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A comprehensive approach to analyzing community dynamics using rank abundance curves

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Abstract. Univariate and multivariate methods are commonly used to explore the spatial and temporal dynamics of ecological communities, but each has limitations, including oversimplification or abstraction of communities. Rank abundance curves (RACs) potentially integrate these existing methodologies by detailing species-level community changes. Here, we had three goals: first, to simplify analysis of community dynamics by developing a coordinated set of R functions, and second, to demystify the relationships among univariate, multivariate, and RACs measures, and examine how each is influenced by the community parameters as well as data collection methods. We developed new functions for studying temporal changes and spatial differences in RACs in an update to the R package library("codyn"), alongside other new functions to calculate univariate and multivariate measures of community dynamics. We also developed a new approach to studying changes in the shape of RAC curves. The R package update presented here increases the accessibility of univariate and multivariate measures of community change over time and difference over space. Next, we use simulated and real data to assess the RAC and multivariate measures that are output from our new functions, studying (1) if they are influenced by species richness and evenness, temporal turnover, and spatial variability and (2) how the measures are related to each other. Lastly, we explore the use of the measures with an example from a long-term nutrient addition experiment. We find that the RAC and multivariate measures are not sensitive to species richness and evenness and that all the measures detail unique aspects of temporal change or spatial differences. We also find that species reordering is the strongest correlate of a multivariate measure of compositional change and explains most community change observed in long-term nutrient addition experiment. Overall, we show that species reordering is potentially an understudied determinant of community changes over time or differences between treatments. The functions developed here should enhance the use of RACs to further explore the dynamics of ecological communities.

Key words: codyn; community composition; long-term data; multivariate analysis; R package; richness; spatial variability; temporal variability.

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Introduction

The dynamic nature of ecological communities, in which abundances of co-occurring species differ over space and change over time, makes them simultaneously fascinating and difficult to study. Ecological communities worldwide are impacted by global change drivers that chronically alter resource availability (nitrogen deposition, altered precipitation, elevated CO_2, etc.). These chronic resource alterations are expected to have large impacts on ecosystem functioning by altering community structure and composition (Smith et al. 2009, Langley and Hungate 2014, Polley et al. 2014, Koerner et al. 2015). Thus, it is imperative that ecologists have the tools needed for predicting and understanding patterns of community change in response to global environmental drivers. Given significant concerns about the global biodiversity crisis (Sala et al. 2000), species richness is often used as one common measure of change at the local scale (Vellend et al. 2013, Dornelas et al. 2014). Yet, species richness alone can be an insensitive measure of ecological dynamics (Wilsey et al. 2005, Avolio et al. 2015, Hillebrand et al. 2017, Jones et al. 2017) because it does not take into account identity or abundance potentially masking complex dynamics, such as turnover and reordering of dominant species within communities (Collins et al. 2008, Avolio et al. 2015, Hillebrand et al. 2017). Conversely, multivariate measures that take into account species identity, such as a dissimilarity index, are abstract and do not detail what exactly about the community is different (Collins et al. 2008). There is a need for methodological approaches to bridge multivariate measures with community structure and composition.

We suggest that using rank abundance curves (RACs) and their derived measures can yield important information in combination with species richness and dissimilarity to more clearly elucidate the complexities of community change across space and over time, and allow for generalizations across different communities (Avolio et al. 2015). In the mid-20th century, RACs became a common way to study communities (MacArthur 1957, Whittaker 1965), because they serve as a useful visualization tool to understand how communities differ in number and abundances of species. They are relatively easy to create using commonly collected species abundance data (e.g., cover, biomass, point intercept, and abundance; Tokeshi 1993, McGill et al. 2007, Ulrich et al. 2010). RACs have mostly been utilized to compare shapes of the curve (curve fitting; Fattorini 2005, Mac Nally 2007, McGill et al. 2007, Ulrich et al. 2010, McGill 2011, White et al. 2012). Yet, RACs yield detail on both community composition and structure when attention is paid to species identity (i.e., the rank and abundance of each species are tracked through time). Comparisons of how RACs differ over space and change over time can provide additional insight into community dynamics that would not be evident by changes in species richness or dissimilarity alone (Avolio et al. 2015). However, approaches to studying RACs—both long-term temporal changes and spatial differences—are lacking beyond investigating the shape of the curve.

We have three objectives in this paper. First, we review common ways of measuring community dynamics and build upon existing approaches for studying RACs by introducing new functions in an update to the library("codyn") R package V.2.0.0 (Hallett et al. 2018) in R (Table 1). We think that this update will strengthen and streamline comparison of communities by incorporating several functions to measure univariate (e.g., species richness), multivariate (e.g., distance between centroids), and RACs (e.g., reordering) changes over time or differences over space. Second, we use two datasets, one simulated and one observational, to examine how a variety of community measures are related to one another when studying changes in community composition and structure over time. This investigation of commonly used multivariate and univariate and underused RAC measures highlights the utility of a comprehensive approach for comparing communities. Lastly, we use a long-term experimental dataset from native tallgrass prairie to illustrate how communities differ in space and change over time in response to altered resource availability.

Table 1. Community change functions in the library("codyn") V2.0.3 release introduced in this paper.

Comparison	CODYN function	Output
None—done for each replicate at a single point in space and time	community_structure (df, time.var, abundance.var, replicate.var, metric)	Calculates species richness and evenness (using specified metric) for each replicate
	community_diversity (df, time.var, abundance.var, replicate.var, metric)	Calculates species diversity (using specified metric) for each replicate
Change—tracks changes of a replicate through time	RAC_change (df, time.var, species.var, abundance.var, replicate.var, reference.time)	Calculates changes in species richness, evenness, species' ranks, gains, and losses for each replicate
	abundance_change (df, time.var, species.var, abundance.var, replicate.var, reference.time)	For each species in a replicate, calculates changes in abundance
	curve_change (df, time.var, species.var, abundance.var, replicate.var, reference.time)	Calculates changes in the shape of the RAC curve for each replicate
	multivariate_change (df, time.var, species.var, abundance.var, treatment.var, reference.time)	Calculates changes in community composition and dispersion of all replicates
Difference—compares differences between replicates at a single point in time	RAC_difference (df, time.var, species.var, abundance.var, replicate.var, treatment.var, pool, block.var, reference.treatment)	Calculates differences in species richness, evenness, species' ranks, shared species between paired samples†
	abundance_difference (df, time.var, species.var, abundance.var, replicate.var, treatment.var, pool, block.var, reference.treatment)	Calculates differences in abundance for each species in paired samples†
	curve_difference (df, time.var, species.var, abundance.var, replicate.var, treatment.var, pool, block.var, reference.treatment)	Calculates differences in the shape of the RAC between paired samples†
	multivariate_difference (df, time.var, species.var, abundance.var, treatment.var, reference.treatment)	Calculates differences in community composition and dispersion of all replicates between treatments

Notes: RAC is rank abundance curve. The default for measures of change calculates changes between paired consecutive years; however, a reference year can be specified (e.g., the first year of data collection can be compared to all other years). The default for the measures of difference calculates differences between all pairwise treatments; however, a reference treatment can be specified (e.g., the controls can be compared to treatments only).

†For the difference functions (RAC_difference(), abundance_difference(), and curve_difference()), it is necessary to specify how replicates should be compared at a given point in time. There are three options: (1) For studies with an experimental block design, within each block pairwise treatment comparisons are made (both block.var and treatment.var need to be specified). (2) All replicates within a treatment can be pooled (the average of each species across all replicates is determined), and then, all pairwise treatment comparisons are made (both treatment.var and pool = TRUE must be specified). This option results in one comparison between each treatment; thus, there is no replication. (3) All pairwise comparisons are made between all replicates (if treatment.var is specified the treatment that each replicate belongs to will also be output). This option results in more comparisons than replicate plots but results in non-independence of replicates.

In this example, we demonstrate how to integrate multivariate measures with RACs to study community dynamics. Our overarching goal is to provide an analytical roadmap that includes RAC measures for enhancing our understanding of the spatial variability and temporal change inherent in ecological communities.

Measures for Studying Communities

Community datasets

A community dataset is often visualized as a matrix with two fundamental components of the species assemblage, species identities (i.e., species names), and their associated abundances, as separate columns (Fig. 1A). Community data are typically collected from replicates arrayed in space and often are repeatedly collected at the same location over time. Here, replicates refer to any single location, plots, sample, etc., in both observational and experimental datasets. Consequently, replicate and time are additional columns in the community data matrix (Fig. 1A). Observational time series will have no additional grouping of the replicates. However, experimental time series will group the replicates into treatments, requiring a fifth column in the data matrix for treatment designation. Thus, we have a data matrix with four columns (time, species, abundance, and replicate) and a fifth optional column that represents treatments (Fig. 1A).

Community datasets collected in space and over time offer two primary pathways for measuring and comparing differences in species composition. First, a single community (which can be a single sample (e.g., a 1-m^2 plot) can be compared to itself over time (Fig. 1B: black arrows), which we will hereafter call change. Conversely, communities of different treatments can be compared to one another

A

Species	Abundance	Time	Replicate	Treatment
A	2	1	1	C
A	8	1	2	T
A	10	2	1	C
A	12	2	2	T
B	30	1	1	C
B	22	1	2	T
B	13	2	1	C
B	11	2	2	T
C	67	1	1	C
C	75	1	2	T
C	63	2	1	C
C	71	2	2	T

B

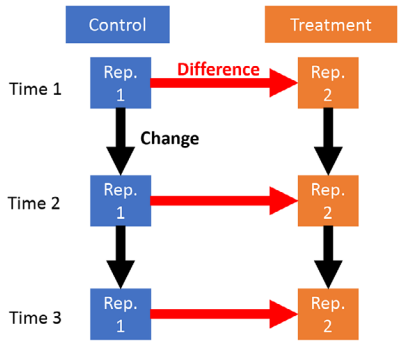

Fig. 1. (A) A hypothetical community dataset that records the time and replicate of the species and their abundances. (B) Long-term experimental community data can be analyzed two ways: (1) How a community (or replicate within a community) changes over time (black arrows) or (2) how a community (or replicate within a community) differs (red arrows) between samples, such as control (C) and treatment (T) replicates, at a given point in time. Both are informative and give rise to unique insights.

at a single time point (Fig. 1B: red arrows), which we consider to be a measure of difference. Both approaches are informative and yield complimentary insights into the spatial vs. temporal dynamics of ecological communities, as discussed below.

Measures of temporal change include change within a replicate between consecutive time points (e.g., Collins et al. 2000). Temporal change measures can also include comparisons of future time points to the original sample (Avolio et al. 2014, Dornelas et al. 2014). Measures of spatial differences include comparisons of how two replicates sampled at the same time differ from one another. In some experimental designs, it is predetermined which replicates to compare across treatments (block design) but in other cases this is less clear. For datasets that have a single or multiple treatments, there are three ways to compare differences: (1) Control and treatment plots can be paired in a block design, (2) all pairwise control–treatment comparisons can be made, with correction for multiple comparisons (Dunnett 1955, 1964), or (3) the abundance of all species in a treatment across replicates can be averaged, allowing for a single comparison between treatment and control plots. The first approach is ideal, the second results in non-independence of difference measures, and the third results in a single comparison prohibiting frequentist statistical tests.

Measures for comparing rank abundance curves

Five aspects of change in RACs can be quantified and compared (Fig. 2): (1) species richness, the length of the RAC; (2) evenness, measured as the slope of the RAC, where steeper slopes reflect greater dominance, or flatter slopes indicate greater evenness (Whittaker 1965); (3) species rank change (or reordering), measures how much species ranks decrease or increase over time (e.g., mean rank shift in Collins et al. 2008); and (4) species loss and/or (5) species gain (e.g., together loss and gains are turnover as in Cleland et al. 2013), both of which are underlying changes in species richness.

RAC_*() functions

The insight from RAC analysis is potentially very powerful, but currently there are not standard analytical approaches. Measures of RACs can be applied to both observational and experimental data. We developed two functions, RAC_change() and RAC_difference(), to study RACs over time or space (Table 1). See Appendix S1 for a RAC change example and Appendix S2 for a RAC difference example. These functions extend the existing rank_change() and turnover() functions in codyn (Hallett et al. 2016).

Species richness comparisons.—Species richness (alpha diversity), the number of species at a given point in space and time, is a simple and widely used measure to describe biodiversity patterns. Our community_structure function calculates species richness (Table 1) for a sample at a single point in space and time. Species richness

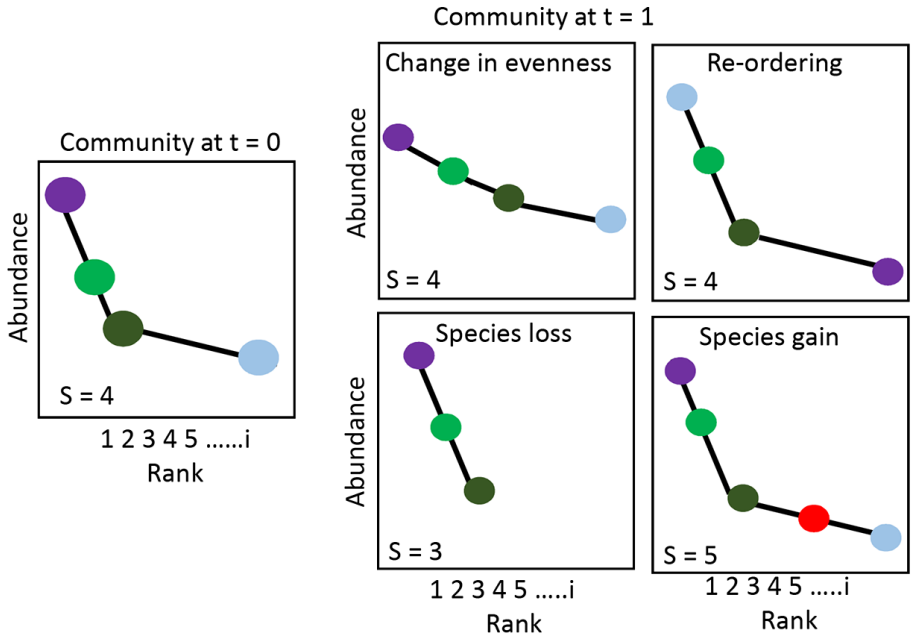

Fig. 2. Demonstration of the five ways a community can change over time as measured by rank abundance curves. Please note that although species richness (denoted as S in the bottom left corner of each panel) is not depicted, species richness also changes with species losses and species gains and that concurrent gains and losses can result in no richness change.

change, ΔS, in the RAC_change() function is calculated as

$$\Delta S = (S_{t+1} - S_t)/S_{\text{tot}},$$

where S is the richness of a replicate, t is time, and S_{tot} is the total number of unique species in both time periods. Species richness difference, S.D., in the RAC_difference() function is calculated as

$$\text{S.D.} = (S_x - S_y)/S_{\text{tot}},$$

where x and y are the two replicates being compared, and S_{tot} is the total number of unique species in both replicates. Since ΔS and S.D. are proportions, they are bound between -1 and 1, where larger values indicate greater changes in species richness. A value of 1 or -1 would occur if there were no species in one the replicates being compared.

Evenness comparisons.—Evenness is a measure of the distribution of species abundances in a community. A perfectly even community is one in which all species have the same abundances, while an uneven community is one where a few species have high abundance and most species have low abundances. Ideally, evenness indices will be independent of species richness. A commonly used evenness measure, J (Shannon's or Pielou's evenness), should not be used as it is highly dependent on species richness (Smith and Wilson 1996). Using our community_structure function (Table 1), the user can specify one of three evenness measures: (1) inverse of Simpson's D, a commonly used evenness measure (Smith and Wilson 1996); (2) E_{Q}, a measure of the slope of a RAC (Smith and Wilson 1996); and (3) E_{var}, a measure of the variance of abundance values (Smith and Wilson 1996). See Appendix S3 for equations and more details. Measures of evenness are bound between 0 (very uneven community) and 1 (perfectly even community). A key difference between these measures is that Simpson's evenness results in an evenness of 1 when there is a single species in a community—a flaw in the measure, as the concept of evenness does not apply to a community with only a single species. Thus, we suggest using E_{Q} or E_{var} as a preferred measure of evenness because they are both fairly intuitive and in our functions result in a NA when there is only one species in a community. Here,

we used E_{var} for all the example analyses and in our RAC_change() and RAC_difference() functions because it results in a more normal distribution of values than E_Q (See Smith and Wilson 1996 for a detailed comparison of evenness measures). Evenness change, ΔE, is in our RAC_change() function using E_{var} and is calculated as

$$\Delta E = (E_{t+1} - E_t),$$

where E is the evenness of a replicate, and t is time. Evenness difference, E.D., in the RAC_difference() function is calculated as

$$\text{E.D.} = (E_x - E_y),$$

where x and y are the two replicates being compared. ΔE and E.D. are bound between -1 and 1, where larger negative values indicate greater decreases in evenness.

Rank comparisons.—Rank change (e.g., species reordering) is a measure of how much species abundances change over time relative to each other. In the RAC_change() function, rank change is similar to the rank_shift() function in the codyn package (Hallett et al. 2018) with two improvements. First, our mean rank change is divided by the size of the species pool making the measure independent of species richness. Second, our measures allow for species that are not in two consecutive time points to be included (see Appendix S1 for details). In the RAC_change() function, rank change, ΔR, is calculated as

$$\mu_R = \frac{\sum_i^N (|R_{i,t+1} - R_{i,t}|)}{S_{tot}} \quad (1)$$

$$\Delta R = \frac{\mu_R}{S_{tot}}, \quad (2)$$

where $R_{i,t}$ is the rank of species i at time t, $R_{i,t+1}$ is the rank of species i at time $t + 1$, and S_{tot} is the total number of unique species in both time periods. For ΔR, the average rank change, μ_R, is divided by S_{tot}. In the RAC_difference() function, rank difference, R.D., compares the rank of species between two replicates and is calculated as

$$\mu_{R.D.} = \frac{\sum_i^N (|R_{i,x} - R_{i,y}|)}{S_{tot}} \quad (3)$$

$$\text{R.D.} = \frac{\mu_{R.D.}}{S_{tot}}, \quad (4)$$

where $R_{i,x}$ is the rank of species R_i in replicate x, $R_{i,y}$ is the rank of species R_i in replicate y, and S_{tot} is the total number of unique species in both replicates. Both ΔR and R.D. are bound between 0 and 0.5, where 0.5 occurs when there are the maximum rank changes allowed in the community.

Species turnover: gains.—A gain occurs when a species that was absent at time t appears in time period $t + 1$. In RAC_change() a gain is calculated as

$$G = \frac{g}{S_{tot}},$$

where g is the number of species gained and S_{tot} is the total number of unique species in both time periods. This returns the same output as the turnover function in library("codyn") with metric "appearance" (Hallett et al. 2018). It is bound between 0 and 1 and is the proportion of species that are gained.

Species turnover: losses.—A loss occurs when a species that was present at time t disappears in time period $t + 1$. In RAC_change() a loss is calculated as

$$L = \frac{l}{S_{tot}},$$

where l is the number of species lost and S_{tot} is the total number of unique species in both time periods. It is bound between 0 and 1 and is the proportion of species that are lost. This returns the same output as the turnover function in library("codyn") with metric "disappearance" (Hallett et al. 2018).

Species difference.—Sometimes it is not possible to infer gains or losses between samples. For example, if a species was never in a treatment plot, but always in the control plot, it cannot have been lost in the treatment. Thus, we calculate a species difference measure in the RAC_difference () function instead of gains/losses. The concept of species differences is most simply understood as Jaccard's index, which is sometimes used as a measure of beta diversity and is calculated as the number of species that are exclusive to either of two communities divided by the total number of species across both communities. However, as has

been documented with dissimilarity-based measures of beta diversity, richness differences influence the outcome of species difference (Baselga 2010, Carvalho et al. 2012). Carvalho et al. (2012) mathematically separated richness differences from species substitution, which summed together equals the Jaccard index. Here, we use the species substitution equation (termed β_{-3} in Carvalho et al. 2012) as our measure of species differences. Species difference is calculated as

$$\text{Sp.D.} = 2 \times \frac{\min(b, c)}{a + b + c},$$

where a is the total number of shared species, b is the number of species that are unique to the first community, and c is the number of species that are unique to the second community. When Sp.D. and the absolute value of richness differences (S.D.) are added, the result is Jaccard's index. Thus, our measure of species differences reflects only compositional differences and not richness differences between two communities.

Curve_*() functions

We developed a new way to compare the shape of two RACs. There is an impressive body of literature on understanding the shape of RACs (or species/rank abundance distributions; SADs or RADs). As noted by Tokeshi (1993), there is a long history of fitting various distributions, such as a log normal or Poisson distribution, to individual RACs (McGill 2011), and there is a robust literature on the best approach (Fattorini 2005, McGill et al. 2007, Ulrich et al. 2010, White et al. 2012). We take a slightly different approach here and ask what is the difference in the curve shape between two communities? A RAC summarizes the abundance of each species in a community and thus simultaneously incorporates species richness and evenness. Our approach was modeled after D^* developed by Collins et al. (2009) to study differences between rank occupancy–abundance profiles. Briefly, for each RAC we calculate (1) the relative rank of a species, where the relative rank of 1 is assigned to the least abundant species and (2) the cumulative community abundance when adding each species to the sample from least to most abundant. We then plot relative rank vs. cumulative abundance using a stepwise function (denoted below as $f_{k,t}(r)$, for relative rank r of the community at location k and time t) and sum the area between the two curves (see Appendix S4 for a worked example). The summed area between the two curves is the curve change or curve difference depending on if the comparisons are temporal or spatial, respectively. Curve changes or differences are larger when using raw instead of relativized abundance data. Curves can be compared for a single replicate over time, and in our function curve_change(), it is calculated as

$$\Delta\text{Curve} = \sum_{i=1}^{N} | f_{k,t}(r_i) - f_{k,t+1}(r_i)|(r_i - r_{i-1}),$$

where N is the number of unique relative ranks among both RACs and the set r is built by taking the union of relative ranks calculated for each RAC, from relative rank 0 to 1, and sorting the result from low to high. RAC curves can also be compared between replicates at a given point in time using our curve_difference() function. The difference between the community at location k from the one at k' is likewise calculated as

$$\text{C.D.} = \sum_{i=1}^{N} | f_{k,t}(r_i) - f_{k',t}(r_i)|(r_i - r_{i-1}).$$

Our approach allows for statistical comparison among treatments. For example, in a multi-year experiment, one could compare the change in curve shape of controls vs. treated plots using a simple t-test.

Measures for performing multivariate comparisons

Multivariate methods generally use species abundance or presence/absence data to assess changes in community composition over time. Here, we only consider using abundance data as it is necessary for all the other community functions that we have developed. Multivariate methods typically involve principal coordinate analysis (PCoA) of community abundance data and have been extensively reviewed (see McCune and Grace 2002, Anderson 2006, Anderson et al. 2008, Legendre and Legendre 2012). Principal coordinate analysis begins by calculating a matrix of pairwise dissimilarities (see Anderson et al. 2011 for a comparison of dissimilarity indices) between communities from distinct replicates, treatments, times, or any combination of these. This matrix can be used

to mathematically determine a point representing each community in a lower-dimensional space, that is, a scatter plot with fewer axes than species. When truncated to sufficiently few axes for actual plotting, the distance between points approximates the dissimilarity between communities (McCune and Grace 2002). When not truncated—excepting certain cases detailed below—the distance between points exactly equals their dissimilarity. Here is the main utility of PCoA: It translates ecologically meaningful indicators, such as the Bray-Curtis dissimilarity, to a space where centroids of clusters and distances associated with those centroids are also meaningful. Clusters are typically a group of replicates from the same treatment or time period, so the two multivariate patterns typically quantified are the distances between centroids and the distances of replicates from their centroid (a.k.a. dispersion, see Fig. 3). These two values correspond, respectively, to comparisons between-group means and within-group variances of univariate analyses (Avolio et al. 2015). Both are measures of beta diversity (dissimilarity of communities), where distance between centroids is turnover beta diversity, and dispersion is variation beta diversity (Vellend 2001, Anderson et al. 2011, Avolio et al. 2015). We provide functions for these multivariate measures to compare changes in a community over time (multivariate_change()) or to compare differences between treatments at a given point in time (multivarite_difference()). Our multivariate_change() function is similar in concept to a recent method development by Legendre (2019) that quantifies the dissimilarity between the composition of a replicate over time

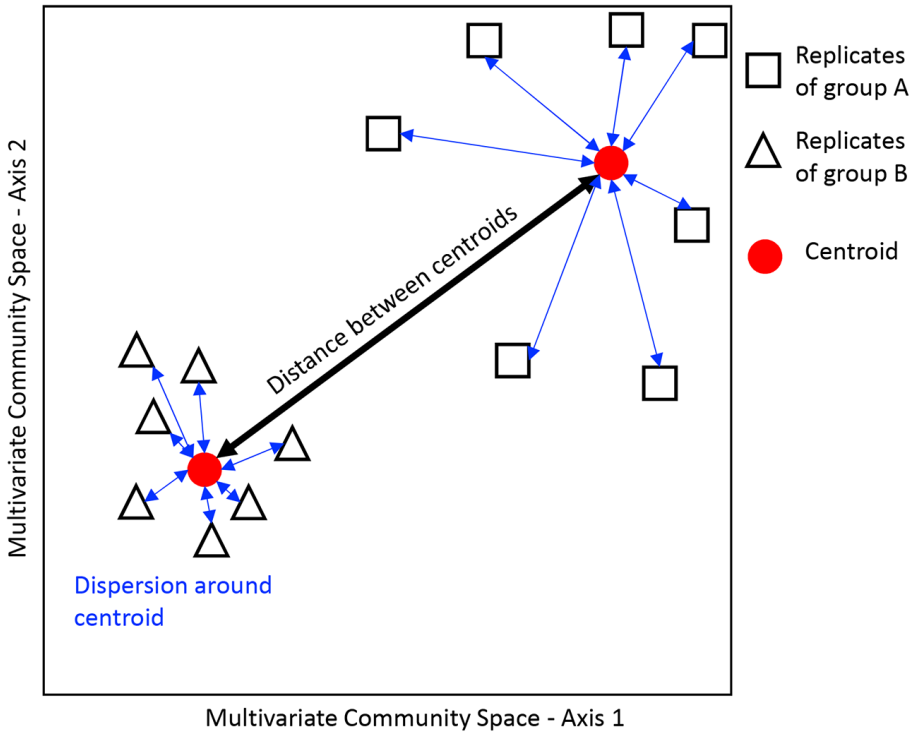

Fig. 3. Example of multivariate community measures. In this figure, there are several replicates in groups A and B, which can represent two time points of the same sample location or two treatments at a single point in time. The length of the black arrow between the two centroids approximates the dissimilarity between an average community within each group, a measure of composition dissimilarity. The length of the smaller blue arrows between replicates and their group centroids approximates the dissimilarity of replicates from their within-group average, a measure of community dispersion. If all of the axes in multivariate community space could be visualized, the arrow lengths would be exact measures rather than approximations.

rather than distance between centroids of all replicates over time.

Multivariate_*() functions

Composition: distance between centroids.—Once the PCoA is computed, pairwise Euclidean distance can be used to quantify shifts in the centroids through time (compositional change) or differences between two treatments (compositional difference), except in cases where the calculated dissimilarity matrix dictates a complex space as we detail below. Our new multivariate_change () and multivariate_difference() functions (Table 1) use the Bray-Curtis dissimilarity, which does in some cases produce dissimilarity matrices with negative eigenvalues, resulting in complex space in a PCoA. As in principal component analysis, eigenvalues from PCoA are weights on their corresponding axes, and negative weights have no clear interpretation, as has been long recognized (Legendre and Anderson 1999, McArdle and Anderson 2001, Anderson et al. 2008, Legendre and Legendre 2012). Whether negative eigenvalues are produced or not, the multivariate_*() function takes the group mean as the centroid and then calculates the sum of squared differences along every principal coordinate axis for specified centroid pairs. When the space is not complex (e.g., no negative eigenvalues), the functions then return the square root of this summation, which is just the Euclidean distance. When the space is complex, the square root is returned if the sum is non-negative (Anderson 2006) and NA is returned if the sum of squares is negative, because as stated above this has no clear interpretation. Anderson (2006) does not address this last situation, except to say that a negative sum of squares is possible but unlikely. The lack of consensus here, demonstrated by contrasting behavior of the vegan package's betadisper()(Oksanen et al. 2018; V2.4-6), which returns a non-negative value as a distance, and Primer7's PERMDISP procedure (V7.0.13), which returns zero, leads us to instead report a missing value.

Dispersion: dispersion around centroids.—The average distance from the group centroid to each replicate in the group is a measure of dispersion, or within-group heterogeneity, and related to the total variance. In the multivariate_change() and multivariate_difference() functions, the method for dispersion comparisons proceeds as above for centroid comparisons, but calculates the sum of squared coordinate differences between each replicate and its centroid. If all sums are positive, then we return the mean of their square root, but if one sum is negative, we return NA for the reason described above. These averages quantify dispersion, and the absolute difference is reported as dispersion change or dispersion difference, depending on whether the pairing corresponds to change of a community over time or to a comparison between treatments.

The Relationship Among RAC and Multivariate Measures, and Their Sensitivity to Species Richness and Evenness

Two fundamental aspects of a community, the species present and their abundances, are measured using species richness and evenness. Other measures of describing communities in space or over time ideally would be independent of species richness and evenness and capture additional attributes of the community. Recently, Ulrich et al. (2018) demonstrated that richness is correlated with many community measures. It is important that each measure used to quantify an aspect of a community is uniquely informative and not redundant with other ways of measuring communities. Additionally, the community measure should not be influenced by data collection methods. We used two datasets to explore (1) how RAC and multivariate community change and difference measures are affected by species richness and evenness, and (2) how the community change measures are related to one another. All code used is available on github (mavolio/RACs_paper).

How are RAC and multivariate measures affected by species richness and evenness?

Methods.—We drew random samples from correlated multinomial distributions to create a simulated dataset. We specified three levels of species richness (5, 20, and 50 species) for each of three levels of evenness (low, mid, and high). Evenness differences were created with a

parameter that controls the difference in sampling probabilities of each species. Thus, we created nine simulated communities covering a wide range of species richness and evenness combinations (see Appendix S5 for methods). For each of these nine richness-evenness combinations, we also simulated two well-studied aspects of community variability (Collins et al. 2018*a*) in all possible combinations: (1) spatial variability, a measure of community heterogeneity or beta diversity; and (2) temporal variability, a measure of compositional change over time or turnover. We simulated these aspects of variability using a parameter that controls temporal autocorrelation and one that controls correlation between replicates at each time point (see Appendix S5: Table S1 and Fig. S1). For each of 36 unique simulation scenarios (three richness levels, by three evenness levels, by four temporal and spatial variability settings), we generated 10 simulated datasets, each containing 10 replicate communities (e.g., plots) sampled at 10-time steps. We averaged over the 10 simulated datasets to create one summary for each of the 36 scenarios, with 10 replicate communities that were sampled 10 times. To study measures of change, we calculated Pearson's product–moment correlation between the simulated species richness and evenness of the community at time 1 with the average change across all replicates in the community from time 1 to time 2 (n = 324). To study measures of difference, we randomly split the replicates into two treatments and then used the pool = T option in RAC_ and curve_difference() and correlated differences between the treatments with the simulated species richness and evenness at that time point. We did not assess correlations with species richness or evenness change or difference as this is what we simulated to be held constant and are not informative in these simulations.

Results.—Species richness and evenness of a community rarely affected the RAC and multivariate measures of community change and difference (Table 2; Appendix S6). For the change measures, only curve change was negatively correlated with species richness and evenness. For the difference measures, dispersion difference was negatively correlated with species richness, and curve difference was negatively correlated with species richness. The effect of richness and evenness of a community on the degree of curve change are not surprising, as curve change only accounts for the shape of the RAC, which is affected by the length (number of species) and steepness (evenness) of the RAC. What drives the influence of species richness and evenness on dispersion difference is less clear. We also found the measures clearly differentiated between the community types (Appendix S6: Table S1), demonstrating that these measures are additional descriptors of spatial and temporal community dynamics; when there are large temporal changes, the measures of change are

Table 2. The relationship between species richness and evenness of a community with RAC and multivariate measures of community change, using the simulated dataset.

Community measure	Correlation across community types
Measures of change	
Effect of species richness	
Rank change	−0.039
Gains/Losses	0.007
Compositional change	0.025
Dispersion change	−0.013
Curve change	**−0.442***
Effect of evenness	
Rank change	0.114
Gains/Losses	0.024
Compositional change	−0.115
Dispersion change	−0.017
Curve change	**−0.270***
Measures of difference	
Effect of species richness	
Rank difference	−0.030
Species differences	−0.050
Compositional difference	0.038
Dispersion difference	**−0.386***
Curve difference	**−0.779***
Effect of evenness	
Rank difference	0.060
Species differences	0.034
Compositional difference	−0.047
Dispersion difference	**−0.363***
Curve difference	−0.040

Notes: For the measures of difference, we pooled the replicates into their respective treatments (replicates were split between two treatments). Shown are correlation coefficients (r), bold, and N = 324 for all correlations. See Appendix S6 for figures of these correlations.

* $P < 0.001$.

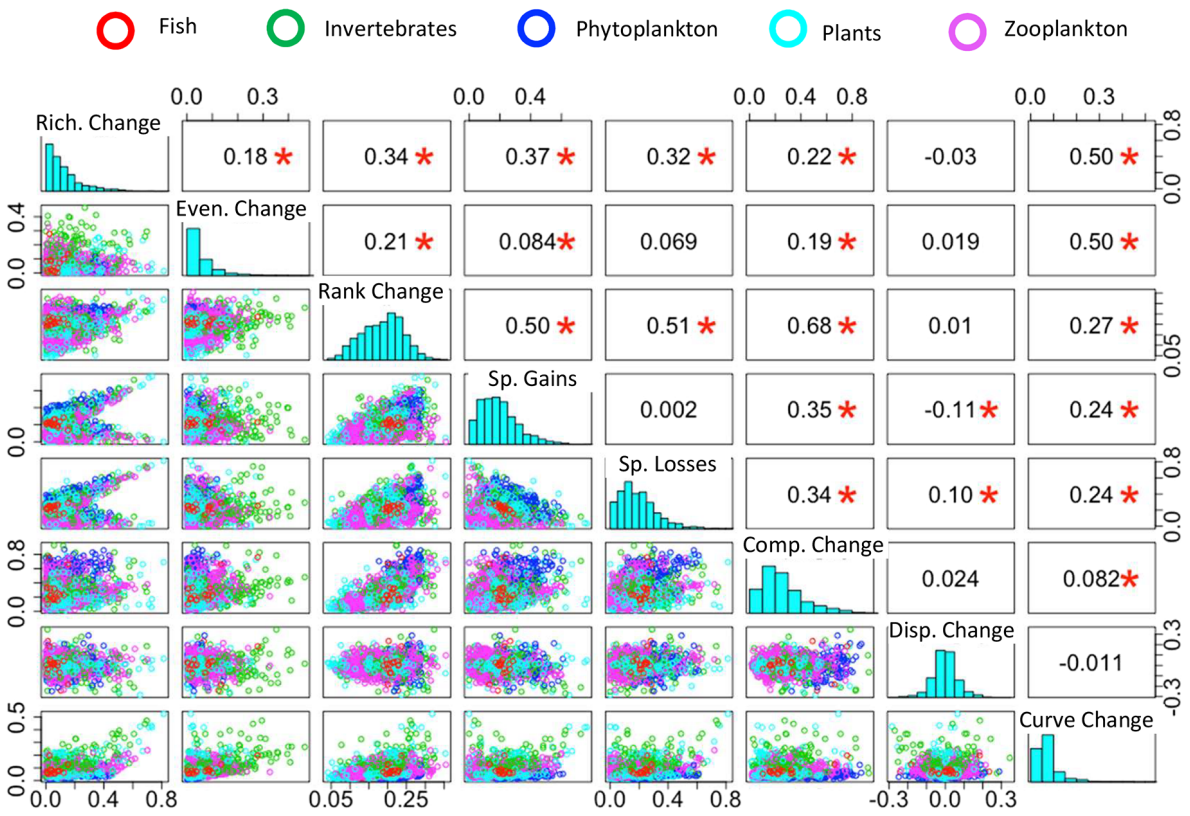

Fig. 4. Correlations among measures of community change with the codyn dataset (https://doi.org/10.6073/pasta/ef4dbad515813be74404a6a87af98f00). Shown are the absolute values from species richness and evenness change. Top triangle is the correlation coefficient (r), and asterisks denote a significant correlation at $P < 0.001$. $N = 1863$ for all correlations. Bottom triangle is the correlation plot with the points colored by taxa. Diagonal are the histograms of the data. $N = 1844$ for all correlations and histograms.

informative whereas measures of difference are informative with large spatial differences.

How are the RAC and multivariate change measures related to one another and affected by data collection methods?

Methods.—For real-world ecological data, we used the codyn dataset that contains spatial and temporal abundance data for 66 communities ranging from primary producers to secondary consumers (Collins et al. 2018*b*). First, we examined the distribution of all change measures and correlations between them across all communities and time points ($n = 1844$). We used the absolute value of species richness and evenness change because we were not interested in the direction of change overtime, just the capacity for change. Next, to examine how the measures related to data collection methods, we calculated the average of each change measure for each community and correlated that value with the spatial extent of the experiment, the number of replicates, and the size of the replicate ($n = 66$). The codyn dataset includes only observational studies, so no measures of difference could be calculated and assessed.

Results.—Overall, there is considerable variability in how communities are changing in these observational datasets (Fig. 4, diagonal). Species richness, evenness, and curve changes are right skewed, indicating that most communities observe little change in these measures while rank and dispersion changes are normally distributed, demonstrating that there is great variability among communities in how these

measures change. Composition change, gains, and losses are all intermediate, with a lesser degree of a right skew. Many of the measures were correlated with one another; however, no measure was redundant with another measure with 85% of the correlation coefficients being <0.5 (Fig. 4, upper triangle). Comparing the measures of RAC changes with the other multivariate measures, we found rank change was most correlated with compositional change followed by species gains and losses. This is not a mathematical artifact, because in the simulated dataset, compositional change is similarly correlated with rank changes (r = 0.73) as it is with species gains and losses (r = 0.69). This finding may suggest that reordering, rather than species gains and losses, is a dominant process in natural communities. Curve change was correlated most strongly with changes in evenness and species richness, which is intuitive as curve change integrates the space of the RAC—a graphical representation of the evenness and richness of a community. For the experimental parameters, only composition change was positively correlated with spatial extent, where larger compositional changes can be detected in experiments that span a greater area (Table 3).

Worked Example in an Experimental Context

Next, we apply RAC and multivariate change and difference measures to a long-term nitrogen and phosphorus addition experiment in tallgrass prairie at the Konza Prairie Biological Station near Manhattan, Kansas, USA (see Avolio et al. 2014, Koerner et al. 2016 for details). In 2002, pre-treatment data were collected, and community composition data have been collected annually thereafter. Here, we investigated community change from the pre-treatment year, to the 9th year of the experiment (2011). To show the versatility of the new R functions for multiple comparisons, we focus on three of the eight treatments in the experiment: control plots (C), plots

Table 3. Influence of experimental parameters on measures of change, using the codyn dataset.

Measures of change	Number of samples	Spatial extent	Sample size
Species richness change	0.180	−0.003	−0.194
Evenness change	−0.195	−0.165	0.249
Rank change	0.018	0.366	−0.196
Species gains	0.075	0.371	−0.253
Species losses	0.083	0.342	−0.239
Compositional change	−0.075	0.541*	−0.044
Dispersion change	−0.079	0.050	−0.028
Curve change	0.170	−0.212	0.035

Notes: Shown are the correlation coefficients (r) between the community measures and experimental parameter. N = 66 for all correlations.
* $P < 0.001$.

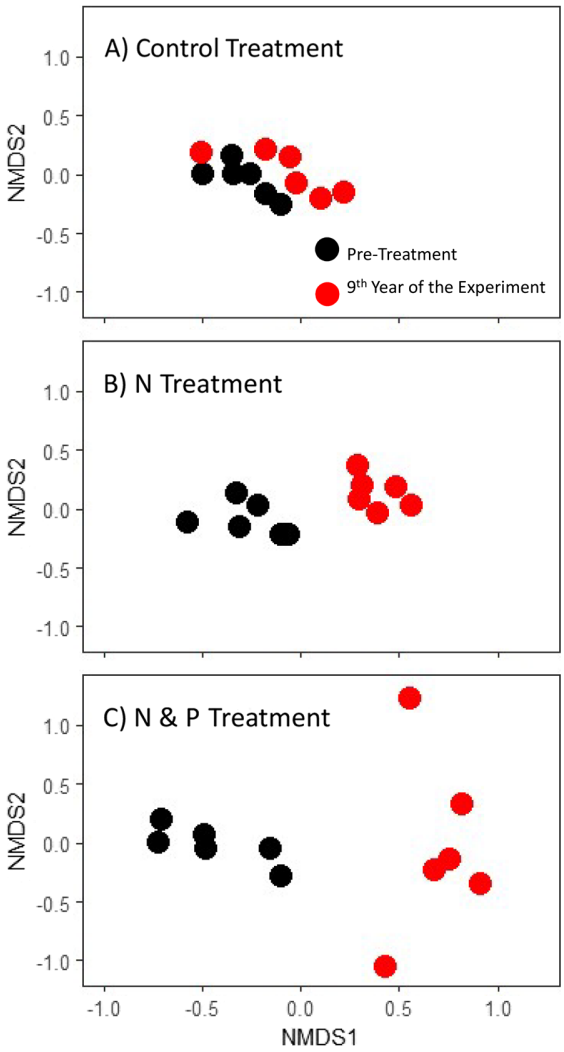

Fig. 5. In a long-term nutrient addition experiment (see Worked Example in an Experimental Context for details), compared with the controls (A) nine years of nitrogen (B) or nitrogen and phosphorus (C) additions resulted in a change in the composition and dispersion of six replicate tallgrass prairie communities.

receiving 10 g/m^2 of nitrogen alone (N), and plots receiving 10 g/m^2 of nitrogen plus 10 g/m^2 of phosphorus each year (N+P).

Over 9 yr, the composition of the community changed in response to N and N+P additions, but there was greater dispersion among N+P-treated replicates compared with control replicates (Fig. 5; Avolio et al. 2014, Koerner et al. 2016) in a non-metric multidimensional scaling (NMDS) plot. We contend that important insight is gained by studying RAC change. To do this, we made RACs for each replicate comparing the pre-treatment and 9th years (Fig. 6). There are few differences in the control communities between the pre-treatment and 9th year (Fig. 6A); however, there were changes in dominant species in the N and N+P replicates (Fig. 6B, C). Thus, the change in composition is driven by new species becoming dominant in the N and N+P plots, and the change in the dispersion is caused by differences in the abundances and identities of those new dominant species in each

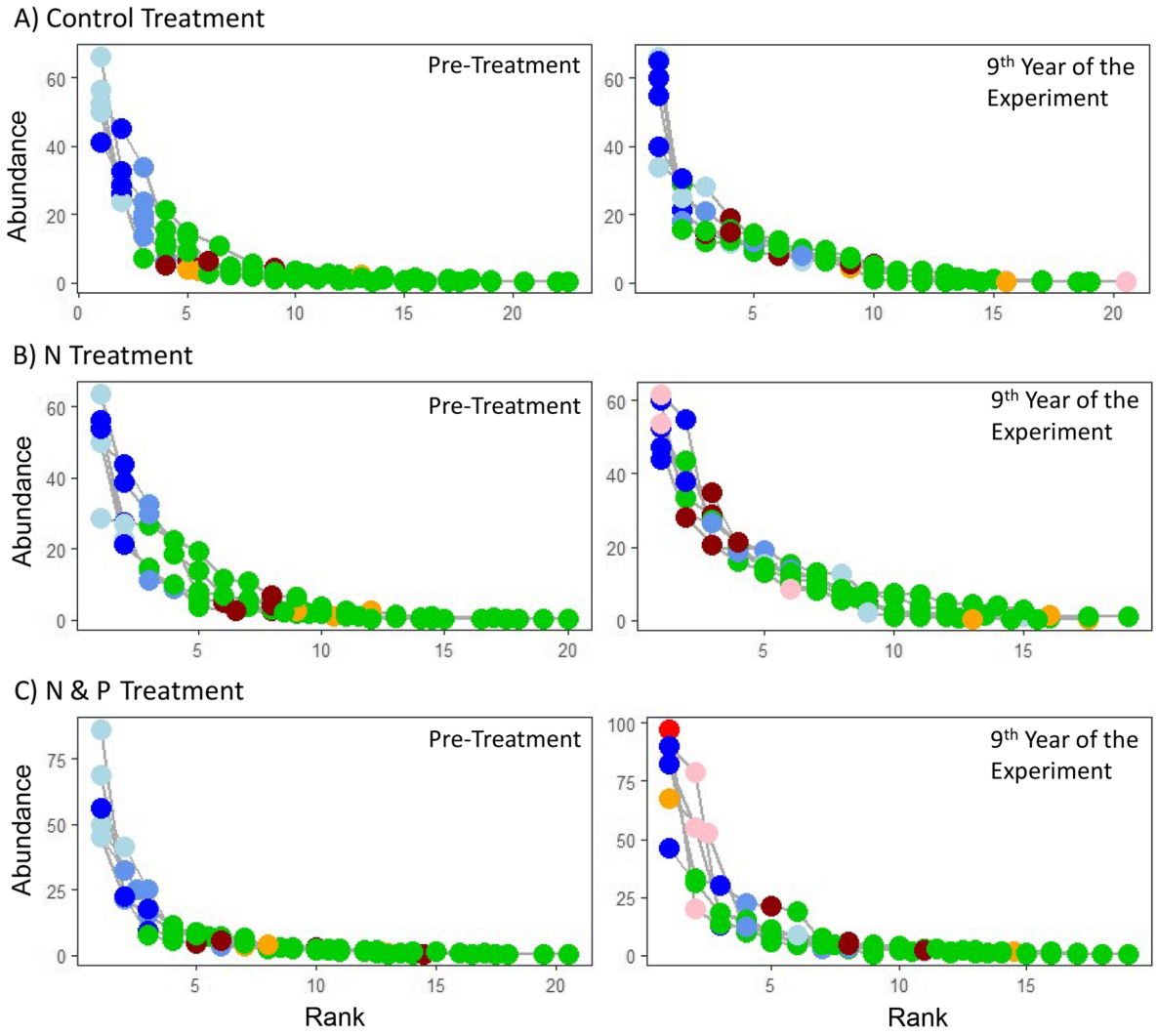

Fig. 6. Rank abundance curves for each replicate in the pre-treatment year and after nine years of nutrient additions demonstrate how the community changed for the controls (A), nitrogen (B), and nitrogen and phosphorus (C) addition treatments. The top three species in the control plots are shades of blue, whereas the top three species in the nitrogen or nitrogen and phosphorus plots in year nine are shades of red, all other species are green. Comparing the years, the identity of the dominant species shifted with nutrient additions.

replicate. We also investigated curve shape differences (Fig. 7), and there are no consistent differences in the shapes of the curve.

We used the RAC_change() and RAC_difference() function to demonstrate how one might use RAC measures to further explore community changes beyond ordination (Fig. 5). First, we investigated changes over time by comparing RACs for each replicate between the pre-treatment year and the 9th year of the experiment. For RAC changes, we find greater reordering in the treated plots compared with the control plots (1-way ANOVA, F-value = 25.44, $P < 0.001$; Fig. 8). For all other measures, there was no statistically significant difference between the treatments (species richness changes: F-value = 0.1, $P = 0.906$; evenness changes: F-value = 3.591, $P = 0.053$; species gains: F-value = 1.116, $P = 0.353$; species losses: F-value = 1.966, $P = 0.174$). There was also no difference for curve change (F-value = 1.659, $P = 0.223$). We then investigated differences among control, N and N+P treatments in the pre-treatment year and in the 9th year of the experiment (Table 4). To do so, species abundances were averaged across all replicates in a treatment to create a single species pool. There were greater species richness differences between C vs. N and N vs. N+P treatments after 9 yr of treatment compared with pre-treatment, but there were similar richness differences between C vs. N+P. Evenness differences were similar over the course of the experiment. Rank differences increased for all treatment comparisons over time, and species differences increased for the control–treatment comparisons but not N vs. N+P treatments. Curve differences also increased over time. When looking over the time-course of the experiment, 2002–2015, the patterns are generally similar (Appendix S7). This investigation demonstrates that large changes in community composition and dispersion in the N and N+P plots shown in NMDS panels in Fig. 5 are mostly driven by reordering of species that already occur in the extant community.

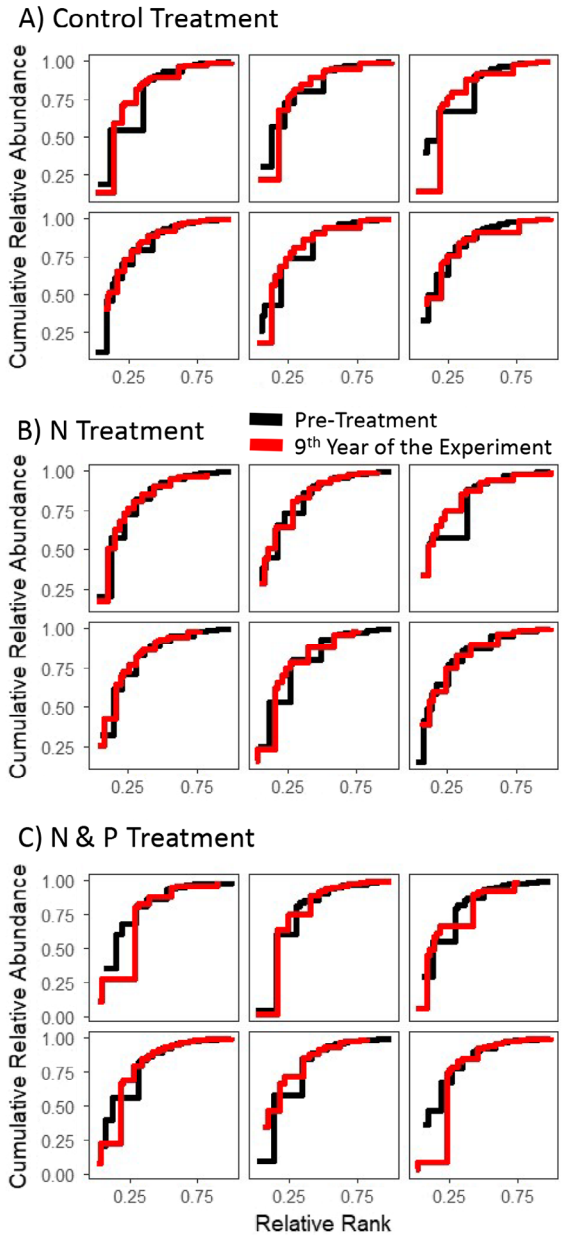

Fig. 7. The relative rank-cumulative abundance curve comparisons of each replicate are shown contrasting pre-treatment and the 9th year of the experiment for the controls (A), nitrogen (B), and nitrogen and phosphorus (C) addition treatments.

Conclusions

Although declines in species richness are of clear concern, there is increasing recognition that species richness alone is not a sensitive indicator of community dynamics (Wilsey et al. 2005, Dornelas et al. 2014, Hillebrand et al. 2017). Compositional changes often occur in the absence of changes in species richness (Dornelas et al. 2014, Jones et al. 2017). Here, we introduce several

new functions to analyze patterns of community change in an update to the library("codyn") R package. Our focus has been specifically on changes and differences in RACs, which we contend give unique insights into patterns of community change over time and differences in communities over space.

A potentially key understudied aspect of communities is the rank of a species in the community. Over time, the rank of a species within a community can change resulting in species reordering. Such changes are particularly important if they involve shifts in the identity of dominant species within the community (Collins et al. 2008, Smith et al. 2009, Koerner et al. 2016, Jones et al. 2017). The new functions we present will help quantify community reordering, which will deepen our understanding of how the phenomenon of species reordering contributes to community change over time. We found reordering correlates most strongly with the multivariate measure of composition change with the

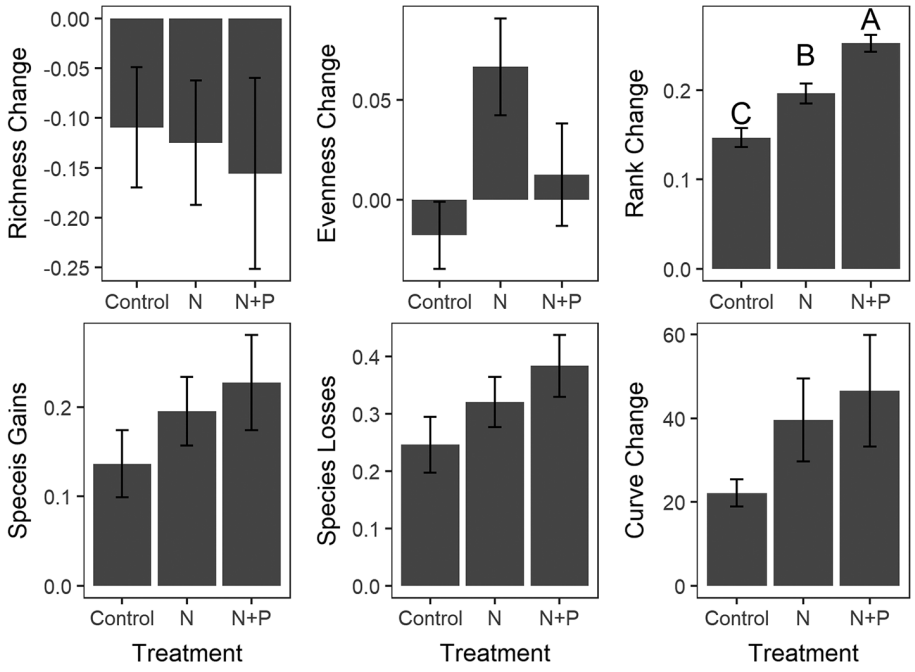

Fig. 8. To better understand what is driving community changes with long-term nutrient additions in tallgrass prairie, we investigated rank abundance curve changes and overall curve change measures, comparing the pretreatment year with the 9th year of the experiment. Letters denote significance at $P < 0.05$ based on a Tukey-HSD test.

Table 4. Differences between control and treatment plots in the long-term N and P addition experiment in tallgrass prairie.

	Pre-treatment year			9th year of the experiment		
Measure of difference	C vs. N	C vs. N+P	N vs. N+P	C vs. N	C vs. N+P	N vs. N+P
Absolute richness difference	0.024	0.048	0.022	0.108	0.049	0.154
Absolute evenness difference	0.007	0.002	0.010	0.011	0.007	0.003
Rank differences	0.108	0.139	0.154	0.202	0.225	0.189
Species differences	0.341	0.333	0.444	0.324	0.390	0.308
Curve differences	4.600	5.33	9.44	28.34	31.11	4.80

Note: Abbreviations are C, control; N, nitrogen addition; N+P, nitrogen plus phosphorus addition.

codyn dataset, and further found that it was the only aspect of community change that differed between the treatments in a long-term N and P fertilization experiment. From our focused exploration of RAC measures, it appears that reordering of species in the community may be a larger driver of community change than species gains, losses, and changes in species richness and evenness. Moreover, such information would not be gained through the more common approach of curve-fitting RACs. Thus, future work is needed to further study the importance of reordering in ecological communities.

The remarkable similarity of RAC shapes within and across systems has intrigued ecologists for decades as the shapes arguably represent a simple yet highly informative representation of community structure (McGill et al. 2007, Ulrich et al. 2010, White et al. 2012). Quantitative RAC curve comparisons have the potential to reveal the ecological factors that drive shape changes or, alternatively, verify that shapes remain constant despite community changes such as rank shifts or species gains and losses. Our measure of curve shape provides a robust way to test for curve differences between two RACs and offers a new way to examine this often-unexplored dimension of ecological communities.

All of the measures introduced in the RAC_change() and RAC_difference() functions are independent of species richness and evenness and together tell a complete story of how a community is changing over time or differs across space. We contend that RACs give unique insights into community dynamics. In particular, multivariate measures are typically used to infer community changes, and while these measures provide insight into how a community changed, in general, they are abstract and it is difficult to pinpoint what aspects of the community have changed (Collins et al. 2008, Avolio et al. 2015). When used alongside these multivariate methods, quantifying RACs yields transparent insight into changes within or differences between communities and together gives a more complete understanding of community dynamics.

In the unprecedented era of anthropogenic change, ecologists are tasked with studying and predicting how communities will respond to novel environmental conditions. The approaches and functions highlighted here and in the library ("codyn") package will offer further insight into the dynamics of ecological communities in long-term observational and experimental datasets.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2881/full