Functional diversity metrics using kernel density *n*-dimensional hypervolumes

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Author contribution

Equal contribution: both authors conceived the idea, developed the code, contributed critically to the drafts, and gave final approval for publication.

Summary

1. The use of kernel density *n*-dimensional hypervolumes [*Global Ecol. Biogeogr.* 23(5):595–609] in trait-based ecology is rapidly increasing. By representing the functional space of a species or community as a Hutchinsonian niche space, this relatively new approach is showing great potential for the advance of functional ecology theory.

2. Functions for calculating the standard set of functional diversity (FD) indexes—richness, divergence, and regularity—have not been developed in the context of kernel density hypervolumes yet. This gap is delaying a full exploitation of the kernel density *n*-dimensional hypervolumes framework in functional ecology, meanwhile preventing the possibility to compare its performance with that of other FD methods.

3. We develop a set of functions to calculate FD indices based on kernel density *n*-dimensional hypervolumes, including alpha (richness), beta (and respective components), dispersion, evenness, contribution, and originality. Altogether, these indexes provide a coherent framework to explore the primary mathematical components of FD within a kernel density setting. These new functions can work either with Hypervolumes objects, HypervolumeList objects, or raw data (species presence or abundance and their traits) as input data, and are versatile in terms of computation speed, which is achieved by controlling the number of stochastic points to be used in the different estimations.

4. These newly developed functions are implemented within the R package BAT, an open platform for biodiversity assessments. As a coherent corpus of functional indexes based on a common algorithm, it opens up the possibility to fully explore the strengths of the Hutchinsonian niche concept in community ecology research.

Keywords: Alpha diversity, beta diversity, functional diversity, functional metrics, Huntchinsonian hypervolume, hyperspace, fundamental niche, traits

Introduction

The past two decades have seen an increasing interest on different facets of biodiversity, namely on the way species interact among them and with their environment, with the resulting exponential growth of functional ecology studies. This push was primarily driven by a few milestone theoretical contributions illustrating a way of reshaping entire areas in ecology from a functional perspective, including population and community ecology (Petchey & Gaston, 2002; McGill, Enquist, Weiher, & Westoby, 2006; Bolnick et al., 2011; Violle et al., 2012), conservation biology (Wellnitz & Poff, 2001; Cadotte, Carscadden, & Mirotchnick, 2011), and biogeography (Violle, Reich, Pacala, Enquist, & Kattge, 2014). The fast development of functional ecology theory has led to a proliferation of approaches for estimating functional diversity (FD) (Legras, Loiseau, & Gaertner, 2018), as well as indexes for measuring different mathematical facets underlying FD (Mouillot, Mason, Dumay, & Wilson, 2005; Villéger, Mason, & Mouillot, 2008; Mouchet, Villéger, Mason, & Mouillot, 2010; Schleuter, Daufresne, Massol, & Argillier, 2010; Cardoso, Rigal, Borges, & Carvalho, 2014).

Three main mathematical objects are typically used to represent FD: functional trees (Petchey & Gaston, 2002), convex hull hypervolumes (Cornwell, Schwilk, & Ackerly, 2006), and kernel density hypervolumes (Blonder, Lamanna, Violle, & Enquist, 2014; Blonder et al., 2018) (Figure 1). In the programming language R—likely the main analytical environment used in ecology and evolution (Tippmann, 2015)—these three frameworks have been implemented, respectively, in the packages *BAT* (Cardoso, Rigal, & Carvalho, 2015; Cardoso, Mammola, Rigal, & Carvalho, 2020), *FD* (Laliberté, Legendre, & Shipley, 2014), and *hypervolume* (Blonder, 2018). The *BAT* package is an open platform that provides an assortment of functions for biodiversity assessment (Cardoso et al., 2015), with a special focus on the estimation of the three main components of biological diversity—taxonomic (TD), phylogenetic (PD) and functional (FD) diversity. For calculating FD, this package uses a functional tree in the sense of Petchey & Gaston

(2002, 2006). The *FD* package is possibly the most widely used R package for functional analyses (over 750 citations as of November 2019 based on Google Scholar metrics). *FD* primarily relies on convex hull for delineating the functional space (Laliberté & Legendre, 2010), although alternative formulations and indexes are implemented as well. Finally, the *hypervolume* package relies on the concept of multi-dimensional niche in the sense of Hutchinson (1957). This is achieved by delineating the shape and volume of the niche hyperspace, whether functional or bioclimatic, using different high-dimensional kernel density estimation methods (Blonder et al., 2018)

Both BAT and FD include a vast collection of functional indexes, allowing a user to explore a functional community based on different mathematical aspects of FD, namely the richness, divergence, and regularity components (Pavoine & Bonsall, 2011; Tucker et al., 2017). As of yet, analogous indexes have not been developed in the context of kernel density *n*-dimensional hypervolumes. This gap is hindering the use of the hypervolumes framework in functional ecology studies and is preventing the possibility to fully compare the performance of these alternative representations of FD. Here, we develop and describe a new set of R functions to calculate the analogous of standard functional metrics with kernel density *n*-dimensional hypervolumes, all available through the R package *BAT* (Cardoso et al., 2020).

New functionalities in BAT

The new functions presented here represent the analogous of the functional indexes that were originally developed in *BAT* for functional trees (Cardoso et al., 2015). Each new function is briefly illustrated below.

INPUT DATA

The calculation of the new indexes requires the user to provide either: i) a 'Hypervolume' class R object; ii) a list of hypervolumes ('HypervolumesList' class R object); or iii) raw data matrices with

species composition of the communities and their functional traits. 'Hypervolume' and 'HypervolumeList' class objects can be constructed using the respective functions of the hypervolume package (Blonder, 2018), namely one of the three algorithms currently implemented for hypervolume delineation (box, gaussian, or svm). Full details on these approaches have been discussed elsewhere (Blonder et al., 2014, 2018; Blonder, 2016). Alternatively, hypervolumes can be constructed directly within the package BAT by feeding the functions with raw data, namely a sites x species matrix with incidence or abundance data about the species in the community and a species x traits matrix.

Note that, although specifically developed for functional hypervolumes, these new functions can also be applied to other input data. For example, the functions *kernel.beta* and *kernel.similarity* could be used to explore the bioclimatic niche overlap between two or more species.

FUNCTIONS FOR ESTIMATING FD IN A KERNEL DENSITY CONTEXT

kernel.alpha

This function allows the user to calculate functional richness in a kernel context. Alpha FD is simply the total volume of the functional niche hyperspace—but see Carmona et al. (2016b, 2016a, 2019) for an alternative estimation based on trait probability density (TPD).

kernel.beta

This function can be used to estimate beta diversity based on the framework recently proposed by Carvalho & Cardoso (2018). The function computes a pairwise decomposition of the overall differentiation among kernel hypervolumes into two components: the replacement (shifts) of space between hypervolumes and net differences between the amount of space enclosed by each hypervolume. This can be used for decomposing beta diversity into its drivers (Carvalho, Cardoso,

& Gomes, 2012; Carvalho, Cardoso, Borges, Schmera, & Podani, 2013) in a similar way as already proposed for functional trees (Cardoso, Rigal, Carvalho, et al., 2014).

kernel.contribution

This function evaluates the contribution of each observation to the total volume of the kernel *n*-dimensional hypervolume. It does so via a leave-one-out approach, whereby the contribution of each observation to the total functional space is calculated as the difference in volume between the full hypervolume and a second hypervolume constructed without that specific observation. Note that, interestingly, the contribution of an individual observation could be negative, if the removal of this observation increases the volume of the total hypervolume (Figure 2). This might happen, although not always, in cases when the presence of a given species decreases the average distance between all the species in the community, i.e., when a given species is close to the "average" species of that community, making that community less diverse in some sense. By definition, this does not happen in the case of functional trees, since contribution can only be positive.

kernel.dispersion

In the kernel context, dispersion can be represented as the average dissimilarity between any two random points of a kernel density hypervolume. Note that this function is the analogous of the function *dispersion* in BAT, based on functional trees. Conversely, in the package FD, the name "dispersion" [Fdis; (Laliberté et al., 2014)] is used to represent the average distance of all functional elements to the centroid.

kernel.evenness

This function measures the functional evenness of an hypervolume, namely the regularity of functional elements distribution within the total functional space (Schleuter et al., 2010). Following

a similar approach to that of Carmona et al. (2016b), evenness is calculated as the overlap between the input hypervolume and a second, imaginary hypervolume where traits and abundances are evenly distributed within their possible range.

kernel.originality

A measure of the originality of each observation used to construct the hypervolume (Pavoine, Ollier, & Dufour, 2005). This is calculated as the average distance between each observation to a sample of stochastic points within the boundaries of the hypervolume. The number of sample points to be used in the estimation is controlled by the *frac* parameter.

kernel.similarity

A versatile function to compare multiple hypervolumes objects, by calculating their pairwise centroid distance, minimum distance, intersection, and Jaccard and Sørensen-Dice similarity. This function is based on a recent simulation study comparing the correlation and performance among these indexes (Mammola, 2019).

Example analysis

To illustrate the usage of the new functions, we provide an example analysis based on a recent study of ground-dwelling arthropods in sampling plots characterized by different levels of urbanization within the municipality of Turin (NW-Italy) (Piano, Giuliano, & Isaia, 2020). R code and databases to generate the analysis are available in Figshare (doi: 10.6084/m9.figshare.11708277). In order to test the effects of patch isolation within the urban matrix on the functional diversity of arthropods assemblages, the authors identified two types of subplots within each plot, where they used pitfall traps to sample the ground-dwelling fauna (spiders and ground beetles). In particular:

i) isolated subplots are patches within a traffic roundabout, surrounded by roads; and

ii) connected subplots are patches in green areas, connected with the surrounding environmental matrix and thus more easily colonized by ground-dwelling arthropods.

We extracted from this database a random subset of 60 subplots, 30 isolated and 30 connected. For each subplot, we extracted abundance data for the spiders community and three functional traits for each species: body length, dispersal strategy, and hunting strategy. Categorization of hunting strategies was based on Cardoso et al. (2011), whereas three type of dispersal (1= non- or sporadic ballooners; 2= ballooners at juvenile stages only; 3= ballooners at all life stages) were assigned by Piano et al. (2020) based on multiple literature sources (Bell, Bohan, Shaw, & Weyman, 2005; Blandenier, 2009; Simonneau, Courtial, & Pétillon, 2016). Note that we analyzed here only spider communities since carabids showed only weak functional signal in their study (Piano et al., 2020).

We used the new kernel-based functions to explore variations in functional diversity between spider communities in isolated versus connected subplots, using *BAT* version 2.0.0. (Cardoso et al., 2020) and *hypervolume* version 2.0.11. (Blonder, 2018). Since spiders' functional traits included two categorical traits (Piano et al., 2020), we used the approach proposed by Carvalho & Cardoso (2018) to incorporate categorical variables in hypervolume estimation. We applied a Gower dissimilarity measure (Gower, 1971) to the complete trait matrix and then, we analyzed the resulting distance matrix through Principal Coordinate Analysis (PCoA) in order to extract orthogonal morphological axes for hypervolume delineation. We retained the first three PCoA axes to construct hypervolumes using the box method and a default bandwidth (Blonder et al., 2018). We then estimated α functional diversity of each community with the function *kernel.alpha*.

While the functional spaces of spider community in isolated versus connected subplots were highly interspersed (Figure 3), we observed that, on average, connected subplots had a higher functional alpha diversity (Figure 4a). This is in accordance with the fact that connected subplots are more easily colonized by a larger number of spider species, that in turn accounts for a greater

diversity of traits. Isolated subplots, on the other hand, are colonized by a subset of specialized species possessing specific dispersal traits that enhance the colonization of these isolated habitats. In fact, traits of spider communities in connected subplots were more dispersed (Figure 4b) and homogeneous (Figure 4c) than those in isolated subplots, as estimated using the functions *kernel.dispersion* and *kernel.originality.*

Furthermore, we used the *kernel.beta* function to explore variations in traits among communities inhabiting the two different types of subplots. Total β functional diversity values were higher in pairwise comparisons between communities in connected subplots, whereas communities in isolated subplots were in general more similar one another (Figure 4d). This result further confirms that only spiders with specific traits—in particular those with higher dispersal potential and probably higher resistance to highly disturbed habitats—are able to reach and survive in isolated subplots. In isolated subplots, the replacement component of β diversity was more preponderant than in connected subplots (Figure 4e), whereas the richness component was higher in connected subplots (Figure 4f). Differential distributions of β diversity values between the two subplot types are attributable to differences in their effective area and environmental conditions. Isolated subplots (roundabouts) are characterized by similar environmental conditions across the study area, and their effective area is smaller than those of connected subplots (Piano et al., 2020). Connected subplots, on the other hand, can be in the middle of both small and large areas. In addition, although being consistently placed in herbaceous environments, these areas are characterized by a greater variety of environmental conditions (Piano E., pers. Comm. 2020), hence explaining the higher differences in β diversity among connected subplots.

By using the function *kernel.contribution*, we further inferred that *Nurscia albomaculata* (Lucas, 1846) (Araneae: Titanoecidae) is the species contributing the most to the functional space in isolated subplots, and *Micaria coarctata* (Lucas, 1846) (Gnaphosidae) the most contributing in connected subplots. This is apparently because *N. albomaculata* was the only species of large size

(>10 mm) and with low dispersal (no ballooning) that fell in pitfall traps in isolated plots in the study by Piano et al. (2020), thus it contributed unique traits to roundabouts communities. We finally used the *kernel.originality* to estimate the functional originality of each spider species included in the dataset (result not shown), finding that average functional originality was not significantly different between isolated and connected subplots (t-test: –1.23, df= 68.2, p= 0.22). This is not unexpected since the pool of spider species found in urban environments are already filtered for a small diversity of traits.

Conclusions

By developing robust functions for estimating the primary facets of FD—the richness, divergence, and regularity components (Pavoine & Bonsall, 2011; Tucker et al., 2017),—we open up the potential to fully exploit the strengths of the Hutchinsonian niche concept in functional ecology research (Blonder, 2019). As in the case of other frameworks for estimating FD (e.g., Mouchet et al., 2010; Junker, Kuppler, Bathke, Schreyer, & Trutschnig, 2016; Carmona et al., 2019), these new functions can be used to answer a large assortment of questions. Alpha and beta FD allow us to understand the richness of a functional hyperspace, and in which components multiple functional hyperspaces differ, namely the pairwise richness or replacement difference in term of functional traits. Contribution and originality allow to understand which are the most unique functional elements, i.e. the species or individuals contributing the most to the overall functional richness of the hyperspace. Therefore, these indexes yield potential to help in targeting keystone species or those of high conservation concern. Dispersion and evenness provide a quantification of the distribution of elements in the functional space enabling, for example, to compare whether multiple assemblages are differentially harmonious/unbalanced in their functional composition.

CITATION

Researchers relying on these functions should cite this article and in addition can also cite the BAT package directly. Updated citation information can be obtained by typing in R the command *citation('BAT')*. The method and parameters used for constructing kernel density *n*-dimensional hypervolumes have also to be specified, referring to the publications by Blonder et al. (2014, 2018).

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Data availability

Data and R scripts to generate the analyses are available in figshare (doi: 10.6084/m9.figshare.11708277).

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Figure captions

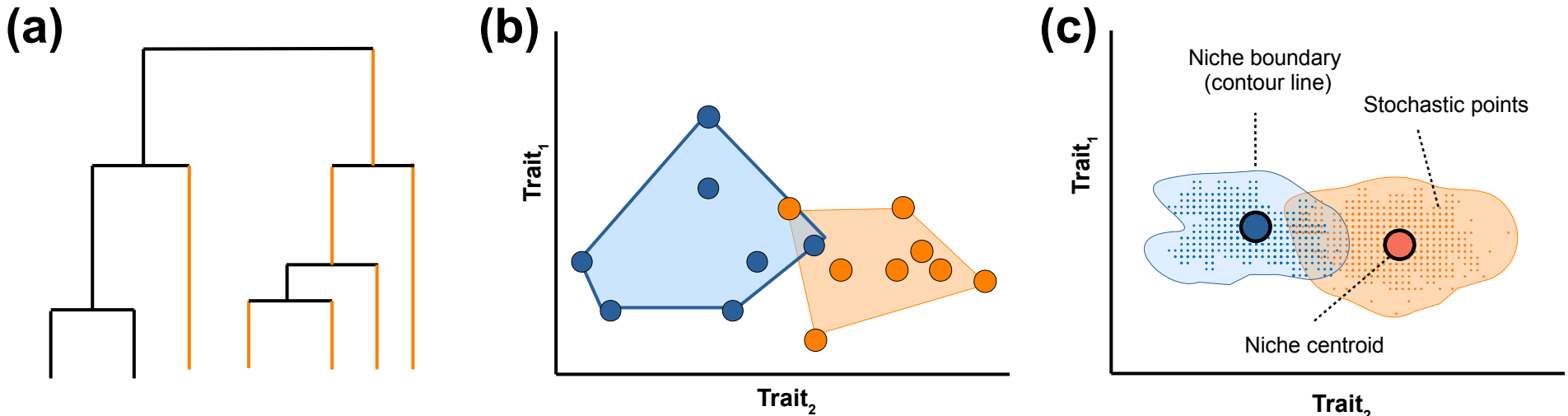
Figure 1. Schematic representation of the three main frameworks for calculating FD – examples are based on two hypothetical traits and two communities, represented in turquoise and orange. **a**) The functional space can be represented as a functional tree, whose construction is based on the distance matrix of the species traits. The alpha diversity of a community can be estimated as the total branch length of a tree linking all species represented in such community—in the example, the FD of a community with 5 species (in orange) is shown. **b**) The functional space can be represented as the convex hull comprising the species occupying the functional space. The alpha diversity of a community can be estimated as the smallest convex volume that contains the set of points. **c**) The functional space can be constructed using kernel density hypervolumes, whereby the functional space is approximated as a cloud of stochastic points sampled based on a set of observations (e.g. the functional elements in the community). The alpha diversity of a community can be estimated as the total volume of the hypervolume.

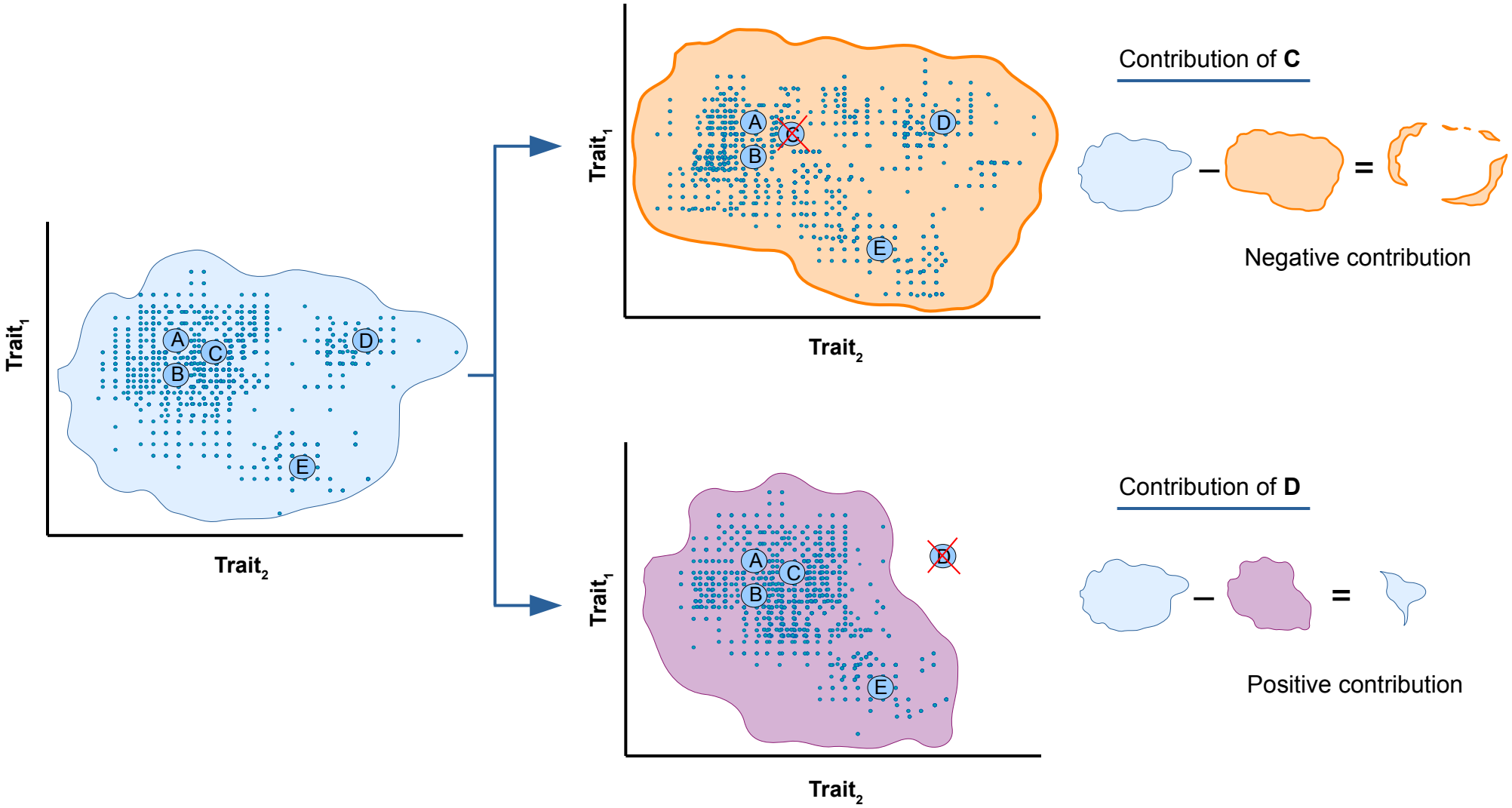
Figure 2. Scheme of the procedure to estimate contribution. A functional 2-dimensional hypervolume is constructed via five observations (A, B, C, D, and E). The contribution of each observation can be computed with a leave-one-out approach, whereby a new hypervolume is constructed leaving out one observation. In turn, the contribution value is quantified as the difference in volume between the original hypervolume and the new one. In this example, the contribution of observation D is positive, because the hypervolume constructed with observations A, B, C, and E is less voluminous than the initial one. Conversely the contribution of C is negative, because the observation C is clustered with A and B, which leads a higher proportion of stochastic points to cluster in the vicinity of these three observations. By removing C, the stochastic points are "freer" to spread in the functional space, which results in a slight increase in the volume. Note that contour lines bounding the stochastic point are only drawn for graphical representation, whereas the real hypervolume volume is based on the stochastic points only.

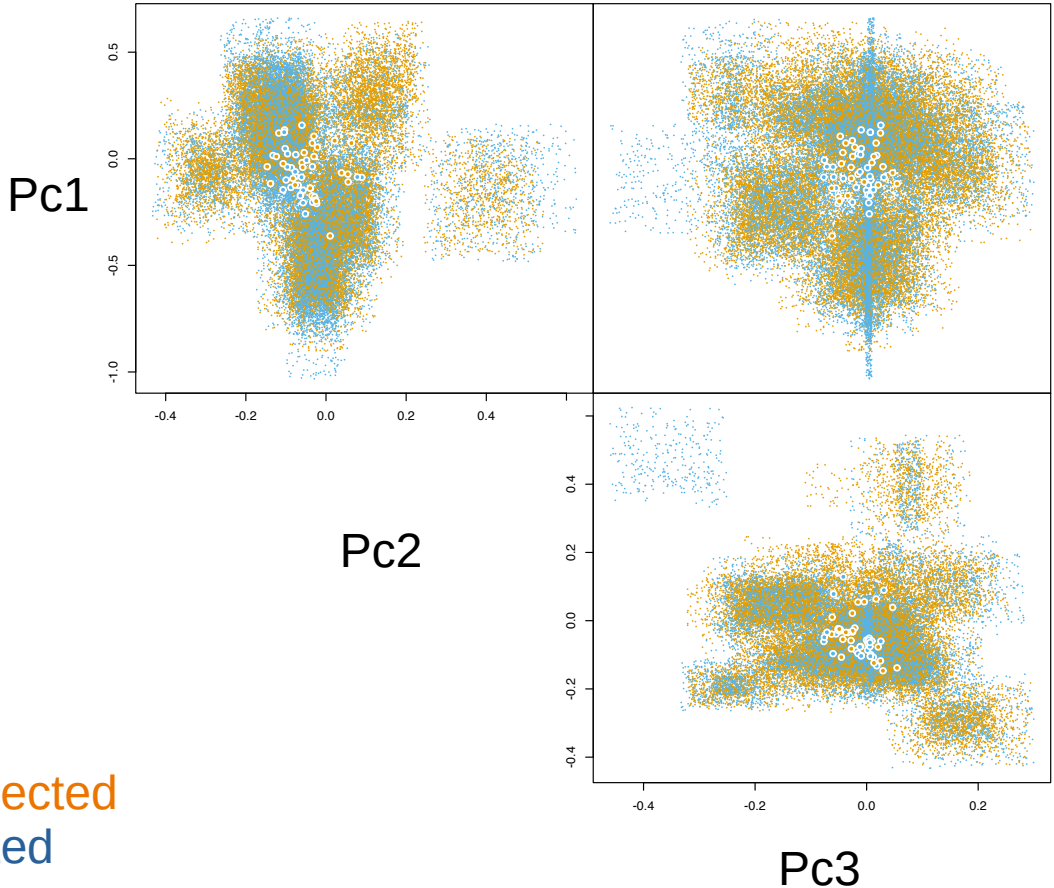
Figure 3. Pairplots representing the estimated 3-dimensional hypervolumes for communities in Isolated and Connected subplots, based on the first three axes of the Principal Coordinate Analysis (PCoA) performed on

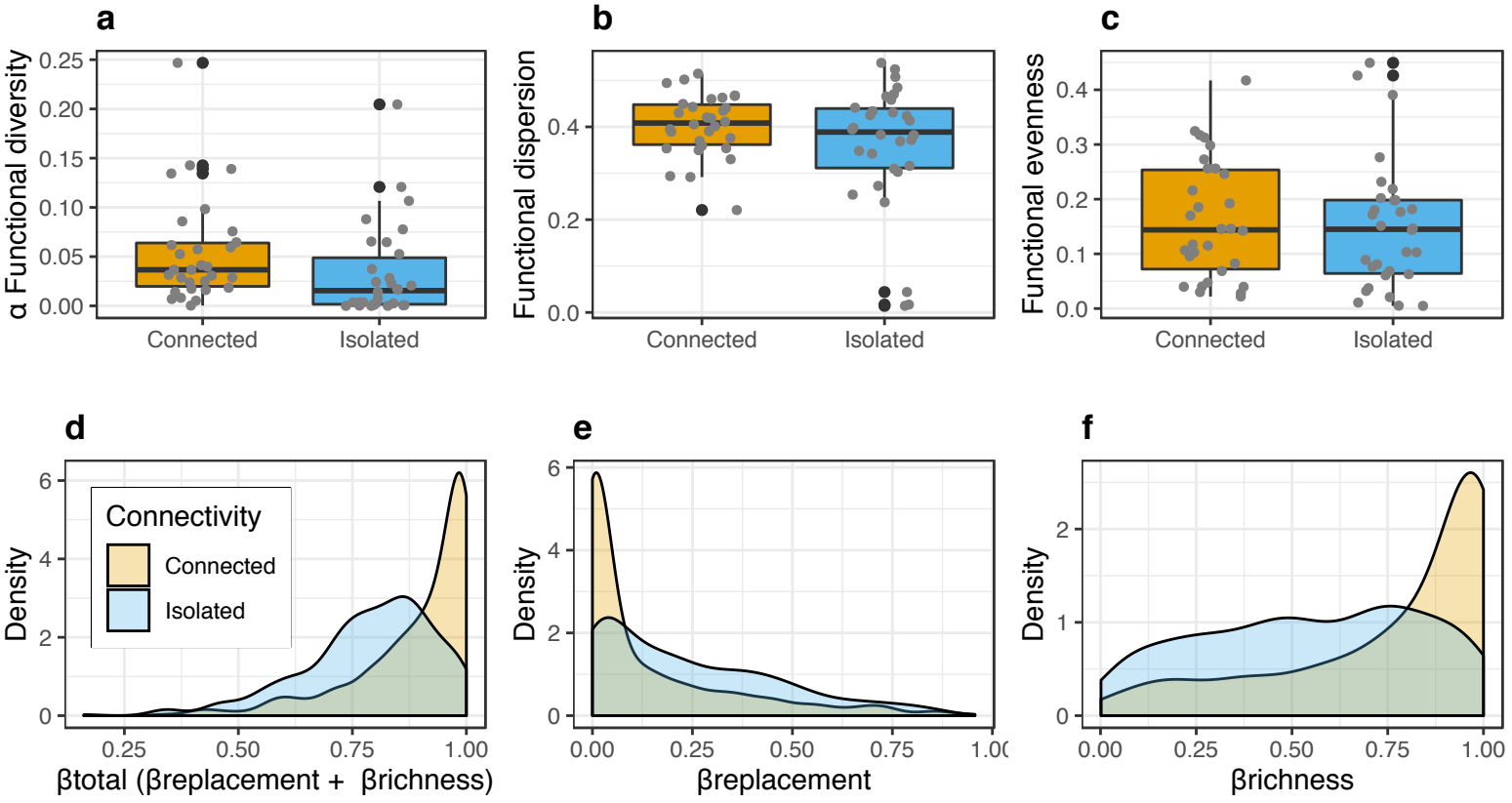
the Gower dissimilarity matrix of the functional traits. Random points are coloured based on the type of plot of each hypervolume.

Figure 4. a–c) Functional richness, dispersion, and evenness of spider communities in connected and isolated plots. **d–f**) Density of β functional diversity values for pairwise comparison of communities in connected and isolated subplots. Total functional β diversity is split in two components: βrichness is the turnover in functional composition explained by species loss/gain alone, and βreplacement is turnover in functional composition explained by replacement of species alone.


(a)
(b)
Trait1
Trait2
(c)
Niche boundary
(contour line)
Stochastic points
Trait1
Niche centroid
Trait2


Trait1
Trait2
A
B
C
D
E
Contribution of C
Negative contribution
Contribution of D
Positive contribution


Pc1
Pc2
Pc3
0.5
0.0
-0.5
-1.0
-0.4
-0.2
0.0
0.2
0.4
Connected
Isolated


a
α Functional diversity
0.25
0.20
0.15
0.10
0.05
0.00
Connected
Isolated
b
Functional dispersion
0.4
0.2
0.0
Connected
Isolated
c
Functional evenness
0.4
0.3
0.2
0.1
0.0
Connected
Isolated
d
Density
6
4
2
0
Connectivity
Connected
Isolated
0.25
0.50
0.75
1.00
βtotal (βreplacement + βrichness)
e
Density
6
4
2
0
0.00
0.25
0.50
0.75
1.00
βreplacement
f
Density
2
1
0
0.00
0.25
0.50
0.75
1.00
βrichness