,
384 and urban); studies where land use was not recorded were omitted. This resulted in 237
385 combinations of source ID and study (some sources had multiple studies, denoted SS in the
386 database), and 418 estimates of change relative to the reference land use category, primary
387 vegetation.
388
389 *Statistical models*
390 Similar models were fit to each data source. For the *Temporal comparisons: natural*
391 *environmental variation* data, total abundance (N) was fit with a model that assumed a lognormal
392 distribution and identity link function, and Poisson distributions with log link functions were fit
393 to S_n, S_{PIE} and S; Poisson distributions were chosen for S_n and S_{PIE} values rounded to integers
394 based on visual assessments that showed lognormal models fit to raw S_n and S_{PIE} values greatly
395 underpredicted the density of ones in the data. For the *Temporal comparisons: experimental or*
396 *natural perturbations* data, S was no longer an integer value after standardising sampling effort,
397 and all metrics were fit with models that assumed lognormal distributions and identity link
398 functions. Both spatial data sets were fit with models that assumed lognormal distributions and
399 identity link functions for total abundance (N), rarefied richness (S_n) and evenness (S_{PIE}), and a
400 Possion distribution and log-link function for species richness (S).
401

402 The *Temporal comparisons: natural environmental variation* models included non-varying
403 intercepts and slopes for year, and varying intercepts and slopes for studies and cells for all
404 responses. To allow for correlations between changes in the different responses, varying study-
405 and cell-level parameters for all responses were drawn from a single multivariate normal
406 distribution for each level (i.e., one for studies, one for cells; see supplement for equations). The
407 models fit to the *Temporal comparisons: experimental or natural perturbations* data similarly
408 included non-varying intercepts and slopes for year, and had varying intercepts for study, site
409 and block fitted separately for each response. For these data, correlations between changes in the
410 different responses were modelled by drawing varying intercepts and slopes for each
411 combination of treatment and study for all responses from a single multivariate normal
412 distribution (see supplement for equations).
413
414 The models fit to the *Spatial comparisons: natural environmental variation* data included non-
415 varying intercepts for data source (i.e., CESTES and McGill). Correlations between the different
416 responses were modelled by assuming varying intercepts and slopes (representing the reference
417 site and departures for all other sites from the reference, respectively) for each study and
418 response came from a single multivariate normal distribution; over-dispersion in the richness
419 response was modelled using an observation-level varying intercept (see supplement for
420 equations). Models fit to the *Spatial comparisons: anthropogenic perturbations* data included
421 non-varying intercepts and slopes (representing the reference [primary vegetation] category and
422 departures from the reference for each land use category, respectively), and varying intercepts
423 for sites and blocks were modelled separately for each response. Correlations between changes in
424 the different responses were modelled by assuming that varying intercepts and slopes (as per the

425 non-varying intercepts and slopes) for each combination of source and study and each response
426 came from a single multivariate normal distribution (see supplement for equations).
427
428 All statistical models were fit using the Hamiltonian Monte Carlo (HMC) sampler Stan
429 (Carpenter et al. 2017), and coded using the 'brms' package (Burkner 2017). Details of all model
430 specifications, and the iterations and warmup periods are provided in the supplement, as are the
431 priors (which were weakly regularising). Visual inspection of the HMC chains and model
432 diagnostics (Rhat < 1.05) showed good mixing of chains and convergence, and model adequacy
433 assessed visually using posterior predictive checks showed that the models were able to make
434 predictions similar to the empirical data (see Supplement Figures S1-4). Code for all analyses is
435 available at https://github.com/sablowes/MulticomponentBioChange, and will be archived
436 following publication.
437
438 **Results**
439 Temporal changes in perturbed environments had the highest percentage of assemblages with at
440 least one component trend (ΔN, ΔS_n, ΔS_{PIE}, or ΔS) that differed from zero (44%), followed by
441 spatial comparisons across land use categories (29%), temporal changes (21%) and spatial
442 comparisons in naturally varying environments (12%). Component changes that differed from
443 zero showed broadly similar patterns across datasets, with one exception: trends differing from
444 zero for multiple components were less common for spatial comparisons between assemblages in
445 naturally varying environments (Figure 3).
446

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.

516 Our general result that changes in the total abundance of an assemblage through time or space
517 are often decoupled from changes in metrics of biodiversity such as species richness also
518 cautions against making "apples to oranges" comparisons in the context of quantifying
519 biodiversity change. For example, some estimates of change are based on either population-level
520 abundance (e.g., Living Planet Index, WWF 2020), or assemblage-level abundance (e.g., insect
521 declines, Wagner 2000, van Klink et al. 2020), whereas other change estimates are based on
522 patterns of the number or identity of species present (e.g., Dornelas et al. 2014, Newbold et al.
523 2015). Our results show that assuming abundance and richness changes are strongly correlated
524 will often be an oversimplification. Moreover, the importance of variation in relative abundances
525 for local biodiversity change means that biodiversity trends may often depend on whether altered
526 relative abundances influence the metrics used (see e.g., Antão et al. 2020b).
527
528 *Patterns of temporal versus spatial biodiversity change*
529 Differences between patterns of temporal versus spatial change emerged from our analyses.
530 Moreover, these differences were generally greater than those found between naturally-varying
531 and perturbed assemblages, for either the temporal or spatial comparisons. In general, the
532 magnitude of changes of all components across space were larger than rates of change through
533 time. Multiple factors likely contributed to the larger effect sizes found for spatial changes. For
534 example, patterns of autocorrelation likely differ between the dimensions, with temporal data
535 more likely to resample individuals than the spatial comparisons, limiting the magnitude of
536 changes possible. Likewise, the units of change differ between temporal (where change was
537 standardised to an annual rate [change per year]) and spatial comparisons (change between
538 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

562 relatively natural environments (Figure 4b). In some cases, this occurred despite countervailing
563 changes in total abundance and evenness (Figure 4a, b). For assemblages where abundance and
564 evenness changed in the same direction, similar estimates of ΔS_n and ΔS indicate that abundance
565 changes were occurring along a relatively flat region of the individual-based rarefaction curve.
566 This shows that changes to the total number of individuals need not strongly influence species
567 richness, even where signs are the same and they have a positive relationship. Instead, richness
568 changes were more strongly associated with altered relative abundances, which has important
569 implications for examining causes and/or consequences of biodiversity change (Hillebrand et al.
570 2008, Crowder et al. 2010). These cases highlight that even where the expected positive
571 relationships between abundance, evenness and richness are found, we can more fully understand
572 assemblage changes when all component changes are examined simultaneously.
573
574 While both approaches, time series and spatial comparisons (or space-for-time substitutions),
575 have contributed to our understanding of biodiversity change, the relative merits of each for our
576 understanding of ecological dynamics has not been discussed much (Adler et al. 2020). The
577 largely decoupled component changes found here for spatial comparisons suggest that too much
578 focus on average changes across assemblages, such as those in total abundance or in species
579 richness, risks masking highly heterogeneous changes occurring within assemblages in multiple
580 components. Moreover, decoupled, heterogeneous component changes complicate using spatial
581 comparisons to infer temporal changes. Our finding of smaller effect sizes for time series
582 indicates greater inertia for assemblage changes occurring through time, compared to site-to-site
583 variation. More generally, the strong role of changes to the SAD for variation in local
584 biodiversity suggests that examining drivers of altered patterns of relative abundance across

585 scales (e.g., are local environmental changes affecting evenness or are changes occurring at
586 broader spatial scales impacting the size of species pool) are an important direction for future
587 empirical work.
588
589 *Conclusions*
590 We found strong correlations between changes in the SAD and species richness changes through
591 time, whereas relationships between abundance and richness changes for both temporal and
592 spatial diversity change were generally weak. Our findings confirm that altered species relative
593 abundances, and/or changes to the size of the species pool, often strongly influence local
594 diversity change (Chapin et al. 2010), even where human impacts are less direct. However, our
595 results also reinforce cautions against examining changes to any one component of biodiversity
596 change in isolation (e.g., Wilsey et al. 2005, Chase et al. 2018, Avolio et al. 2021).
597
598 To be most useful, variation in the different components of biodiversity need to be coherently
599 conceptualised. Individual-based rarefaction curves and associated metrics provide an intuitive
600 and illustrative characterisation of relationships among changing components of local
601 biodiversity. Whilst ecologists are increasingly looking beyond species richness to quantify
602 biodiversity change (e.g., Dornelas et al. 2014, Hillebrand et al. 2018), different components of
603 biodiversity and its change within assemblages are most often analysed independently, and with
604 metrics lacking conceptual unification. Our results emphasise that changes to the most frequently
605 quantified aspects of biodiversity, including changes to the numbers of individuals, and the
606 relative abundance and total numbers of species are highly interdependent. Examining how
607 within-assemblage component changes covary with potential drivers could reveal insights

608 masked by independent aggregate estimates of change and provide new information for

609 understanding biodiversity change in the Anthropocene.

610

611 **Open research statement**: All data used in the manuscript are already in the public domain. The
612 BioTIME database is accessible through the BioTIME website (http://biotime.st-andrews.ac.uk)
613 and a Zenodo repository (https://zenodo.org/record/1095627). Perturbed time series were
614 compiled using the data portal of the Environmental Data Initiative
615 (https://portal.edirepository.org/nis/home.jsp); code for compilation and standardisation available
616 at https://github.com/chase-lab/BioTIMEx. PREDICTS is available at
617 https://www.predicts.org.uk/. McGill SAD data were previously archived at:
618 https://doi.org/10.6084/m9.figshare.6945704. CESTES database is available at
619 https://doi.org/10.25829/idiv.286-21-2695. Code for all analyses is available at
620 https://github.com/sablowes/MulticomponentBioChange, which will be archived when accepted.
621

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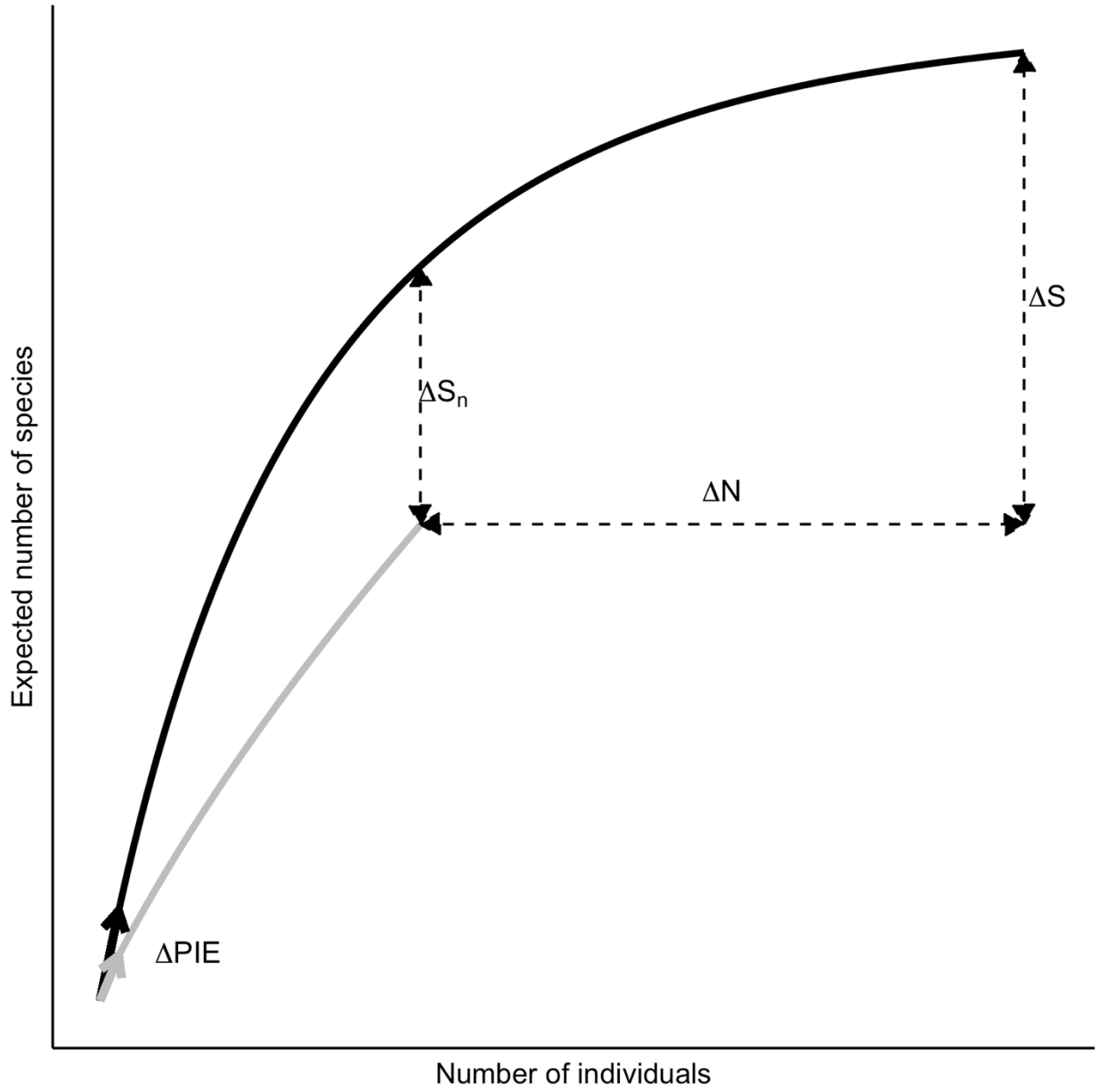
Figure 1: Individual-based rarefaction (IBR) curves for samples from two hypothetical assemblages. We characterise diversity change using four components of the IBR curve: altered numbers of individuals (ΔN), changes in species richness (ΔS), and two metrics that capture changes to the SAD – changes 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).

829 **Figure 3**: Summary of assemblage diversity components with a high probability of change (90%
830 credible interval did not overlap zero) for (a) temporal changes in naturally varying
831 environments, (b) temporal changes in perturbed environments, (c) spatial changes relative to an
832 arbitrary reference, (d) spatial changes relative to primary vegetation. Assemblages with no
833 component changes different from zero are reported as insets for clarity. Metric abbreviations:
834 total number of individuals (N), expected number of species for n individuals (S_n), numbers
835 equivalent transformation of the Probability of Interspecific Encounter (S_{PIE}), and total species
836 richness (S). Number following each bar is the count of assemblages for that category.
837
838 **Figure 4**: Relationships between four components of local diversity change. Change in species
839 richness as a function of changes in the numbers of individuals (left column), rarefied richness
840 (middle column), and evenness (right column) for (a-c) study-level estimates of temporal
841 changes in naturally varying environments; (d-f) estimates of temporal change for combinations
842 of study and treatment in perturbed environments; (g-i) estimates of spatial changes within
843 studies from an arbitrary reference site along natural environmental gradients; and, (j-l) estimates
844 of spatial change within studies between primary vegetation and different land use categories.
845 Coloured concentration ellipses show 10% increments (5 – 95%) of the posterior distributions.
846 Dotted grey lines are x = y = 0, and x = y for visual reference. See Supplementary Figure 5 for
847 remaining pairwise relationships. NB: Scale of x- and y-axes vary between panels; one estimate
848 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)
849 for clarity.
850

851 **Figure 5**: Component correlations among studies within each data source. Density plots for the
852 posterior distribution of pairwise correlations between component changes for (a) temporal
853 comparison in naturally varying environments, (b) temporal comparisons in perturbed
854 environments, (c) spatial comparisons along natural gradients, and (d) spatial comparisons
855 between different land use categories. NB: correlations estimated separately for sites and land
856 use categories relative to the references were combined here for clarity on (c) and (d).
857

858 **Figure 1**



859

860

Figure 2

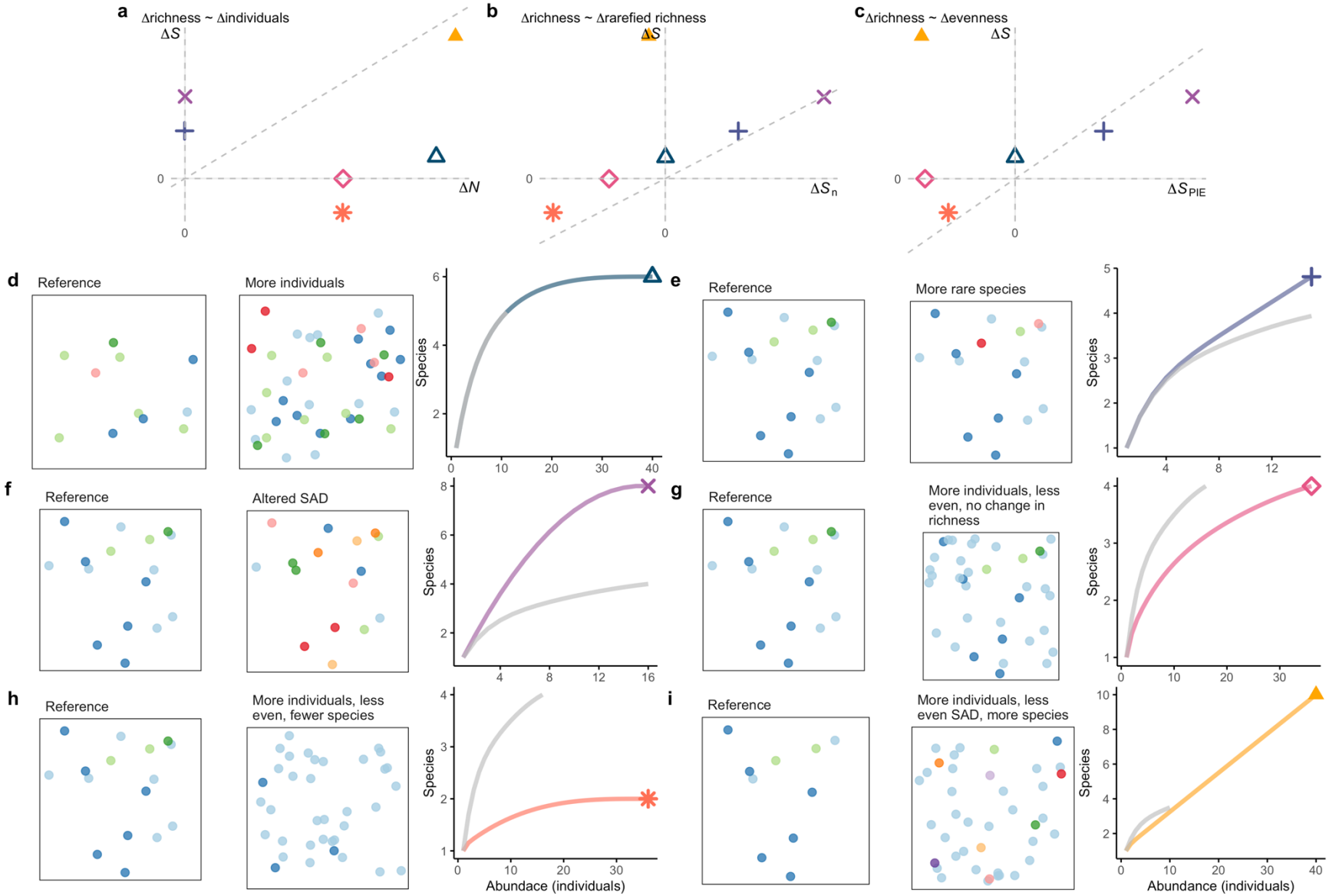

a
Δrichness ~ Δindividuals
ΔS
ΔN
b
Δrichness ~ Δrarefied richness
ΔS
ΔSn
c
Δrichness ~ Δevenness
ΔS
ΔSPIE
d
Reference
More individuals
Species
e
Reference
More rare species
Species
f
Reference
Altered SAD
Species
g
Reference
More individuals, less even, no change in richness
Species
h
Reference
More individuals, less even, fewer species
Species
Abundace (individuals)
i
Reference
More individuals, less even SAD, more species
Species
Abundance (individuals)

Figure 3

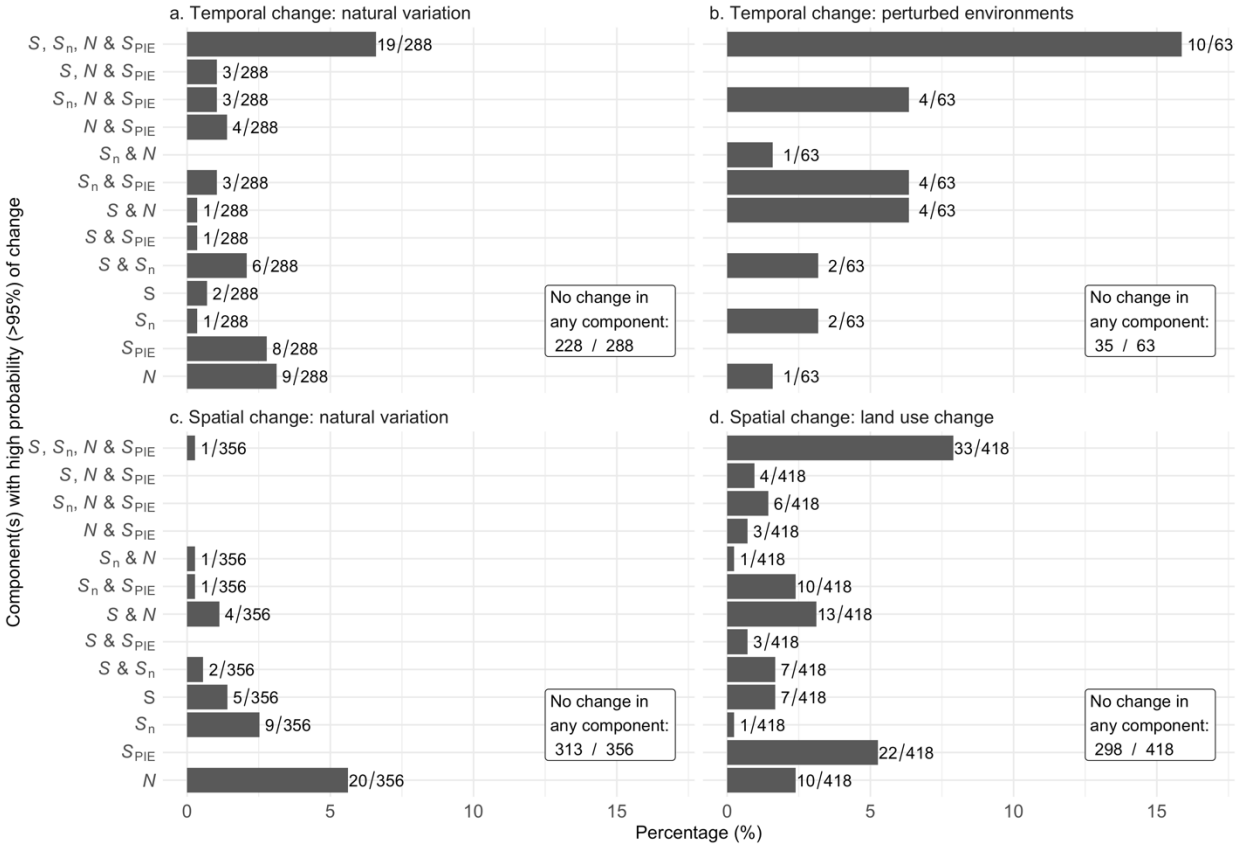

a. Temporal change: natural variation
b. Temporal change: perturbed environments
c. Spatial change: natural variation
d. Spatial change: land use change
Component(s) with high probability (>95%) of change
S, Sn, N & SPIE
S, N & SPIE
Sn, N & SPIE
N & SPIE
Sn & N
Sn & SPIE
S & N
S & SPIE
S & Sn
S
Sn
SPIE
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

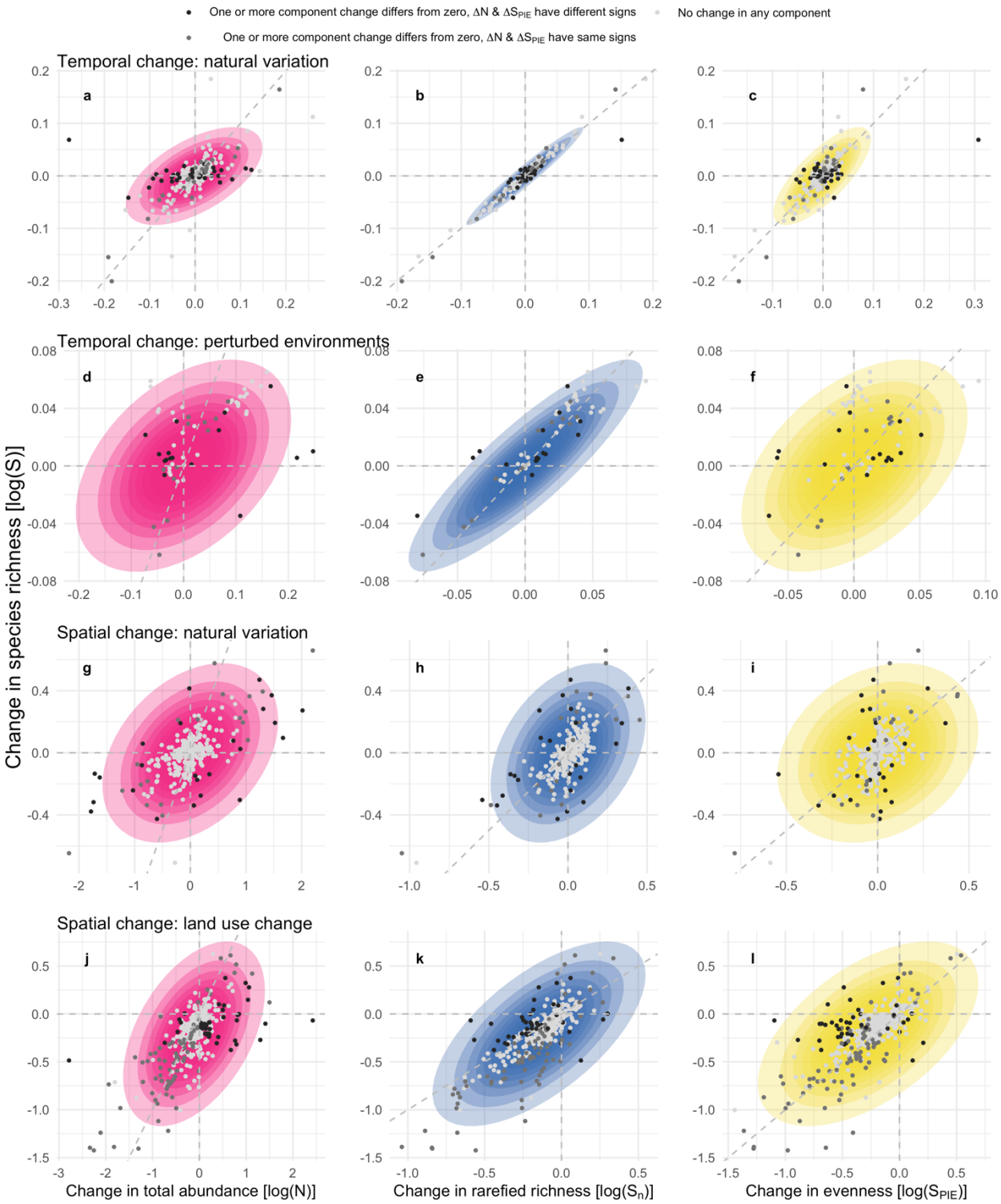
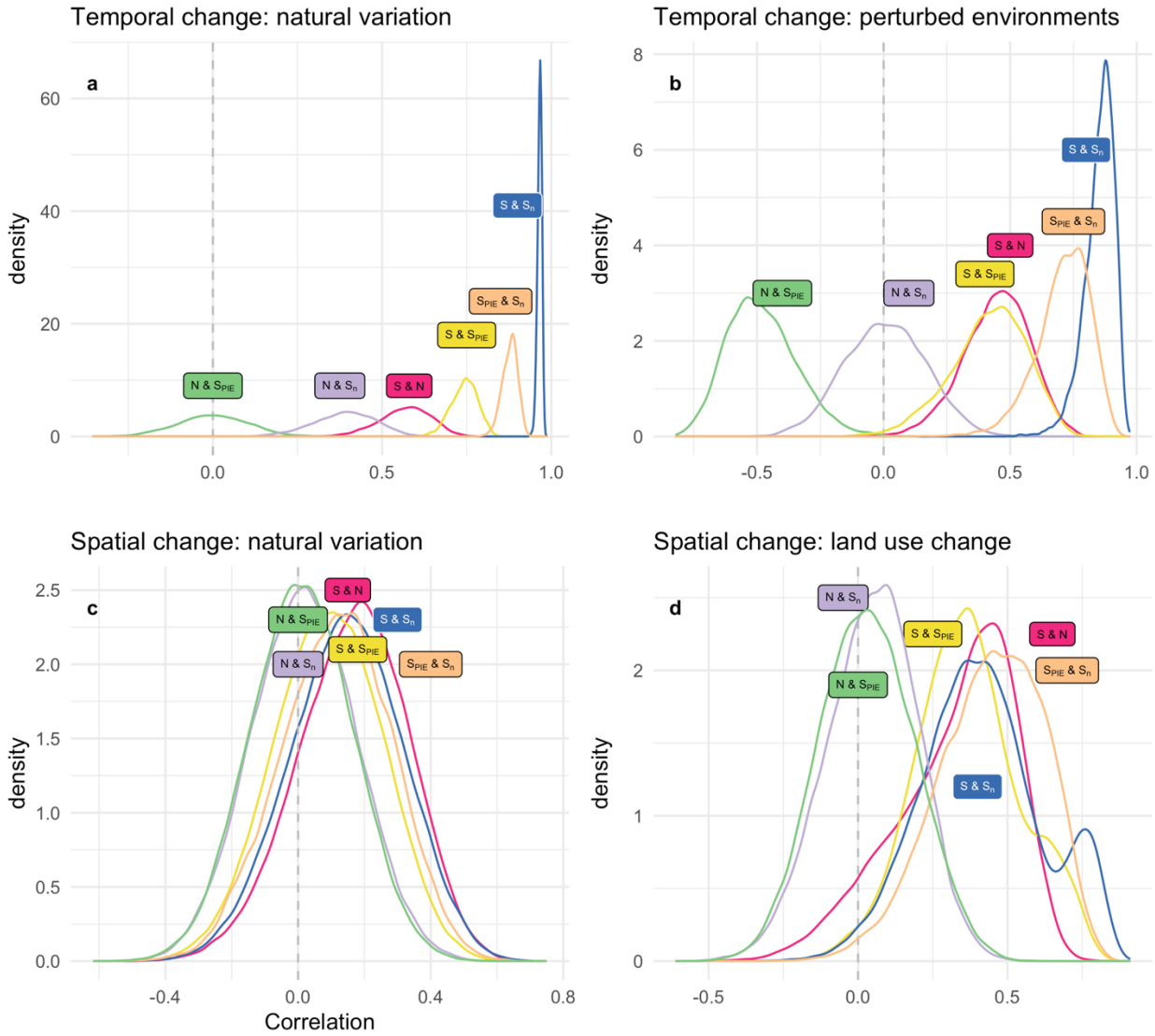

One or more component change differs from zero, ΔN & ΔS_PIE have different signs
No change in any component
One or more component change differs from zero, ΔN & ΔS_PIE have same signs
Temporal change: natural variation
Temporal change: perturbed environments
Spatial change: natural variation
Spatial change: land use change
a
b
c
d
e
f
g
h
i
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
N & S_{PIE}
N & S_n
S & N
S & S_{PIE}
S_{PIE} & S_n
S & S_n
Temporal change: perturbed environments
b
Spatial change: natural variation
c
Spatial change: land use change
d
Correlation