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A simulation tool to scrutinise the behaviour of functional diversity metrics

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Abstract

1. Many indices have been proposed to measure functional diversity and its four distinct dimensions: functional richness, evenness, divergence and redundancy. Identifying indices that reliably measure the functional diversity dimension(s) of interest requires careful testing of how each index responds to species' traits and abundance distributions. In the absence of a convenient simulation tool, tests with artificial data have to date explored only a limited number of scenarios or have altered trait and abundance distributions only indirectly based on principles of evolution and community assembly.

2. We provide *simul.comms*, an R function that allows users to test the efficacy of functional diversity indices by easily creating artificial species communities with user-specified abundance and trait distributions for continuous, ordinal and categorical traits. To illustrate the function's utility, we examine the performance of *R*, a recently published abundance-sensitive index for functional redundancy. We use two approaches to designing simulation tests for this example analysis. The first uses *simul.comms* to create six separate sets of artificial communities to qualitatively assess how *R* responds to predictable changes in functional redundancy. The second uses *simul.comms* to independently alter seven community composition parameters, whose influence on *R* is then examined quantitatively via effect sizes in linear regression.

3. Our analyses indicate that *R* broadly mirrors expected changes in functional redundancy and predictably responds to changes in community composition parameters. *R* appears, however, to primarily reflect trait distributions, responding minimally to variance in abundance and counter-intuitively to abundance range. Further refinement of tools to measure functional redundancy may therefore be desirable.

4. The R tool we provide should assist with refining functional diversity measures, a critical step towards improving our ability to understand and mitigate the impacts of biodiversity loss on ecosystem functioning. Because *simul.comms* simply produces two linked matrices, a species-by-traits matrix and a site-by-species abundance matrix, it may be equally valuable in exploring questions and analytical approaches in other areas of community ecology.

KEYWORDS

abundance distributions, artificial ecological communities, functional diversity, functional redundancy, index reliability, R code, simulations, site-by-species abundance matrix, trait distributions, traits matrix

1 | INTRODUCTION

Accurately quantifying functional diversity – the values and range of functionally important traits in a community (Tilman, 2001) – is of fundamental importance for understanding how biodiversity loss impacts ecosystem functioning. Perhaps for that reason, indices to measure functional diversity abound (Mouchet, Villéger, Mason, & Mouillot, 2010; Schleuter, Daufresne, Massol, & Argillier, 2010; Weiher, 2010), with new ones being added at regular intervals (e.g. Ricotta et al., 2016; Scheiner, Kosman, Presley, & Willig, 2017).

The multitude of available indices partly reflects the fact that functional diversity comprises four distinct dimensions: functional richness, evenness, divergence and redundancy (Table 1). Each dimension characterises a separate aspect of the distribution of organisms in functional space, is thought to interact with ecosystem functioning in distinctive ways (Fonseca & Ganade, 2001; Mason, Mouillot, Lee, & Wilson, 2005), likely responds differently to environmental controls and disturbances (Pakeman & Stockan, 2014; Villeger, Mason, & Mouillot, 2008), and therefore is pertinent to different research questions (Tucker et al., 2017; Table 1).

The choice of index, hence, should first and foremost be guided by the functional diversity component of interest. But multiple indices are available for each component, and yet other, synthetic indices summarise functional diversity as a whole. Existing reviews (Mouchet et al., 2010; Schleuter et al., 2010; Weiher, 2010) provide researchers with some guidance as to the advantages and disadvantages of individual metrics, but inevitably omit newer indices. Moreover, no review to date provides detailed information on how sensitive different indices are to the number of traits, the nature and distribution of trait values, or abundance frequencies. A better understanding of these sensitivities would allow researchers to link diversity indices back to the underlying properties of ecological communities, and so facilitate choosing the index best suited to a particular study's purpose.

Here, we introduce *simul.comms*, a custom-written R function (R Core Team 2017) that simulates artificial ecological communities to examine the sensitivities of functional diversity indices. For a regional species pool of user-specified size, the function creates a species-by-traits matrix for which users can specify the number and type of traits and the density function of the underlying trait values. The function then draws a user-specified number of replicate communities from this regional pool. Users regulate the species richness of these communities, whether included species should be drawn at random or predominantly comprise taxa with either rare or common traits, whether certain trait values should be excluded, how many duplicate taxa (species with identical trait values) should be represented, what density function drives abundance values and whether abundance values are assigned randomly or favour species with either rare or common traits. To illustrate the utility of *simul.comms*, we use it to examine the behaviour of *R*, an index of functional redundancy recently proposed by Ricotta et al. (2016).

2 | R FUNCTION FOR SIMULATING ECOLOGICAL COMMUNITIES

The function *simul.comms* creates artificial species communities, allowing users to manipulate characteristics of the regional species pool and individual communities via 14 input arguments (enclosed within square brackets below). Fully executable R code and a detailed manual are provided at https://github.com/baumlab/sim-ecol-communities and in Appendix 1. The function would typically be run multiple times with some arguments held constant and others altered to generate communities with differing trait and abundance characteristics.

Each time the function is run, it creates an artificial regional species pool with [p] species, each bearing [t] traits whose values are drawn independently according to the sample distribution(s) specified in [tr.method] and interpreted as a continuous variable or otherwise converted to ordinal or categorical depending on settings in [tr.type]. Currently enabled trait sampling distributions include normal and lognormal with user-specified standard deviation, or uniform with user-specified range. From the regional species pool thus generated, the function draws [r] replicate communities with as many species as specified in [s] (users can specify multiple values for [s] in a single function call, yielding [r] replicate communities for each value of [s] specified). Species for each community are drawn from the regional species pool either at random or with preference given to species with rare or common traits, depending on settings in [presence]. Species are assigned abundance values based on the sampling distribution specified in [abun.method], with sampled values assigned either randomly or such that they favour species with rare or common traits, depending on settings in [abundance]. Currently enabled abundance sampling distributions include normal, lognormal and uniform (again with user-specified standard deviation or range, respectively); alternatively users can set all abundances to a fixed value. The degree to which trait values in the regional species pool are represented within individual communities can further be manipulated via [commin] and [commax], which allow minimum and maximum values to be set for each trait (e.g. to shorten the represented trait range), or [comnot] and [comnot.type], which allow individual trait values or a range of trait values to be excluded from representation (e.g. to create holes in the represented trait range). Finally, by setting [dups]>0, users can force communities to include pairs of duplicate species that are identical to one another in all traits, mimicking the presence of recently split or otherwise functionally similar congenerics.

The function returns three outputs. The first, T, is a species-by-traits matrix that represents the regional species pool generated by the function call. The second, A, is a site-by-species abundance matrix that details the artificial communities generated from the regional species pool. T and A together provide the input required for computation of most functional diversity indices; many recently developed indices provide executable R code. The third output, S, returns the settings that determined the composition of the artificial communities created, and also provides summary statistics about the resulting traits and abundance distributions observed in each community that can help

TABLE 1 The four dimensions of functional diversity and their pertinence to ecological research: their definition, interpretation, and illustrative examples of research questions that consider them as either a response (a) or explanatory variable (b)

Dimension	Functional richness	Functional evenness	Functional divergence	Functional redundancy
Definition	How large is the functional space occupied by the species or individuals in a community?	How regularly are individuals or biomass distributed within occupied functional space?	How strongly do individuals or biomass cluster towards the extremes of occupied functional space?	How much overlap exists between species, individuals or biomass in occupied functional space?
Interpretation	What is the breadth of functions represented within the community?	Are different functions equally well represented or is functionality concentrated in distinct clusters?	Given the breadth of functions present, do the more abundant species in the community have maximally distinct traits?	How similar are species within the community, i.e. how likely are they to fulfil equivalent functional roles?
Example questions	(a) Functional diversity as the response variable • Does functional diversity reflect energy availability? • Is drought-induced environmental filtering stronger in seasonally or permanently dry environments? (b) Functional diversity as an explanatory variable • Do functionally richer forests provide greater per hectare carbon storage? • Is extant functional richness higher in older evolutionary lineages?	• Is functional evenness higher in seasonally variable environments? • Which fishing methods minimise impacts on functional evenness? • Does fruiting success vary with the functional evenness of pollinators? • Are functionally more even communities less prone to invasive species?	• Does predator removal alter competition-induced trait divergence among prey? • Does periodic disturbance decrease functional divergence? • Are competitive interactions weaker in more divergent communities? • Are species in highly divergent communities more prone to climate change-induced extirpation?	• Does habitat heterogeneity increase redundancy? • How scale-dependent is functional redundancy? • Does greater redundancy confer increased stability in ecosystem function? • Are more redundant ecosystems less productive?

Excepted change in redundancy	Parameters manipulated	Constant parameters	Observed change in *R*
(a) Test 1: Is *R* sensitive to trait density functions & insensitive to species richness? (*n* = 40 × 100)			
Redundancy should be largely insensitive to species richness, although slight increases with species richness may occur because more species mean tighter species packing given a limited regional traits pool. At any given species richness, redundancy should be higher when the trait density function encourages trait overlap.	- Species richness (10, 20, 30, …, 90, 100) - Density function of trait values in species pool (uniform 0–1, uniform 0–5, normal with *SD* = 1, normal with *SD* = 5)	*r* = 100, *p* = 1,000, *t* = 3, tr.type = c("con", "ord","cat"), presence="random", abun.method = "lnrom:1", abundance = "random", commin = commax = comnot = NULL, dups = 0	
(b) Test 2: Is *R* sensitive to duplicate species? (*n* = 55 * 100)			
Redundancy at each level of species richness should increase with the number of duplicates.	- Species richness (s = 10, 20, 30, …, 90, 100) - Number of duplicate species (5, 10, 15, …, 45, 50, but only up to ½*species richness)	*r* = 100, *p* = 1,000, *t* = 3, tr.method = "norm:1", tr.type = c("con", "ord", "cat"), presence="random", abun.method = "fixed", abundance = "random", commin = commax = comnot = NULL	
(c) Test 3: Is *R* sensitive to reductions in the represented trait range? (*n* = 135 × 100)			
Redundancy at each level of species richness should increase with increasing reductions in the range of traits represented in the community, because a compressed trait range implies greater similarity among species. Whether reductions in range affect minima, maxima or both should not matter.	- Species richness (30, 70, 100) - Range of trait values (reductions of 0.1, 0.2, … 0,5, 0.6% achieved by manipulating represented trait minima, maxima or both for each of 3 traits in turn*)	*r* = 100, *p* = 1,000, *t* = 3, tr.method = "unif:1", tr.type = c("con", "ord", "cat"), presence="random", abun.method = "lnrom:1", abundance = "random", comnot = NULL, dups = 0 * For the categorical trait, we varied which levels were excluded	
(d) Test 4: Is *R* insensitive to gaps in observed trait values? (*n* = 108 × 100)			
Gaps in continuous and ordinal traits should not affect redundancy because closer similarity among species within clusters at either end of the gap likely compensates for increased between-cluster distances. Gaps in categorical traits equate to fewer unique trait values and thus higher overall similarity, so redundancy may increase with increasing categorical gaps.	- Species richness (30, 70, 100) - Gaps within the range of trait values (gaps equating to 0.1, 0.2, 0.3, 0.4% of trait range in the centre, lower or upper half of the trait range for each of 3 traits in turn*)	*r* = 100, *p* = 1,000, *t* = 3, tr.method = "unif:1", tr.type = c("con", "ord", "cat"), presence="random", abun.method = "lnrom:1", abundance = "random", commin = NULL, commax = NULL, dups = 0 * For the categorical trait, we varied which levels were excluded	
(e) Test 5: Is *R* sensitive to how abundances are distributed among traits? (*n* = 120 × 100)			
Under variable abundance, redundancy should be highest when abundance favours common traits, intermediate when abundance is assigned at random and lowest when abundance favours rare traits. This pattern should be strongest where abundance density functions allow for greater variance and range.	- Species richness (10, 20, 30, …, 90, 100) - Density function for abundance values (uniform, normal, lognormal) - Assignment of abundance values (random, or favouring rare or common traits)	*r* = 100, *p* = 1,000, *t* = 3, tr.method = "norm:1", tr.type = c("con", "ord", "cat"), presence="random", commin = commax = comnot = NULL, dups = 0	
(f) Test 6: Is *R* sensitive to how species presence is distributed among traits? (*n* = 30 × 100)			
Redundancy at each level of species richness should be higher when selection favours common rather than random or rare traits, because species with common traits should be most similar to each other.	- Species richness (10, 20, 30, …, 90, 100) - Species selection (random or favouring common or rare traits)	*r* = 100, *p* = 1,000, *t* = 3, tr.method = "norm:1", tr.type = c("con", "ord", "cat"), abun.method = "lnrom:1", abundance = "random", commin = commax = comnot = NULL, dups = 0	

FIGURE 1 Simulation approach one: six separate simulation tests that qualitatively examine how *R* complies with predictable changes in functional redundancy (*n* = number of unique scenarios × number of replicates)

FIGURE 2 Simulation approach two: linear regression results summarising the expected (*y*-axis labels) and observed (plotted symbols) direction and relative strength (standardised parameter estimate) of influence that characteristics of community composition exert on redundancy index *R*. Parameter estimates <0.05 (left of broken line) counted as weak effects
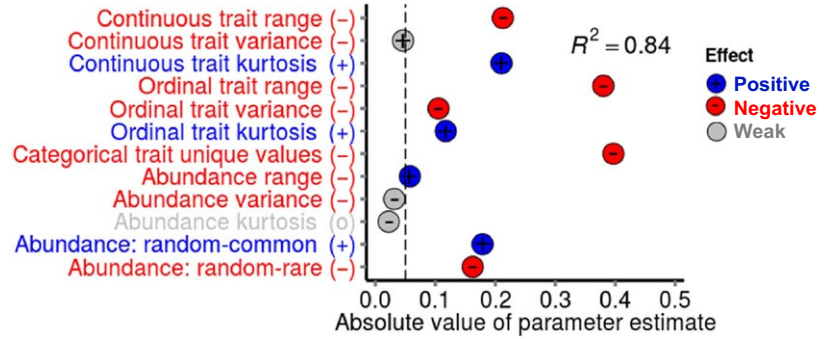
identify what community composition parameters functional diversity indices are sensitive to.

It is sometimes desirable to retain a specific regional species pool but impose different restrictions on how individual communities are sampled from this pool. We therefore also provide a second version of our function, *simul.comms.2*, which expects a species-by-traits matrix produced by *simul.comms* under input [tr.pool] in lieu of arguments [p], [t], [tr.method] and [tr.type], but otherwise works identically.

3 | EXAMPLE WORKFLOW

Step one involves selecting the functional diversity index or indices whose behaviour is to be examined or compared. For illustration, imagine we seek to measure functional redundancy, the overlap in species' ecological traits (a proxy for the overlap in species' contributions to ecosystem functioning). Greater overlap should improve the stability of ecosystem functioning because when one species declines or is lost, others can compensate (Fonseca & Ganade, 2001). One candidate for measuring functional redundancy is the recently proposed index *R* (Ricotta et al., 2016). *R* derives from two well-supported measures of diversity, Simpson's index *D* (Simpson, 1949) and Rao's quadratic entropy *Q* (Rao, 1982), and computes redundancy as $1 - Q/D$ (Ricotta et al., 2016).

Step two involves identifying desirable characteristics that the index or indices should have, given what they intend to measure. Any measure of redundancy should ideally be insensitive to species richness. It should increase as the range and variance of trait values represented in a community shrinks relative to trait values in the species pool, or greater local overlap emerges due to elevated kurtosis in trait values or the selection of species with identical or similar traits. While most functional redundancy measures ignore abundance, it seems likely that an ecosystem process performed by three extremely rare species is more vulnerable than one executed by two very abundant taxa (Mouillot et al., 2013). Ideally, therefore, an index of functional redundancy should be abundance-sensitive, declining when abundance is highly variable or concentrated in species with uncommon traits. Equivalent expectations for responses of indices of functional richness, functional evenness and functional divergence are outlined in Table S1 (Appendix 2).

Step three involves translating these expectations into specific tests with the help of *simul.comms* by creating a variety of artificial communities that differ in those community composition parameters

that should or should not affect the index or indices of interest. For our example, we illustrate two different designs of simulation test.

The first design focuses on two or three community composition parameters at a time to test for six desirable (in)sensitivities, as detailed in Figure 1. Each community was sampled from an artificial regional species pool of 1,000 taxa with one continuous, one ordinal and one categorical trait each, and replicated 100 times. *R* was then calculated based on Gower distances (Podani & Schmera, 2006) among species, and its response to changes in community composition checked visually using the plots in Figure 1 to qualitatively assess its compliance with expectations (also detailed in Figure 1).

While such specific tests can be useful in verifying desirable properties, it is important to recognise that default settings for un-manipulated parameters may affect simulation outcomes and their interpretation. Our second simulation design therefore varied seven community composition parameters independently, yielding 104,676 unique communities. The regional species pool stayed constant at 1,000 species with one continuous, ordinal and categorical trait each. Trait density distributions, however, varied ([tr.method] set to standard normal, lognomal or uniform). The species richness of individual communities ([s]) varied from 10 to 100 species (in steps of 10), picked either randomly or favouring rare or common traits ([presence]), with up to 50 duplicate species ([dups]). Abundance distributions varied ([abun.method] set to standard normal, lognormal, uniform or fixed) and were also assigned either randomly or based on traits ([abundance]). Trait values represented in communities for any one trait in turn either included the full range of values in the species pool or had restricting minima ([commin]), maxima ([commax]), or both, or value gaps in the lower, central or upper range ([comnot]). Each combination of parameters was replicated across 100 communities.

The corresponding values of *R* then served as the response variable in linear regression models designed to determine which of the following predictors (all available in *simul.comms*' output) most influenced the index, with expected positive (+), negative (−), or weak (o) effects: the range (−), variance (−) and kurtosis (+) of the continuous trait, range (−), variance (−) and kurtosis (+) of the ordinal trait, number of unique values in the categorical trait (−), whether abundance favoured common (+) or rare (−) as opposed to random trait values, and the range (−), variance (−), and kurtosis (o) of abundance values. We used linear regressions because our predictions regarding the expected responses were purely directional. We built models with all possible subsets of the predictors using function *dredge* in R package MuMIn (Barton, 2013),

but the full model emerged clearly as the top model (ΔAICc > 1,000). We therefore used the full model's coefficient of determination (R^2) to quantify how predictably R varied with community composition, and its standardised parameter estimates as a measure of each predictor's effect size. Parameter estimates were standardised using predictors' partial standard deviations (Barton, 2013). Parameter estimates less than 0.05 counted as weak effects.

4 | RESULTS

R mostly complied with the expected direction of change in the six qualitative tests (Figure 1), although it responded only weakly to the presence of duplicate species in test 2 (Figure 1b), and for the ordinal trait proved unexpectedly sensitive to the position of range reductions (test 3, Figure 1c) and representation gaps (test 4, Figure 1d). In the linear regression model, R behaved quite predictably (R^2 = .84), changing in accordance with expectations for 9 of 12 predictors (Figure 2). It was most influenced by the number of unique categorical trait values and the range (and kurtosis) of the continuous and ordinal traits. Only its lacking response to variance in the continuous trait and in abundance, and (mild) positive response to range in abundance were counterintuitive. We conclude that R provides a decent measure of functional redundancy, but further refinement may be warranted given the desirable characteristics for redundancy measures we outline above.

5 | DISCUSSION

Identifying reliable measures of functional diversity constitutes a critical step in improving our ability to understand and mitigate the impacts of biodiversity loss on ecosystem functioning. Given the multitude of indices available, careful scrutiny is important and is best accomplished via simulations. Beyond representing an accessible way to test and illustrate known mathematical properties, simulations may reveal previously unrecognised sensitivities.

Naturally, simulations to assess the behaviour of functional diversity indices are not new. To date, however, such simulations have generally examined a limited number of scenarios without replication (Chiu & Chao, 2014; Ricotta et al., 2016; Scheiner et al., 2017; Schleuter et al., 2010), have considered traits with only a single density function (Laliberté & Legendre, 2010; Lefcheck, Bastazini, & Griffin, 2015; Villeger et al., 2008), or have manipulated trait and abundance distributions only indirectly by either modifying real ecological data through sequential removal of information for individual species or sites (Májeková et al., 2016; Pakeman, 2014), or by basing community composition on evolutionary principles and community assembly rules (Maire, Grenouillet, Brosse, & Villéger, 2015; Mason, de Bello, Mouillot, Pavoine, & Dray, 2013; Mouchet et al., 2010). The latter model-based simulations are attractive for their grounding in ecological theory, but limit exploration of sensitivities not directly related to processes captured in the underlying model. The purely statistically driven simulations facilitated by *simul.comms* risk creation of ecologically implausible scenarios; judicious use, however, can elucidate the impact of both realistic ecological

phenomena (e.g. varying dominance patterns) and methodological constraints (e.g. inability to measure traits on a continuous scale).

Further refinements to *simul.comms* are no doubt possible. It may be desirable, for example, to implement correlation among two or more simulated traits, specify the presence of multiple (rather than just two) species with identical traits, force duplicate species to split a single abundance value, or set a community's total abundance. We welcome further suggestions and encourage programming-savvy users to implement additional functionality via Github (https://github.com/baumlab/sim-ecol-communities). As use of *simul.comms* grows, we hope that it will help refine the quality of analyses and insights in functional diversity research. Beyond that, *simul.comms* may prove useful in other areas of community ecology, where carefully customised artificial data on species traits and community composition may help to scrutinise observed patterns or methodological approaches.

AUTHORS' CONTRIBUTIONS

J.M.M. and J.K.B. conceived the ideas; J.M.M. performed the writing of the code and manuscript. L.A.Y. contributed to the implementation of example analyses. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

All data used in this manuscript was simulated, using R function *simul.comms*. The function's R script and manual to allow for replication are available online:

- R script: uploaded as online supporting information and also available at https://github.com/baumlab/sim-ecol-communities (https://doi.org/10.5281/zenodo.831710).
- R manual: uploaded as online supporting information and also available at https://github.com/baumlab/sim-ecol-communities (https://doi.org/10.5281/zenodo.831710).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.