

# ECOGRAPHY

## Research article

### A mismatch between community assembly and abundance-based diversity indices

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Long-term ecological studies have consistently reported slower than expected changes in biodiversity over time. One explanation for this phenomenon is that commonly used diversity measurements such as species richness are too coarse to detect mechanisms shaping community assembly. Theory suggests that similar phenomena may occur in abundance-based diversity measurements, but the extent of this problem is currently unclear. We confront this theoretical prediction with field data by studying temporal changes in abundance-based diversity indices across 3341 observations from 880 plots in 15 long-term vegetation plot studies. We then partition diversity change into mechanisms of interest to ecologists: selection, drift, and immigration. We show that these resulting changes in relative abundances often produce non-linear changes in diversity. These non-linearities lead counterintuitive effects that are easy to miss when directly analysing changes in diversity. To resolve this we show that explicit partitioning of diversity change leads to one further, less-studied partition: ‘rarity shifts’. Rarity shifts measure how an individual’s contributions to diversity changes over time. These rarity shifts are responsible for counter-intuitive effects, for example when radical changes in community composition lead to negligible changes in diversity. We found rarity shifts are an important component of diversity change across many studies. Furthermore, rarity shifts tend to oppose selection, drift and immigration. Therefore, rarity shifts explain why changes in relative abundance do not consistently result in changes in abundance-based diversity measurements. Ultimately, using rarity shifts can lead to a more accurate understanding of the temporal rate and nature of diversity change in ecology and conservation.

Keywords: biodiversity, Gini-Simpson’s, immigration, mechanistic models, partition, selection, Shannon entropy, species richness

#### Introduction

A central goal of ecology is to understand biodiversity change over time (MacArthur 1965, McGill et al. 2015, Dornelas et al. 2018, Chase et al. 2019, Dornelas et al. 2019).

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Biodiversity represents the variety of living organisms found in a given place. Biodiversity is a key concept in conservation, used to assess ecosystem health in response to management or anthropogenic stressors and to prioritize areas for protection (McGill et al. 2015, Hillebrand et al. 2018). Despite disruptive anthropogenic environmental changes, many long-term ecological studies show surprisingly little change in biodiversity within locations (Sax et al. 2002, Vellend et al. 2013, 2017, Hillebrand et al. 2018). For example, analyses of vegetation plots show no overall decline in local scale biodiversity over time (Vellend et al. 2013). Surprisingly, this apparent stasis concealed important trends in community assembly: the rate of extinctions increased over time, but this effect was obscured by an increase in the rate of colonisations (Dornelas et al. 2019). Given the need to detect anthropogenic impacts and predict shifts in biodiversity (Urban et al. 2016), there is a need to understand the extent of this mismatch.

Species richness, the most widely studied diversity measurement, may give an overly coarse picture of diversity change (Hillebrand et al. 2018). This is because richness provides no explicit information about species abundances, and many of the mechanisms that operate in communities act on abundances (MacArthur 1965, Urban et al. 2016, Godsoe et al. 2023). The logical alternative is abundance-based diversity indices such as Shannon entropy and Gini-Simpson's (Jost 2006). These metrics incorporate information on the evenness of species' relative abundances in addition to richness. By relative abundance we mean the proportion of all individuals in a given community which belong to a particular species.

When studying changes in abundance-based diversity indices, it makes sense to focus on mechanisms that change relative abundances at the species level such as selection and drift (Vellend 2016). A major advantage of this approach is that selection describes changes in relative abundances and diversity summarizes information on relative abundances (Jost 2006). In contrast, species interactions such as competition or predation are characterized by their effects on absolute abundances (i.e. the total number of individuals in each species). Competition, for example, decreases the absolute abundance of interacting species, while predation increases the absolute abundance of predators and decreases the absolute abundance of prey (Holland and DeAngelis 2009). By focusing on selection and drift, we are implicitly capturing some of the consequences of species interactions (Vellend 2010). Vellend (2016) has argued that, particularly when teaching community ecology, it is helpful to organize ecological processes into four fundamental mechanisms: selection, drift, immigration and speciation. Many of his examples highlight how individual species respond to these mechanisms (Vellend 2010). But because multiple processes can still produce similar patterns of diversity change (Godsoe et al. 2023), it remains challenging to quantify the effects of these mechanism on biodiversity as a whole.

Evolutionary theory provides tools to quantify the effects of selection, drift and immigration using a technique known as partitioning. Partitioning focuses on a quantitative attribute of a group of organisms, then divides total change in this

attribute into distinct, biologically interpretable partitions. In ecology some of the most familiar examples of partitions examine how changes in diversity alter ecosystem function (Loreau and Hector 2001, Fox and Kerr 2012, Harrison et al. 2022). However, partitioning techniques are intended to solve a much broader array of problems (Price 1995, Luque 2017), including analyzing change in abundance-based diversity measurements (Godsoe et al. 2021). This approach starts by measuring each individual's contribution to a diversity index, with individuals belonging to rare species scoring higher than individuals belonging to common species. The scores of these individuals are then averaged to produce a measure of diversity (Patil and Taillie 1982, Roswell et al. 2021). Diversity change over time can be decomposed into changes in individual contributions. For example, diversity increases in response to species-level selection when individuals belonging to rare species have higher fitness than individuals belonging to common species. Diversity decreases in response to species-level selection when individuals belonging to common species have higher fitness than individuals belonging to rare species. Species-level drift shapes diversity when chance events lead to differences in the number of descendants produced by individuals belonging to rare species relative to common species. Note that in small observational studies stochasticity (i.e. drift) can have substantial impacts and therefore distinguishing drift and selection is challenging. This problem can be mitigated by large sample sizes such as laboratory experiments with microbes or repeated observations under similar conditions. The datasets we analyse are observational and so the term we describe 'selection' implicitly includes drift. See Godsoe et al. (2022), for a simulation-based test for the distinct effects of drift in larger plots.

Under some circumstances, partitioning suggests that changes in diversity closely match the effects of selection/drift and immigration. For example, Figure 1 illustrates changes in relative abundances in observations of forest plots in Brazil (Farah et al. 2014) from the BioTIME database (Dornelas et al. 2018). In the first plot, the relative abundance of a rare species *Psychotria vauthieri* slightly increased, while the relative abundance of a common species *Ixora gardneriana* (Fig. 1a) slightly decreased between 1994 and 1999. This leads to a small increase in diversity (Fig. 1c). There was no immigration in this community, and the total change in diversity is more or less equal to the increase in selection from the rare species becoming more common in the plot (Fig. 1e). Under other circumstances, partitioning reveals a mismatch between total change in diversity and changing species' relative abundances. For example, the right column in Fig. 1 illustrates a forest plot with far more dramatic changes in relative abundances (Fig. 1b). In 1994 *Plinia cauliflora* is the rarer species while *Croton floribundus* is more common. However, *P. cauliflora* increases in relative abundance to become more common than *C. floribundus* in 1999. This dramatic flip in relative abundances produces a small change in diversity (Fig. 1d) which is similar to the diversity change recorded in the first forest plot (Fig. 1c). This is because the success of the rare species, which is captured by the selection term increasing diversity, is counteracted by the rapid changes in rarity

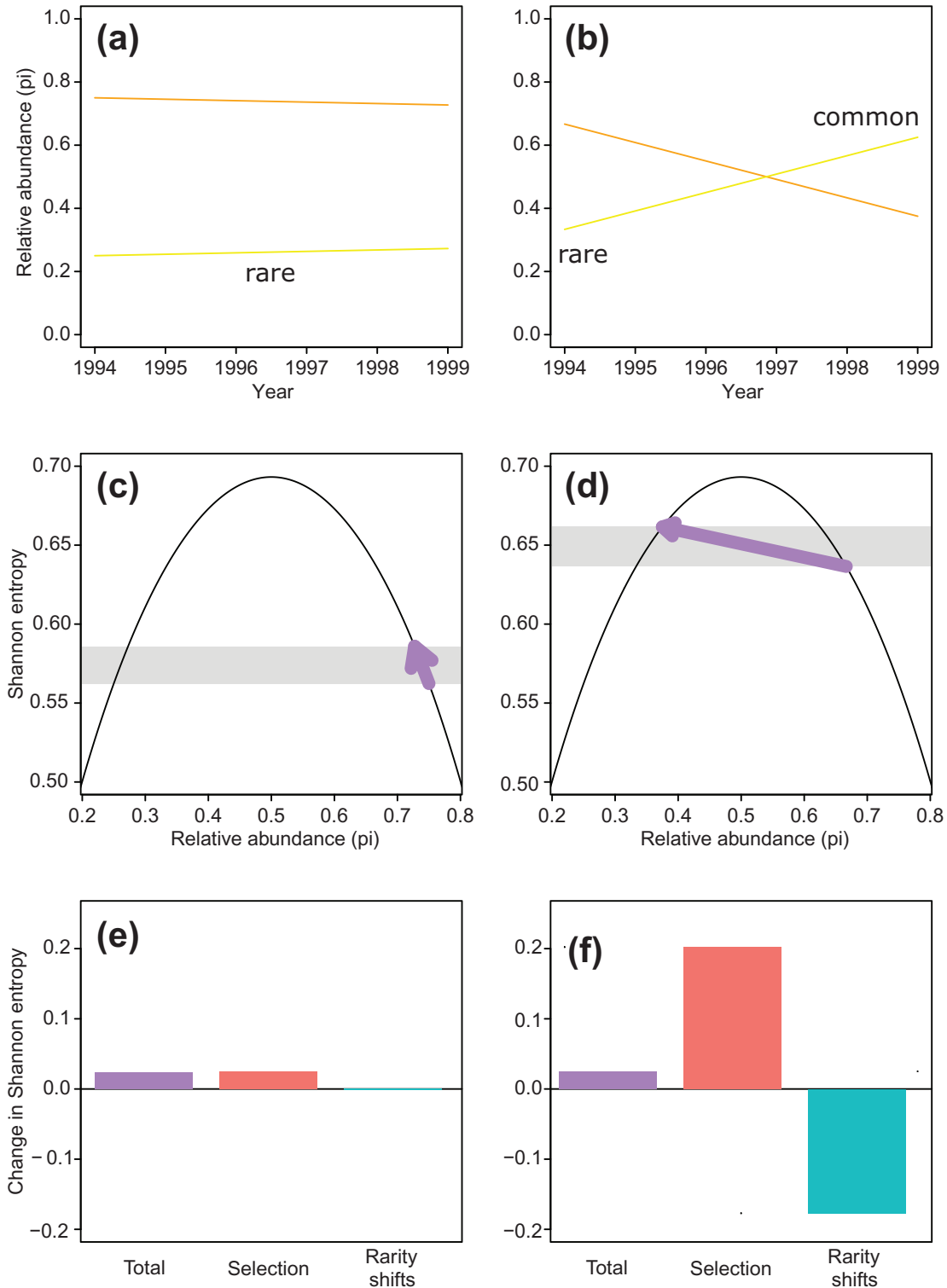


Figure 1. Small changes in diversity may obscure strong changes in relative abundance, as shown between 1994 and 1999 (indicated by grey bands) in Santa Genebra Forest, Brazil (Farah et al. 2014). (a) illustrates small changes in relative abundances for species *Ixora gardneriana* (orange) and *Psychotria vauthieri* (yellow); (b) illustrates comparatively large changes in relative abundances for species *Croton floribundus* (orange) and *Plinia cauliflora* (yellow); (c) The changes in abundances in (a) lead to relatively small changes in diversity. Here, the arrow indicates the change in the community with the diversity change highlighted in grey; (d) The large changes in abundances in (b) also lead to a surprisingly weak effect on diversity change; (e) Partitioning the total change in diversity shows the effects of selection and rarity shifts (blue, but barely visible). This highlights the primary role of selection in the example presented in (a); (f) In contrast, partitioning of change in example (b) shows selection increases diversity, while rarity shifts simultaneously decrease diversity. This interplay of selection and rarity shifts leads to a modest change in diversity.

shifts decreasing diversity. The opposing directions of rarity shifts and selection in this example explained why diversity changes were smaller in magnitude than expected, highlighting how a mismatch between relative abundances and diversity change may arise (Fig. 1f).

Analyses of rarity shifts have focused on developing theory (Godsoe et al. 2021, 2022, 2023). Until now, there has not been a systematic test of the importance of rarity shifts. To better understand how much observed changes in diversity reflect rarity shifts, we analyse 15 terrestrial vascular plant studies (Table 1). Vegetation plots are ideal for our purposes because plants are sessile, meaning immigrants are rarer and less likely to be confused with descendants. This makes it easier to spot the role of rarity shifts (Fig. 1). Using these data we calculate the change over time in Shannon entropy and Gini-Simpson's diversity. We then use partitioning to decompose total diversity change into selection/drift, immigration, and rarity shifts to address three questions. 1) Are rarity shifts a large component of diversity change? We address this by comparing the distribution of measured rarity shifts to overall diversity change across all observations. 2) Are rarity shifts equally common across studies? We address this by comparing the range of rarity shifts observed in each study. 3) How does the strength of rarity shifts change with the strength of the other partitions? We address this by using a generalized additive model to predict when rarity shifts are most common.

## Material and methods

### The model

To analyse change within a plot we use the partitioning approach from Godsoe et al. (2021). Within a given plot

the absolute abundance of each species is  $n_i$  and the relative abundance of each species is  $p_i = n_i / \sum_i n_i$ . For many diversity indices, the contribution that each individual makes to diversity can be defined as  $z_i$ , the rarity of the species to which it belongs. For Shannon entropy, the measure of rarity is  $z_i = -\log(p_i)$ . Because we are interested in change between one period and another we can define rarity scores for Gini-Simpson's diversity as  $z_i = -p_i$  (Godsoe et al. 2021). Diversity is an average measurement of rarity across all individuals in a plot (Patil and Tailie 1982) (Eq. 1). For Shannon entropy, the arithmetic mean of rarity scores are weighted by the relative abundance of each species (Jost 2006, 2007, Cover and Thomas 2012).

$$D = \sum_i p_i z_i. \quad (1)$$

Total change in diversity over time is the difference between a measurement of diversity in the present and diversity in the past (Eq. 2). Here and elsewhere,  $\Delta$  describes change over time and the prime superscript (') denotes present measurements (Frank 2012).

$$\Delta D = D' - D. \quad (2)$$

To understand the effects of immigrants on diversity change, we further divide the present community into two components:

$$D' = \omega \sum_i p_i' z_i' + \mu \sum_j a_j z_j^*. \quad (3)$$

Table 1. Summary of the 15 long-term vegetation plots analysed from the BioTIME database.

Citation	Study ID in BioTIME	Location	Description	Years between samples	Plot size (m <sup>2</sup> )	Plant density (m <sup>-2</sup> )
Webb and Scanga (2001)	10	USA (Minnesota)	Windthrow on mixed hardwood–evergreen forest	3	4	6.025
Zachmann et al. (2010)	18	USA (Idaho)	Old, natural temperate sagebrush scrub	1–3	1	141.500
Barreto (2016)	302	Brazil (Sao Paulo)	Semi-deciduous subtropical broadleaf forest	3, 6	400	0.115
(Salami et al. 2014)	303	Brazil (Lages)	Subtropical, broadleaf forest.	4	200	0.184
Farah et al. (2014)	322	Brazil (Sao Paulo)	Semi-deciduous, subtropical, forest structure	5, 11	100	0.122
Venturoli et al. (2011)	324	Brazil	Regenerating semi-deciduous saplings	1	16	0.288
Venturoli et al. (2011)	325	Brazil	Regenerating semi-deciduous forest	1	25	0.556
Pelissier et al. (2011)	329	India	Evergreen dipterocarp mature forest	3–5	3600	0.117
Ernest et al. (2009)	336	USA (Arizona)	Flowering desert shrubs - seasonal	0.5	2500	1.348
Lightfoot (2011)	340	USA (Arizona)	Flowering desert shrubs	1	1	264.600
Sanquetta (2008)	346	Brazil (Sao Paulo)	Subtropical grass or shrubland	3, 6	400	0.206
Myster (2007)	352	Peru	Flooded rainforest	1	25	1.436
Bradford et al. (2014)	356	Australia (Queensland)	Mature rainforest	Varies	5000	0.009
Thorn et al. (2016)	465	Germany (Bavaria)	Vascular plants after windfall	1	200	0.078
Thorn et al. (2016)	548	Germany (Bavaria)	Vascular plants after windfall	1	200	0.071

The first term represents individuals that are not immigrants ('descendants'). They may represent individuals that were in the community in the first survey or their offspring. Here  $\omega$  is the proportion of individuals in the present community that descended from the past community. Among descendants the proportion belonging to species  $i$  is  $p'_i$ , and the rarity score of species  $i$  is  $z'_i$  (note this is rarity as a proportion of total individuals across both time steps). The second term describes the contribution of immigrants, where  $\mu$  is the proportion of individuals in the present community which immigrated to the community since the initial measurement. In practice, we treat individuals in the present community that belong to species that were absent in the past community as immigrants. It is likely that some other individuals were immigrants, but were more difficult to detect. Among immigrants, the proportion belonging to species  $i$  is  $a'_i$ , and the rarity score of species  $j$  is  $z_{j^*}$  (note this is rarity as a proportion of all individuals, not just immigrants).

Overall diversity change in Eq. 2 can then be partitioned using extensions of the Price equation (Price 1970, Kerr and Godfrey-Smith 2009). This leads to explicit definitions for the effects of selection/drift, immigration and rarity shifts on diversity (Eq. 4).

$$\Delta D = \underbrace{\omega \sum_i \Delta p_i z_i}_{\text{Selection (+drift)}} + \underbrace{\mu \left( \sum_j a_j z_j^* - \sum_i p_i z_i \right)}_{\text{Immigration}} + \underbrace{\omega \sum_i p'_i \Delta z_i}_{\text{Rarity shifts}} \quad (4)$$

In Eq. 4, the first term describes the effect of selection, where the tendency of species  $i$  to leave more descendants increases its frequency relative to other descendants ( $\Delta p_i = p'_i - p_i$ ). In this framework, selection on species identity emerges either by leaving more offspring or having higher survival (Vellend 2016). This term implicitly includes effects of drift because both mechanisms change species' relative abundances (Rice 2004). Drift emerges when one species increases in relative abundance due to stochastic sampling. The second term describes immigration, which changes diversity when diversity among immigrants  $\sum_j a_j z_j^*$  is different from the diversity among resident ancestors. The final term denotes rarity shifts where the rarity score for descendants is different from the rarity scores of ancestors  $\Delta z_i$ , as in (Fig. 1c). For Eq. 4, it is natural to interpret rarity shifts as an indirect consequence of changes caused by selection and immigration. As such it is not an 'independent mechanism'. Instead rarity shifts are way to quantify non-linear changes in diversity that are difficult to intuit by directly studying selection, drift and immigration. However, the rarity shift partition corresponds to a term known as 'transmission bias' in evolutionary theory. Partitioning is a very general technique applicable to problems ranging from quantitative genetics, to ecological evolutionary dynamics to analyses of diversity-productivity relationships (Loreau and Hector 2001, Ellner et al. 2011, Queller 2017). In these applications transmission bias is treated as separate mechanism (Frank 2012, Luque 2017,

Godsoe et al. 2022), but this choice may be unhelpful for analyses of diversity change because rarity shifts are an indirect consequence of changes in relative abundances.

We have presented diversity indices that are familiar and easy to partition on a linear scale. More complexities emerge when analysing Hill numbers, a re-scaled version of diversity indices expressed in the equivalent number of uniformly distributed species needed to produce the observed diversity index (Jost 2006, 2007). Both Shannon entropy and Gini-Simpson's diversity indices can be converted into Hill numbers. While not used in this paper, the numbers equivalent Shannon entropy can be partitioned by exponentiation of Eq. 4 (Godsoe et al. 2022). This conversion changes the scale of measurement from additive to multiplicative but preserves many of the qualitative patterns. Techniques are available to partition other Hill numbers such as the Hill number equivalent of Gini-Simpson's diversity (Frank and Godsoe 2020), but these techniques are only valid in the absence of immigration. Adding immigration dramatically increases the complexity of partitioning (Kerr and Godfrey-Smith 2009). This problem has been addressed when investigating quantities that are arithmetic means (such as Shannon entropy) but Hill numbers are complex generalizations of these means.

## The data

We analysed the causes of biodiversity change from plots in terrestrial vegetation studies compiled in the BioTIME database (Dornelas et al. 2018). As of December 2021, the BioTIME database contained 361 studies, 201 of which were terrestrial surveys. We selected vegetation studies with multiple plots of area greater than 1 m<sup>2</sup>, including observations from three or more time periods, five or more species, and counts of individuals (as opposed to biomass, presence or vegetation cover). This resulted in a database of 3341 observations of diversity change drawn from 15 studies. Our analyses were done in R (www.r-project.org, Oksanen et al. 2009, Wickham et al. 2016).

To compare the effect of rarity shifts with other partitions, we calculated the change in Shannon entropy and Gini-Simpson's diversity within each plot across each time step using Eq. 1–2. To do this, we treat change in diversity was partitioned using Eq. 4. We then used histograms to compare the prevalence of rarity shifts relative to other sources of diversity change (Q1 and 2).

To determine how the strength of rarity shifts changes with other partitions (Q3), we used a generalized additive model (GAM). We modelled the strength of rarity shifts as a smoothed non-linear function of selection and immigration, with study and plot treated as random effects. Increasing effective degrees of freedom (edf) indicate greater model complexity, where edf = 1 indicates a straight line. The model was fit in the mgcv package (Wood and Wood 2015) using restricted maximum likelihood (REML). Rarity shifts had an extremely long tail and so to improve the interpretability of Fig. 4, ~3% of the data with the lowest rarity shifts were removed from the analysis of Shannon entropy. We also removed one

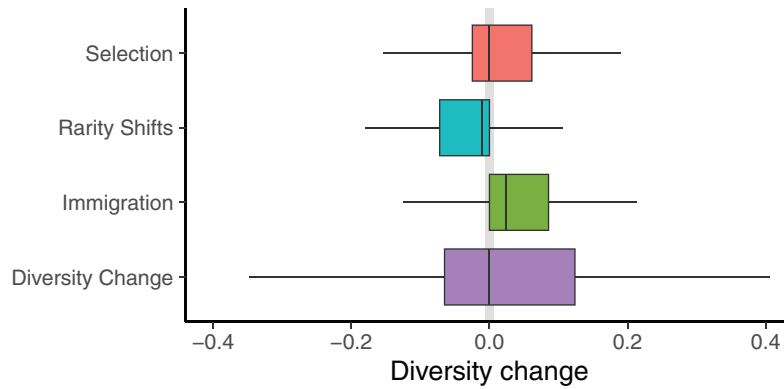


Figure 2. Summary of partitions from 3341 observation periods for Shannon entropy change including selection, rarity shifts, immigration and total diversity change across all plots and from the 15 studies. Each boxplot represents the number of observations where a given partition was of a particular magnitude. Boxplots show median values, interquartile range and values exceeding 1.5 times past the interquartile range.

unusually large estimate of selection, leaving us with 3244 observations. Example code can be found in an online repository: <https://figshare.com/s/cf8b20276ff930b64c76>.

## Results

All partitions contributed substantially to diversity change across the 3341 observations examined. For Shannon entropy, selection had a wide-ranging effect on diversity change (Fig. 2). Selection could either increase or decrease diversity (median: 0, inter quartile range:  $-0.025$  to  $0.061$ ). Immigration tended to increase diversity (median:  $0.024$ , inter quartile range:

$0-0.085$ ) (Fig. 2), this makes intuitive sense since the immigrants we observe are new species, and the arrival of new species tends to increase diversity. Immigration occasionally decreased diversity when highly diverse communities were replaced by a new community of immigrants with lower diversity, or when new immigrant species became the most dominant species. Rarity shifts commonly decreased diversity (median:  $-0.011$ , inter quartile range:  $-0.072$  to  $0$ ) (Fig. 2). Total diversity change was centered on zero (median:  $0$ , inter quartile range:  $-0.065$  to  $0.124$ ) (Fig. 2). Gini-Simpson's diversity showed similar trends (Supporting information).

Patterns of diversity varied across the 15 studies (Fig. 3). Many studies showed little diversity change, particularly

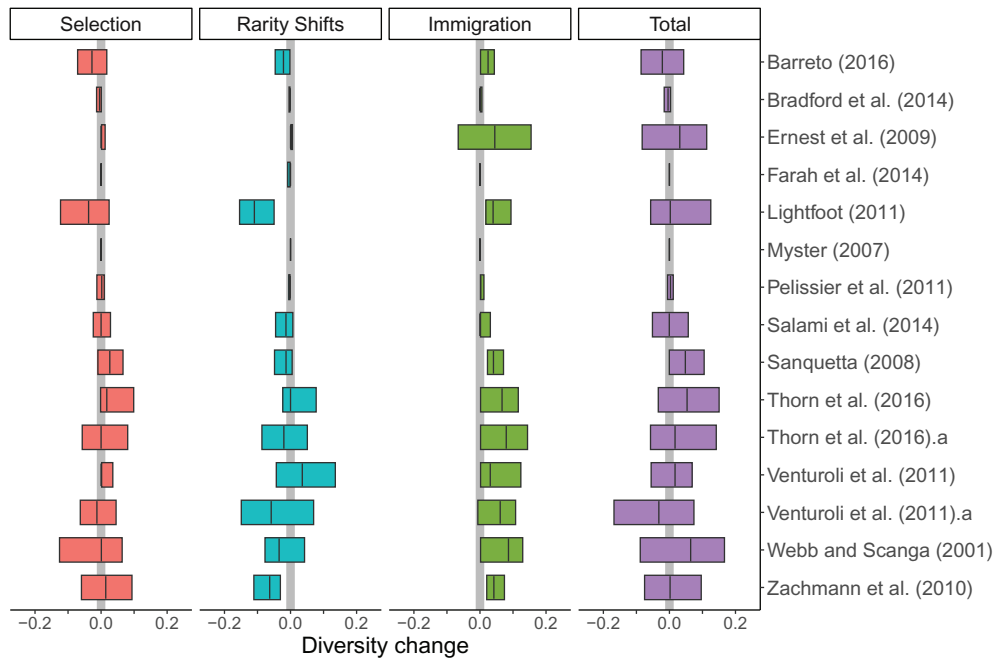


Figure 3. Partitions of Shannon entropy change across all plots and time periods for each of the 15 studies. Diversity change (purple) is partitioned into selection (red), immigration (green) and rarity shifts (blue) as is described in Eq. 4. The grey line represents zero diversity change. Boxplots summarize median and inter quartile range. Studies are ordered by diversity change. See supporting information for more details and Gini-Simpson's diversity comparison.

studies of long-term forest plots (Bradford et al. 2014). In these studies, total diversity change is typically zero and the contribution of each partition is negligible. Other studies are far more dynamic, such as communities experiencing disturbance regimes (Webb and Scanga 2001, Thorn et al. 2016) or regeneration (Venturoli et al. 2011), and many of these experienced strong rarity shifts. In these studies, all partitions could make a substantial contribution to diversity change. A notable example is Ernest et al. (2009) who studied seasonal flowering xeric shrubland communities in the deserts of Arizona each summer and winter. In these sites, the annual plants in a summer survey could represent different seasonal communities from plants in subsequent winter surveys. This increased diversity strongly in some plots and decreased diversity strongly in others (Baldwin et al. 2002). A similar experiment examines flowering plant communities in the desert of Arizona within plots where small mammal have been excluded (Lightfoot 2011). Immigration tends to increase diversity, rarity shifts tend to decrease diversity and selection appeared to take a wide range of positive and negative values. In this community, the most abundant species is the Creosote bush, *Larrea tridentata*. This species is perennial and its abundance changes little over the course of the study. Many of the rarer species are annuals whose abundances fluctuate dramatically from one season to another.

Generalized Additive Models indicate that there is a non-linear relationship between the strength of rarity shifts related and the strength of other partitions. Rarity shifts were close to zero when selection was zero, but tended to become negative when selection was non-zero. Rarity shifts were close to zero when immigration was close to zero and was slightly positive when immigration was non-zero (Fig. 4). Each term in each model required a relatively complex spline with many effective degrees of freedom (selection edf=7.8, immigration edf=8.8). Only a modest amount of variation was explained

by the model ( $R^2_{\text{adjusted}}=0.345$ ). Supporting information shows similar trends in Gini-Simpson's diversity.

## Discussion

Our work highlights how abundance-based diversity indices may not reveal real changes in community assembly. We quantified this effect by measuring rarity shifts, and showing how this effect can counteract more familiar sources of diversity change such as selection (Fig. 1). Therefore, abundance-based diversity indices and not just richness-based observations of diversity change can obscure changes in ecological communities and reveal slower than expected changes in diversity (Urban 2015, Urban et al. 2016, Chase et al. 2019, Dornelas et al. 2019).

Our results indicate that strong changes in relative abundances can lead to rarity shifts. Rarity shifts tended to oppose increases in selection and decreases in immigration (Fig. 4) resulting in a mismatch between changes in community assembly and diversity commonplace across all studies (Fig. 2) and accounts for why a negligible diversity change was observed in dynamic communities (Fig. 3).

We have shown that rarity shifts are commonplace across many datasets (Fig. 3), particularly in studies where changes in relative abundances are high. This includes studies experiencing environmental disturbances (Webb and Scanga 2001, Thorn et al. 2016) or regeneration (Venturoli et al. 2011). Additionally, studies of annual plant communities in the Arizonan desert by Ernest et al. (2009) and Lightfoot (2011) showed strong rarity shifts because measurements intervals matched or exceeded the seasonal lifespan of the community, meaning diversity measures reflected the high mortality and rapid emergence of plant species.

One idiosyncrasy of our analysis is that rarity shifts (and the other partitions) were uncommon in long-term forest

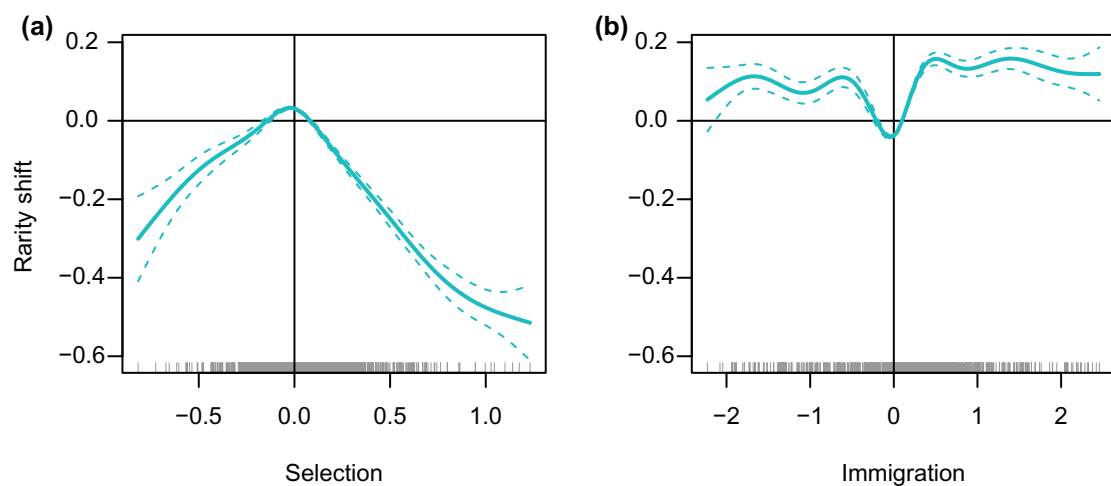


Figure 4. Predictions of the strength of rarity shifts for Shannon entropy derived from Generalized Additive Models. (a) When selection is close to zero, rarity shifts are close to zero. Selection values further away from zero lead to negative rarity shifts. Blue lines indicate predictions, dashes indicate 95% confidence intervals, and grey vertical bars indicate observations. (b) When immigration's effects on diversity are close to zero rarity shifts are close to zero. When immigration's effects on diversity are more extreme, rarity shifts tend to be slightly positive.

plots where changes in community composition and diversity are slow (Bradford et al. 2014). Some might choose to ignore these observations because they use a short sampling interval relative to the rate of change in the community. Nevertheless, we elected to analyse the data using these observations. This choice is likely conservative, as picking longer intervals would increase shifts in relative abundances, increasing the importance of rarity shifts. By analysing the sampling intervals in the original data, our results illustrate how gradual changes in diversity sometimes imply rarity shifts and sometimes indicate negligible overall change.

Considering rarity shifts may help us to understand the impacts of shifts in relative abundances. These shifts may produce less change in diversity than we expect and this has implications for many other ecosystem properties. For example, the rarity shift illustrated in Fig. 1b highlights how a substantial change in relative abundances leads to a negligible change in diversity. Considering only relative abundances we might note that a rare species has succeeded and therefore assume that diversity will increase along with some facets of community stability and ecosystem functioning (Tilman 1999, Cardinale et al. 2012). In reality, species diversity has changed little, by implication so has its impact on other community-level properties.

Our results are one of several recent applications of diversity partitions. Many of these papers have highlighted how ideas from the partitioning literature can clarify temporal changes in diversity. Examples include new methods to quantify the effects of biotic homogenization (Tatsumi et al. 2020, 2021, Godsoe et al. 2022), and how to relate biotic interactions such as competition to shifts in diversity (Godsoe et al. 2021, 2023). Arguably the biggest insight has been the realization that seemingly slow changes in species richness obscure substantial species turnover (Dornelas et al. 2019). We have added to this literature by showing that an analogous phenomena affects abundance-based diversity indices.

For generations, ecologists have sought to understand the relationship between changes in diversity and the fates of individual species (MacArthur 1965, Blowes et al. 2019). This debate has become more urgent as we have confronted our limited ability to explain shifts in diversity in nature (McGill et al. 2015, Socolar et al. 2016, Urban et al. 2016, Vellend et al. 2017). Many of us expect that contemporary methods will allow us to understand the causes of diversity change, by studying species' abundances (Gonzalez et al. 2023). Our work provides an important caveat: changes in relative abundances often produce non-linear changes in diversity. Such counterintuitive effects are easy to miss when directly analysing changes in diversity (Dornelas et al. 2019). Because it is not clear that existing methods will be able to tease apart these non-linear effects, we have proposed that partitioning be used to separate shifts in rarity from mechanisms that alter species' relative abundances. We have provided examples from individual plots that highlight how these rarity shifts can obscure selection (Fig. 1). We have shown that rarity shifts are comparable in magnitude to selection and immigration across the 15 studies (Fig. 2 and 3). Finally, we have

shown that rarity shifts can oppose selection and immigration (Fig. 4). Our results highlight how abundance-based diversity measurements can give an impression of slow diversity change, even in communities with rapid shifts in relative abundances. Therefore, reliable predictions of diversity change will require a more nuanced understanding of the role of rarity shifts.

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### Author contributions

**Matthew Vere Edmonds:** Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Software (equal); Visualization (equal); Writing – original draft (equal); Writing – review & editing (equal). **Jennifer L. Bufford:** Formal analysis (equal); Methodology (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **William Godsoe:** Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

### Transparent peer review

The peer review history for this article is available at <https://publons.com/publon/10.1111/ecog.06987>.

### Data availability statement

Data and code are available from the Figshare Repository: [https://figshare.com/articles/dataset/A\\_mismatch\\_between\\_community\\_assembly\\_and\\_abundance-based\\_diversity\\_indices/24503683](https://figshare.com/articles/dataset/A_mismatch_between_community_assembly_and_abundance-based_diversity_indices/24503683) (Godsoe et al. 2023).

### Supporting information

The supporting information associated with this article is available with the online version.

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