

A mismatch between community assembly and abundance-based diversity indices

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Abstract

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. It remains unclear whether abundance based diversity measurements are susceptible to the same problem. To test this, we study temporal changes in abundance based diversity indices across 3341 observations from 880 plots from 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 mechanisms are an imperfect predictor of temporal diversity change, creating a mismatch between changes in species abundances and changes in diversity, particularly when shifts in diversity are rapid. To resolve this mismatch, we quantify a less studied mechanism “rarity shifts”, which measure how an individual’s contributions to diversity changes over time. We found rarity shifts are an important component of diversity change across many studies. Furthermore, rarity shifts tend to oppose other mechanisms, particularly selection. Therefore, rarity shifts obscure changes in relative abundance from abundance based diversity measurements, revealing why diversity changes appear slower than expected. Ultimately, understanding rarity shifts can lead to a more accurate understanding of the rate and nature of temporal diversity change in ecology and conservation.

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than expected. Ultimately, understanding rarity shifts can lead to a more accurate understanding of the rate and nature of temporal diversity change in ecology and conservation.

Key Words: Biodiversity, species richness, mechanistic models, partition, selection, immigration, Shannon entropy, Gini-Simpsons

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). 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, Vellend et al. 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 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.

When studying changes in abundance based diversity indices, it makes sense to focus on mechanisms that change relative abundances such as selection and drift at the species level (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. Competition, for example, decreases the absolute abundance of some species at the expense of others, 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), but multiple species interactions can have indistinguishable effects on diversity (Godsoe et al. 2023).

To quantify the effects of mechanisms that alter diversity, Godsoe et al. (2021) proposed partitioning diversity change for abundance-based diversity measurements. This approach starts by measuring each individual's contribution to a diversity index, with individuals belonging to rare species contributing more than individuals belonging to common species (Patil and Taillie 1982, Roswell et al. 2021). Overall diversity change is then decomposed into changes in individual contributions. For example, species-level selection occurs when individuals belonging to rare species have higher fitness than individuals belonging to common species. Species-level drift occurs 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 drift and selection can produce similar effects (i.e. a change in the relative abundances of individuals from species that were already in the community). For this reason, we describe drift under the term "selection", but see Godsoe et al. (2022), for a simulation-based test for the effects of drift in larger plots.

Under some circumstances, partitioning emphasizes the role of mechanisms familiar to ecologists. 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 this case, the relative abundance of a rare species *Psychotria vauthieri* slightly increased, while the relative abundance of a common species *Ixora gardneriana* (Figure 1A) slightly decreased between 1994 and 1999. This leads to a small increase in

diversity (Figure 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 rare species becoming more common in the plot (Figure 1E). In contrast, rapid changes in relative abundances can lead to a mismatch between total change in diversity and mechanisms changing relative abundances. For example, the right column in Figure 1 illustrates forest plots with far more dramatic changes in relative abundances. 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 (Figure 1 D) which is similar to the diversity change recorded in the first forest plot (Figure 1C). This is because the success of rare species, which is captured by the selection term, increasing diversity, is counteracted by the rapid changes in rarity exhibited. The opposing mechanisms 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 (Figure 1 F).

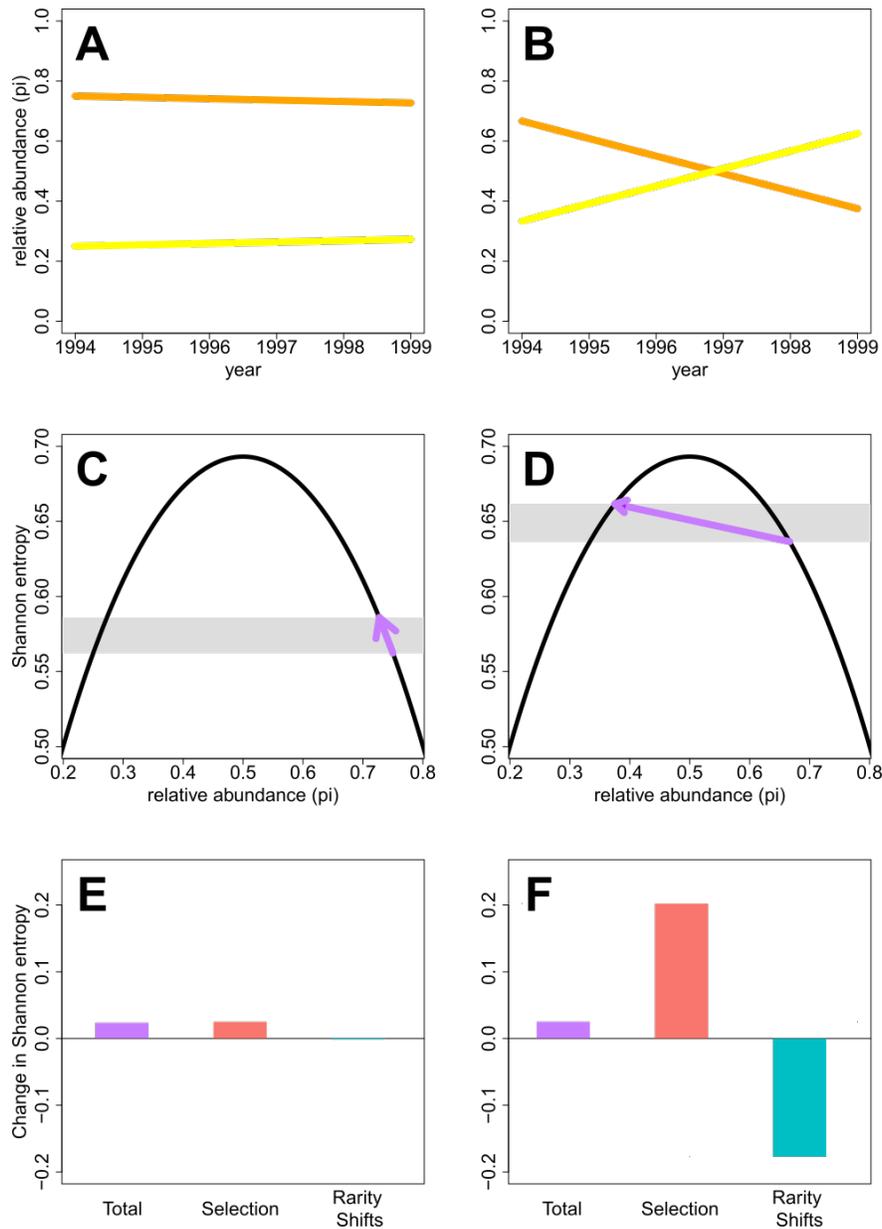


Figure 1: Gradual changes in diversity may obscure strong changes in relative abundance, as shown between 1994 and 1999 (indicated by grey bands) in Santa Genebra Forest, Brazil (Farah et al. 2014). A) illustrates gradual changes in relative abundances for species *Ixora gardneriana* (orange) and *Psychotria vauthieri* (yellow). B) illustrates comparatively rapid changes in relative abundances for species *Croton floribundus* (orange) and *Plinia cauliflora* (yellow). C) The gradual 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 rapid changes in abundances in B also lead to a surprisingly weak effect on diversity change. E) Partitions total change in diversity into an effect 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.

To better understand the importance of rarity shifts we analyse 15 terrestrial vascular plant studies. Vegetation plots are ideal for our purposes because plants are sessile, meaning new arrivals are unlikely to be confused with descendants (Table 1). We use partitioning to decompose total diversity change into selection, immigration, and rarity shifts. We then 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 contrasting the distribution of rarity shifts across each study. 3) We then asked how the strength of rarity shifts changes with the strength of the other mechanisms? 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 (Equation 1). 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 Taillie 1982); 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).

$$D = \sum_i p_i z_i.$$

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

$$D = D' - D.$$

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

$$D' = \omega \sum_i p'_i z'_i + \mu \sum_j a_j z_j^*.$$

The first term represents what we will call “descendants”, individuals that are not immigrants. They may represent individuals that were in the community in the first survey, or their offspring. Here ω 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 in both time steps). The second term describes the contribution of immigrants, where μ is the proportion of individuals in the present community which immigrated to

the community since the initial measurement. Among immigrants, the proportion belonging to species i is a_j' , 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 equation 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, immigration and rarity shifts on diversity (Equation 4).

$$(4) D = \text{Selection} + \text{immigration} + \text{rarity shifts}$$

In Equation 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 ($p_i = p_i' - p_i$). This term implicitly includes effects of drift because both mechanisms change species' relative abundances (Rice 2004). In this framework, selection on species identity emerges when one species tends to leave more descendants than another either by leaving more offspring or having higher survival (Vellend 2016). 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 z_i , as in (Figure 1 C).

We have presented diversity indices that are familiar and easy to partition on a linear scale. More complexities emerge when analysing so called “Hill numbers”, a re-scaled version of diversity indices expressed in common units. Both Shannon entropy and Simpsons diversity indices can be converted into common units the equivalent number of uniformly distributed species needed to produce the observed diversity index (Jost 2006, 2007). While not used in this paper, the numbers equivalent Shannon entropy can be partitioned by exponentiation Equation 4 (Godsoe et al. 2022). This conversion changes the scale of measurement from additive to multiplicative but preserves many of the qualitative patterns. At present, techniques exist to other Hill numbers into selection and transmission terms, in the absence of immigration (Frank and Godsoe 2020), but this condition is unrealistic for most observations in our study.

The Data

We analysed the causes of biodiversity change from plots in 15 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 m², including observations from 3 or more time periods, 5 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, with each observation representing the difference in diversity between one sample and a previous sample.

To compare the effect of rarity shifts with other mechanisms, we calculated the change in Shannon entropy and Gini-Simpson's diversity within each plot across each time step using Equations 1 and 2. This change in diversity was partitioned using Equation 4. We used histograms to compare the prevalence of rarity shifts relative to other sources of diversity change.

To determine how the strength of rarity shifts changes with other mechanisms, we used a generalized additive model (GAM). This was done using the `mgcv` package (Wood and Wood 2015) where the strength of rarity shifts is modelled 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 using Restricted Maximum Likelihood (REML). Rarity shifts had an extremely long tail and so to improve the interpretability of Figure 4, ~3% of the data with the lowest rarity shifts were removed from the analysis of Shannon entropy. We also removed one unusually large estimate of selection.

Results

All mechanisms contributed substantially to the 3341 observations of diversity change examined. For Shannon entropy, selection had a substantial effect on diversity change (Figure 2 A). Selection could either increase or decrease diversity (median: 0, inter quartile range: -0.025 - 0.061). Immigration tended to increase diversity (median: 0.024, inter quartile range: 0 - 0.085) (Figure 2 B), Intuitively, immigration increases diversity because the number of species increases as new species enter a community. Immigration occasionally decreased diversity when highly diverse communities were replaced by a new community of immigrants with lower diversity, or when the new immigrant species became the most dominant species. Rarity shifts commonly decreased diversity (median: -0.011, inter quartile range: 0.072 - 0) (Figure 2 C). Total diversity change was centered on zero (median: 0, inter quartile range: -0.065 - 0.124) (Figure 2 D). Gini-Simpsons diversity showed similar trends (Supporting information).

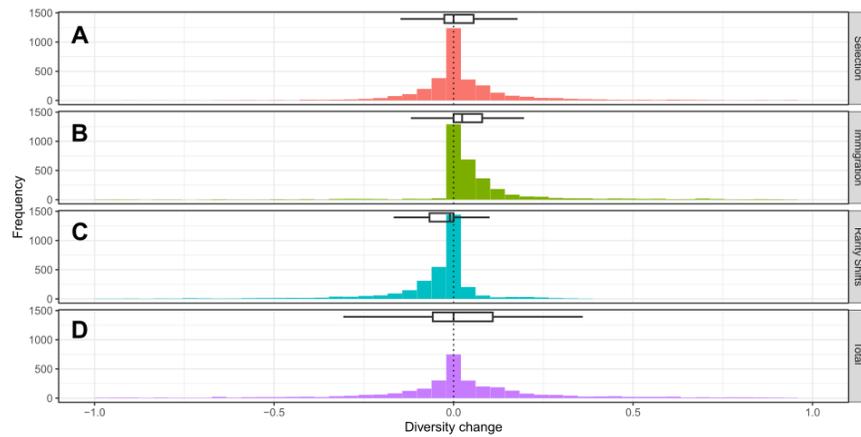
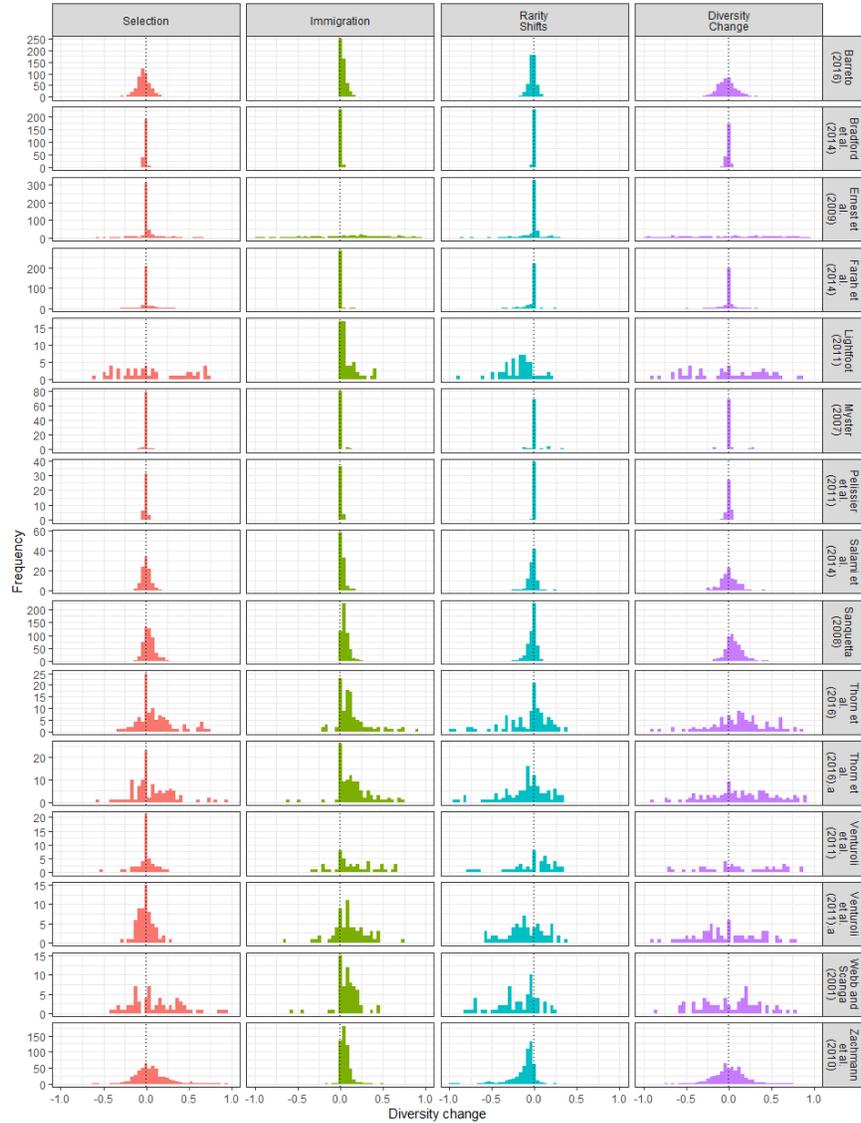


Figure 2: Histograms plot 3341 observation periods for Shannon entropy change including A) selection, B) immigration, C) rarity shifts and D) total diversity change across all plots and from the 15 studies. Each histogram represents the number of observations where a given partition was of a particular magnitude. To improve readability, we set the x-axis from -1 to 1, excluding a small number (3.7%) of values (see supporting information for further details). Boxplots show median values, interquartile range and values exceeding 1.5 times past the interquartile range.



Patterns of diversity varied across the 15 studies (Figure 3). Many studies showed little diversity change, particularly studies of long-term forest plots (Bradford et al. 2014). In these studies, total diversity change is typically zero and the contribution of each mechanism 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) experienced strong rarity shifts. In these studies, all mechanisms could make a substantial contribution to diversity change. Ernest et al. (2009) studies seasonal flowering xeric shrubland communities in the deserts of Arizona each summer and winter. Immigration had an unusually strong influence on diversity. Immigration increased diversity strongly in some plots and decreased diversity strongly in others. The high immigration rate reflected the high turnover in species, with the dominant species frequently being replaced, largely due to the dramatic fluctuations in precipitation (Baldwin et al. 2002). A similar experiment examines flowering plant communities in the desert of Arizona within plots where small mammals have been excluded (Ernest et al. 2009). 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. Figure 3: Partitions of Shannon diversity 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 Equation 4. The dotted line represents zero diversity change. To improve readability, we set the x-axis from -0.5 to 0.5 , excluding (3.7%) of values. See supporting information for more details and Gini-Simpsons diversity comparison.

Generalized Additive Models indicate that there is a non-linear relationship between the strength of rarity shifts related and the strength of other mechanisms. 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 (Figure 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-Simpsons diversity.

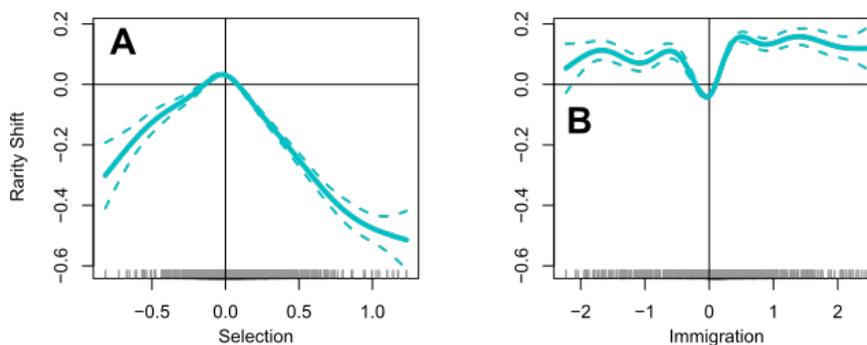


Figure 4: Predictions of the strength of rarity shifts for Shannon entropy derived from Generalized Additive Models. A) When selection is close to zero, rarity shifts are close to zero. Selection values further away from zero lead to negative rarity shifts. Blue lines indicate predictions, dashes indicate 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.

Discussion

Our work highlights how abundance-based diversity indices can obscure 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 (Figure 1). This insight extends the observation that richness based observations of diversity change can obscure changes in communities (Chase et al. 2019, Dornelas et al. 2019); (Urban 2015, Urban et al. 2016). Our results indicate that strong changes in relative abundances can lead to large shifts in species’ rarity. These shifts produce the illusion of negligible diversity change in dynamic communities.

Rarity shifts tended to oppose increases in selection and decreases in immigration (Figure 4). Increases in diversity from selection and decreases in diversity from rarity shifts oppose overall diversity change (Figure 1). This mismatch is commonplace across all studies (Figure 2). We have shown that rarity shifts are commonplace across many datasets (Figure 3), particularly in studies where changes in relative abundances are high studies such as 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) experienced strong rarity shifts because

measurements matched or exceeded the seasonal lifespan of the community, meaning diversity measures reflected the high mortality and rapid emergence of plant species. Rarity shifts were uncommon in long-term forest plots where changes in community composition and diversity are slow (Bradford et al. 2014). Nevertheless, we elect to analyse the data using the observations, as they were collected, even if, in retrospect, the sampling periods used may have been comparatively brief. This choice is likely conservative, as picking longer intervals would likely 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.

The observations in the previous paragraph highlight the benefits of focusing on diversity change in plants. Plants are sessile which lowers the chance that descendants of one species will be confused with immigrants of the same species. Long-term vegetation plots are available in many model systems. As a result, data in our study represents 5 continents - North America, South America, Asia and Australia and Europe. It is of course possible that other sources of change dominate in other taxa. We suspect for example that immigration will be more important in other systems.

Our results are one of several recent applications of diversity partitions. These include analyses of why empirical observations show seemingly slow shifts in diversity over time (Dornelas et al. 2019), how to quantify the effects of biotic homogenization (Tatsumi et al. 2020, Tatsumi et al. 2021, Godsoe et al. 2022), and how to relate biotic interactions such as competition to shifts in diversity (Godsoe et al. 2021). We have added to this literature by showing that rarity shifts, a mechanism derived from partitioning (Godsoe et al. 2021), is an important source of diversity change.

For generations, ecologists have sought to understand the relationship between changes in diversity, ecosystem functioning, 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). To help resolve this problem, we have shown how abundance-based diversity indices can be influenced by shifts in species rarity. We have provided examples from individual plots that highlight how these rarity shifts can obscure selection (Figure 1). We have shown rarity shifts are comparable in magnitude to selection, and immigration across the 15 studies (Figure 2 and Figure 3). Finally, we have shown rarity shifts can oppose selection and immigration (Figure 4). Our results highlight how abundance based diversity measurements can give a disconcertingly slow impression of 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

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

Citation	Number in Biotime	Location	Description	Years between samples	Plot size (m ²)	Plant density (m ⁻²)
Webb and Scanga (2001)	10	Minnesota USA	Windthrow on mixed hardwood-evergreen forest	3	4	6.025
Zachmann et al. (2010)	18	Idaho USA	Old, natural temperate sagebrush scrub	1, 2, 3	1	141.5
Barreto (2016)	302	Sao Paulo Brazil	Semi-deciduous subtropical broadleaf forest	3, 6	400	0.115

Citation	Number in Biotime	Location	Description	Years between samples	Plot size (m ²)	Plant density (m ⁻²)
Salami et al. (2014)	303	Lages Brazil	Subtropical, broadleaf forest.	4	200	0.184
Farah et al. (2014)	322	Sao Paulo Brazil	Semi-deciduous, subtropical, forest structure	5, 11	100	0.122
Venturoli et al. (2011)	324	Brazil	Regenerating semi-deciduous saplings	1	16	0.2875
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, 4, 5	3600	0.1172
Ernest et al. (2009)	336	Arizona USA	Flowering desert shrubs - seasonal	0.5	2500	1.3478
Lightfoot (2011)	340	Arizona USA	Flowering desert shrubs	1	1	264.6
Sanquetta (2008)	346	Sao Paulo Brazil	Subtropical grass or shrubland	3, 6	400	0.2062
Myster (2007)	352	Peru	flooded rainforest	1	25	1.436
Bradford et al. (2014)	356	Queensland Australia	mature rainforest	varies	5000	0.0092
Thorn et al. (2016)	465	Bavaria Germany	Vascular plants after windfall	1	200	0.078
Thorn et al. (2016)	548	Bavaria Germany	Vascular plants after windfall	1	200	0.0705

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