Concepts and applications in functional diversity

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ABSTRACT

The use of functional analyses in ecology has grown exponentially over the past two decades, broadening our understanding of biological diversity and its change across space and time. Virtually all ecological sub-disciplines recognize the critical value of looking at species and communities from a functional perspective, and this has led to a proliferation of methods for estimating contrasting dimensions of functional diversity. Differences between these methods and their development generated terminological inconsistencies and confusion about the selection of the most appropriate approach for addressing any particular ecological question, hampering the potential for comparative studies and meta-analyses. We show that two general mathematical frameworks for estimating functional diversity are prevailing: those based on dissimilarity matrices (e.g., Rao entropy, functional dendrograms) and those relying on multidimensional spaces, constructed as either binary (convex hulls) or probabilistic hypervolumes. We review these frameworks, discuss their strengths and weaknesses, and provide an overview of the main R packages allowing to perform these calculations. In parallel, we propose a 'periodic table' of functional diversity metrics quantifying the richness, divergence, and regularity of species or individuals under each framework. Therefore, this overview offers a roadmap for confidently approaching functional diversity analyses both theoretically and practically.

Keywords: alpha diversity, beta diversity, disparity, evenness, functional dendrogram, functional divergence, functional dispersion, functional hyperspace, functional regularity, functional richness, biological traits, functional originality, functional uniqueness

INTRODUCTION

The idea that organisms are not equal in their attributes and functions—that is, the range of things they do (Petchey & Gaston, 2006)—can be traced back to the concept of ecological niche (Elton, 1927; Grinnell, 1917, 1924; Hutchinson, 1957) and the subsequent emergence of functional ecology as a scientific discipline (Calow, 1987; Keddy, 1992). Over the past two decades, we have witnessed an exponential growth of trait-based studies (>13,500 published papers as of 2019; Figure 1). This was largely driven by a number of seminal essays that illustrated a way of rethinking entire ecological fields from a functional perspective, from population and community ecology (Bolnick et al., 2011; Lavorel & Garnier, 2002; McGill, Enquist, Weiher, & Westoby, 2006; Violle et al., 2012), to biogeography (Violle, Reich, Pacala, Enquist, & Kattge, 2014), along with conservation biology (Cadotte, Carscadden, & Mirotchnick, 2011; Rosenfeld, 2002; Wellnitz & Poff, 2001). Stemming from this intellectual legacy, the use of functional diversity in the study of ecological patterns across different spatial and temporal scales has now become routine (Carmona, de Bello, Mason, & Lepš, 2016b; Jarzyna & Jetz, 2018; Kamran et al., 2011; Kraft & Ackerly, 2010; Lamanna et al., 2014; Mammola & Cardoso, 2020; Mason & De Bello, 2013).

This fast theoretical development was accompanied by a proliferation of methods for studying functional diversity (Legras, Loiseau, & Gaertner, 2018). There is nowadays a wide variety of algorithms and frameworks (hereafter ‘methods’) that can be used to delineate the trait space occupied by a given species or community, each based on particular mathematical objects—raw data, distance matrices, trees, convex hulls, kernel density hypervolumes, etc (see Table 1 for a glossary). Once the trait space is generated, an even larger set of indexes (hereafter ‘metrics’) is available to calculate specific properties of the system (Pavoine & Bonsall, 2011; Schleuter, Daufresne, Massol, & Argillier, 2010). Albeit this broad availability of methods and metrics is fueling gigantic leaps forward in our understanding of ecosystem functionality, it has been pointed out that it is also “*[...] causing much confusion in selecting appropriate methods for specific questions”* (Carmona et al., 2016b).

In our view, this confusion is the direct consequence of two drivers. First, there have been few efforts to compare each method to illustrate their strengths, weaknesses, and limitations. Our experiences as reviewers and editors of manuscripts, readers of the existing literature, and instructors of early-career scientists have led us to think that most users routinely use a single method or metric just because it has been published in a famous paper or it appears in the first page of Google, and not because it better fits their question and data. Second, researchers developing the statistics underlying functional diversity approaches often provided the user with a limited selection of functions for calculating functional metrics or used different denominations to metrics with similar properties.

In the last decade or so, there have been subsequent attempts to categorize functional metrics and explore their usefulness in discriminating different processes (e.g., Mason et al., 2005; Mouchet et al., 2010; Ricotta, 2007; Villéger et al., 2008). Building upon this ground, Pavoine & Bonsall (2011) provided a broad clarification of the mathematics underpinning this plethora of metrics, categorizing them under three independent dimensions of richness, divergence, and regularity (Box 1). The Pavoine-Bonsall scheme is compelling, as it allows to group taxonomic, phylogenetic, and functional metrics under a common umbrella and thus it well encapsulates a modern view on biodiversity (Jarzyna & Jetz, 2016). Yet, the classification still presents limitations (e.g., it does not fully account for a beta-diversity level; Box 1) and was not fully incorporated in the available statistical packages for functional diversity calculation, which often provide the user with an incoherent set of metrics to explore these three dimensions.

Altogether, these shortcomings generate a fertile ground for terminological and conceptual confusion, which leads to a parallel confusion about the selection of the most appropriate methods and metric for addressing any particular ecological question. This hampers the potential for comparative studies and meta-analyses, meanwhile preventing to fully understand the eco-evolutionary rationale beyond functional diversity estimation. We aim, therefore, to propose a classification of the existing jungle of functional methods, dimensions, and metrics. To achieve this goal, we first review the main frameworks and R packages for estimating functional diversity that are emerging in trait-based ecology. We explain the ecological logic underpinning each framework (that is, how each method relates to the concept of niche) and discuss their pros and cons. We then illustrate the meaning of the three dimensions of functional diversity—richness, divergence, and regularity (Box 1)—in the context of each of these methods. Finally, we present the metrics quantifying each dimension within each method and which R packages allow to calculate them. Our ultimate goal is to develop a roadmap to select the best possible functional diversity approach depending on the question under study.

Box 1. The Pavoine–Bonsall scheme for classifying taxonomic, phylogenetic, and functional metrics.

Pavoine and Bonsall (2011) proposed a semantic framework for classifying taxonomic, phylogenetic, and functional metrics under a unified scheme. This classification was further improved by Tucker et al. (2017), who identified three distinct dimensions of diversity: *richness*, *divergence*, and *regularity*. These three dimensions capture the primary mathematical operation inherent to each metric, namely:

i) the ‘richness’ dimension encompasses metrics reflecting the sum of difference among observations (sum);

ii) the ‘divergence’ dimension encompasses metrics reflecting the average difference among observations (mean); and

iii) the ‘regularity’ dimension encompasses metrics reflecting how regular the difference among observations are (variance).

Note that these dimensionss loosely correspond to respectively trait space’s size, position and density discussed in an evolutionary biology context in Guillerme et al (2020).

This scheme is general as it can be applied to both abundance and presence/absence formulations, and provides a simple and intuitive rationale for grouping functional metrics. The classification scheme is also split on a second axis of information, reflecting the level of data organization at which each metric is calculated (Group). In their classification of phylogenetic indexes, Tucker et al. used two levels of organization, depending whether each metric is calculated within a set (e.g., individuals within a species or species within a community; so-called α-diversity) or between sets (e.g., comparison of multiple species or communities in space and time; so-called β-diversity). Here, we expanded this second axis of information to three levels of organization, namely:

i) ‘Observation level’, representing the distinct functional elements within a set (e.g., an individual, population, or species);

ii) ‘Within groups’, representing all the *Observation level* elements within a set (e.g., functional diversity within a population, species, community, or region); and

ii) ‘Between groups’, comparing multiple *Groups* (e.g., comparison of multiple populations, species, communities, or regions in space and time).

MATHEMATICAL METHODS FOR FUNCTIONAL DIVERSITY ESTIMATION

Stemming from the concept of ecological guild (Root, 1967), the simplest mathematical estimation of functional diversity can be achieved using a raw data matrix of traits, whereby total functional richness is calculated as the number of unique functional combinations (guilds) in a given set of observations (Blondel, 2003). Although the idea of guild provides an intuitive representation of functional diversity, researchers soon felt that this approach was too simplistic (Legras et al., 2018). A plethora of more sophisticated methods has since been developed to represent the observed diversity of traits in a system and their relations. We will refer to this representation of the diversity of traits as the 'trait space' throughout this review (see Table 1).

Rather than overviewing all published and used methods, which would probably create further confusion, we seek to illustrate a way to frame the plethora of possibilities for trait space analyses. We chose to only discuss methods that:

i) are open and free, which today practically coincide with packages and functions implemented and maintained in R (Lai, Lortie, Muenchen, Yang, & Ma, 2019);

ii) are accessible to the largest possible audience, namely methods that are thoroughly documented and thereby do not require a high level of knowledge in statistics or programming; and

iii) are based on robust mathematical concepts that provide an easy-to-understand representation of the trait space.

In our view, two general mathematical approaches for estimating the trait space and its properties are prevailing in recent literature: those based on non-ordinated matrices (non-dimensional representation) and those based on ordinated multidimensional spaces (i.e., multidimensional representation). Note, however, that the distinction between dissimilarity-based and multidimensional may become blurry when the data used to build a multidimensional space are first converted to a dissimilarity matrix to deal with non-continuous traits (see "Input data & data preparation” in Figure 2). We hereafter briefly describe each of these methods, discuss their strengths and weaknesses (Table 2), and list the main R packages that can be used for practical calculations.

Methods based on non-dimensional representation

All these methods rely on converting the trait matrix to a dissimilarity matrix; in turn, this transformed matrix serves to delineate the trait space and explore its properties. Here, we distinguished between methods and metrics that attempt to measure the entropy of the trait space as the dissimilarity among observations directly (mean dissimilarity methods) and those that use a distance-based dendrogram object to represent the trait space.

Whereas all these methods have several features that may make them advantageous over multidimensional frameworks, there are at least two main caveats that apply to all. Foremost, they do not relate well with the classical concept of niche *sensu* Hutchinson (1957). Second, as discussed by Podani and Schmera (2006), the choice of the distance measure to use is not trivial, especially because a trait matrix is frequently a mixture of different datatypes—continuous, ordinal, categorical, and binary data—and this can significantly affect results (see also Lloyd, 2016).

Mean dissimilarity methods

The methods in this category are based on the notion that functional diversity represents the extent of trait differences between species (de Bello, Carmona, Lepš, Szava-Kovats, & Pärtel, 2016). These methods do not allow to visualize the trait space directly [but see, e.g., Micó et al. (2020) for a work-around], and are more a collection of metrics measuring entropy-based properties of the trait matrix. The three most commonly used are:

i) Rao quadratic entropy (Rao), representing the expected dissimilarity between two different individuals, populations, or species sampled at random (Botta-Dukát, 2005);

ii) functional dispersion (FDis) *sensu* Laliberté & Legendre (2010), representing the mean distance of individual species to the centroid of all species; and

iii) mean pairwise dissimilarity (MPD), representing the expected dissimilarity between two randomly-sampled individuals from different species (Weiher & Keddy, 1995).

The differences between these metrics are subtle, but with important practical consequences. Both Rao and FDis have the same mathematical basis as variance (Pavoine & Bonsall, 2011), so that they are considered to be fundamentally equivalent (de Bello et al., 2021). Conversely, in MPD the expected dissimilarity is estimated only considering individuals from different species, thus it does not allow to account for intraspecific variability, unlike Rao. The great advantage of using mean dissimilarity methods versus others, is their clear link with taxonomic and phylogenetic diversity. Rao is in fact a generalization of the Simpson index of taxonomic diversity (Rao and Simpson are equivalent if the dissimilarity between all pairs of species is equal to 1; de Bello et al., 2016). This provides the basis to estimate taxonomic, phylogenetic (if using evolutionary instead of functional dissimilarities between species), and functional diversity under a common mathematical framework (De Bello, Lavergne, Meynard, Lepš, & Thuiller, 2010; Hevia et al., 2016). Another advantage is that all these indexes allow to incorporate information on species abundances on estimations of functional diversity, as well as using trait data containing missing information (as long as the dissimilarity index chosen allows for it).

Yet, they present disadvantages as well (Table 2). Besides the general caveats discussed before, probably the main limit is that there is no single mean dissimilarity method able to measure the richness, divergence, and regularity components of the trait space. While Rao and related metrics are well suited to estimate the divergence component, they do not serve well in other research scenarios. Also, a consequence of the mathematical relationship between Rao (and, as a corollary, of FDis) and Simpson's index is that Rao is not independent of species richness, but rather have an asymptotically-increasing relationship with it (Carmona, Guerrero, Morales, Oñate, & Peco, 2017). However, this may also be seen as a strength, as we are not always interested in functional diversity indices that are independent from species richness.

There are several R packages providing functions to calculate mean dissimilarity metrics. Rao is implemented, although with different formulations, in `adiv` (Pavoine, 2020), `FD` (Laliberté, Legendre, & Shipley, 2014), and `TPD` (Carmona, 2019). FDis is available in the `FD` package. MPD is implemented in the `picante` package (Kembel et al., 2010); however, when the abundance of species is considered, the MPD values estimated in this implementation are equal to Rao—see de Bello et al. (2016) for a discussion and a function to estimate abundance-weighted MPD values that reflect the definition of MPD that we provided above.

Functional dendrograms

In a milestone paper, Petchey and Gaston (2002) proposed to represent the trait space of a given community or site as the dendrogram of the functional relationships (distances) among species, whereby total functional richness can be calculated as the total branch length of the tree. A dendrogram representation of the trait space is graphically intuitive, allowing to visualize functional relations among species or individuals. Moreover, this way of calculating the trait space is strongly linked with tree-based phylogenetic diversity (Faith, 1992), thereby offering a congruent framework based on tree objects for comparing different dimensions of biodiversity (taxonomic, phylogenetic, and functional diversity; Jarzyna & Jetz, 2016). As previously discussed, a dendrogram-based representation of the trait space presents, of course, disadvantages as well (Table 2).

As far as R is concerned, tree-based calculation of the trait space is available through `adiv` (Pavoine, 2020), `BAT` (Cardoso, Mammola, Rigal, & Carvalho, 2020; Cardoso, Rigal, & Carvalho, 2015), and `vegan` (Oksanen et al., 2018), besides many other packages that focus on phylogenetic diversity (e.g. `ape`; Paradis & Schliep, 2019). While `vegan` and other packages currently allow calculating only the richness component of functional diversity, `BAT` allows to explore richness, divergence, and regularity dimensions.

Methods based on multidimensional spaces

Making the closest analogy with the Hutchinsonian niche, Rosenfeld (2002) defined functional diversity as the distribution of observations in a multidimensional space whose axes represent the traits of interest. In other words, the position of observations in a multidimensional space can be used to characterize the boundaries of a multidimensional object (hypervolume) encompassing all trait values observed in the group.

The interest in multidimensional representations of the trait space (and of the ecological niche; Holt, 2009) is raising. Beyond trait-based ecology (Blonder, 2019), hypervolumes have been applied to fields as diverse as environmental risk assessment (Yemshanov et al., 2017), invasion biology (Zhang, Mammola, McLay, Capinha, & Yokota, 2020), and cybersecurity (Gonzalez-Granadillo, Garcia-Alfaro, & Debar, 2017). It has been ironically pointed out that there are now probably "*as many definitions of these multidimensional spaces [...] as there are questions that can be tackled with such methods*" (Guillerme, 2018). Here, in a way of synthesis, we grouped methods in two families: those that achieve a binary description of the trait space depending on whether it is occupied or not, and those that achieve a probabilistic description of the trait space by modeling the density of observations.

Binary hypervolumes

A binary hypervolume, or convex hull, is the smallest convex polyhedron surrounding a set of observations. It is arguably one the simplest type of hypervolume and provides an intuitive geometrical representation of the trait space that easily embodies the often continuous nature of species' traits (Cornwell, Schwilk, & Ackerly, 2006). This approach was first introduced by Cornwell (2006) and later popularized by Villéger et al. (2008) who described a way to use convex hulls for functional richness estimation and to explore turnover among communities (Villéger, Grenouillet, & Brosse, 2013). A convex hull has a great advantage over rectangular representation of the trait space (e.g., Ricklefs & Travis, 1980) in that it excludes the "missing corners" of irregular distributions. In n≥ 2 dimensions, it also reduces the amount of empty space compared to (hyper-)cubes or (hyper-)spheres (Cornwell et al., 2006).

Yet, convex hulls have several shortcomings in functional ecology (Table 2). Foremost, the assumption that there is no empty space within extreme values of traits of a convex hull implies that adding unique combinations of traits does not always affect functional richness or other metrics if the new combinations fall within the existing trait space (Blonder, 2016; Mammola & Cardoso, 2020). Convex hulls are also extremely sensitive to outliers and they can only be used to explore the richness dimension of functional diversity (see Table 3). Owing to these and other pitfalls, Podani (2009) reached the conclusion that "*the measurement of functional diversity [...] can do very well without convex hull, because a plethora of methods [is] available already.*"

Despite these critiques, the trajectory of functional ecology research has been different: `FD`, the R package that introduced convex hull in functional ecology, has accumulated over 1000 citations in Google Scholar as of October 2020, affirming itself as one of the most used statistical environments for functional analyses. There are other packages allowing to build and/or analyses convex hulls, including `BAT`, and `betapart` (Baselga, Orme, Villeger, De Bortoli, & Leprieur, 2018), and several others not been specifically developed for functional analyses.

Probabilistic hypervolumes

Rather than assuming that the trait space is homogeneous, as in the case of a convex-hull, density-based approaches allow detecting areas of higher or lower density in the multidimensional space (Blonder, 2016). Thus, probabilistic hypervolumes reflect the notion that not all areas within the boundaries of a given trait space are filled with the same intensity. The popularity of probabilistic hypervolumes is steadily increasing in functional ecology, as testified by the number of R algorithms published in recent years allowing to delineate and/or analyze probabilistic hypervolumes (Blonder, Lamanna, Violle, & Enquist, 2014; Blonder et al., 2018; M. J. M. Brown, Holland, & Jordan, 2020; Carmona, de Bello, Mason, & Lepš, 2019; Carvalho & Cardoso, 2020; Junker, Kuppler, Bathke, Schreyer, & Trutschnig, 2016; Mammola & Cardoso, 2020; Swanson et al., 2015).

Inevitably, these representations of the trait space, like any other, also present shortcomings, at least in their present formulation (Table 2). The plot density will depend on the method and parameters used, and there are no clear guidelines on the best options (Mammola, 2019). Furthermore, these methods are computationally demanding, especially in high dimensions (Mammola & Cardoso, 2020).

While a number of approaches are available for estimating probabilistic hypervolumes, the two R packages that allow characterizing the trait space in the domain of richness, divergence, and regularity are `BAT` and `TPD` (Table 3). In its current version, `BAT` relies on a kernel density estimation of the trait space as in the package `hypervolume` (Blonder, 2018); once the trait space is generated, several custom metrics can be used to explore its properties (Mammola & Cardoso, 2020). `TPD` implements instead a delineation of the trait space based on probability density functions that can be estimated (and composed) at different hierarchical scales. These functions represent, for each point of the trait space, the relative abundance of the corresponding trait values at the considered scale (Carmona et al., 2016b, 2019).

DIMENSIONS OF FUNCTIONAL DIVERSITY FOR SPECIFIC RESEARCH QUESTIONS

Most often than not, the reason for characterizing a trait space is to explore its properties in relation to a research question of interest (Figure 2). This can be achieved by interrogating the trait space at a specific level of organization under the domain of richness, divergence, and regularity. Here we propose a way to group existing functional metrics using a simple, unifying scheme. This 'periodic table' of functional diversity (Table 3) is an attempt towards providing some order to the avalanche of available metrics, useful for applying the richness, divergence, and regularity notions (Box 1) to different level of organisation and spatial scales. Interestingly, besides emphasizing how there is both complementarity and redundancy in the metrics for exploring the trait space, this exercise of classification allowed us to point to the existence of gaps in what is currently available, potentially stimulating future developments of new metrics.

Richness

The richness dimension is arguably the most intuitive component of functional diversity. When estimating functional richness one tries to answer questions related to the amount of trait space occupied by assemblages as well as how it varies in space and time. This include questions such as what ecological processes and ecosystem services we lose if suddenly a community is wiped out (Cadotte et al., 2011; Cooke, Eigenbrod, & Bates, 2019), the filtering effect of a given habitat on species traits (Martínez et al., 2020; Micó et al., 2020), and how does the functionality of a community varies through seasons (Rocha, Vasseur, & Gaedke, 2012). At a broader, macroecological scale, many studies have explored variations in functional richness along gradients of thermal seasonality (latitude) (Lamanna et al., 2014; Schumm et al., 2019), glacier cover (L. E. Brown et al., 2018), or urbanization (Buchholz, Gathof, Grossmann, Kowarik, & Fischer, 2020; Sol et al., 2020). Mapping the richness of traits can also serve to identify areas of conservation priority based on criteria beyond species richness (Brum et al., 2017; Strecker, Olden, Whittier, & Paukert, 2011) and even to compare extinction risk across different taxa (Carmona et al., 2020). We refer the readers to the comprehensive overview by Lagres et al. (2018) for further reading on the richness component.

Divergence

Metrics classified under the divergence component of functional diversity seek to measure the extent to which observations spread across the occupied trait space (Anderson, 2006), usually relative to a mean or centroid (Mason et al., 2005; Villéger et al., 2008). Measuring dispersion allow answering questions related to community assembly processes and the general organisation of the trait space (Mason et al., 2005). A high dispersion often translates to a high degree of niche differentiation and/or relaxed ecological filters, and consequently low competition for space and resources. In a similar vein, some authors interpreted dispersion as a measure of the functional redundancy (see Rosenfeld, 2002b; Wellnitz & Poff, 2001). Theoretically, less redundant communities should be those characterized by more relaxed ecological filters, and *vice versa* (Ricotta, Laroche, Szeidl, & Pavoine, 2020). From the perspective of biological conservation, more functionally redundant systems should show greater resilience to perturbation, e.g., when facing the extinction or disappearance of a single species, the roles performed by it can easily be done by functionally close species.

Regularity

The regularity component, or evenness, is probably the least intuitive measurable property of functional diversity, reflecting the regularity of observations' distribution within the trait space (Mouillot, Mason, Dumay, & Wilson, 2005; Schleuter et al., 2010). In terms of raw data, regularity often measures the skewness of trait values; graphically, it can be seen as a measure of how harmonious the shape of the occupied trait space is—the symmetry of branches in a functional dendrogram or the regularity of the shape of a probabilistic hypervolume. Biologically speaking, regularity is used to examine the degree to which there is an effective use of the entire range of resources available to a given niche space (Mason et al., 2005). A practical example comes from cave ecosystems, where the permanent darkness and the consequent lack of photosynthetic primary producers skew the total trait space towards the over-expression of traits of detritivorous and predators (Gibert & Deharveng, 2002) or towards species employing particular hunting strategies (Cardoso, 2012).

LEVEL OF ORGANISATION

Existing metrics are furthermore divided according to the level of data organization at which they are calculated. Metrics can be calculated for individual observations (individuals, populations, or species), within groups (e.g., individuals within a species or species within a community; so-called α-diversity) or between groups (e.g., comparison of multiple species or communities in space and time; so-called β-diversity).

Observations

Observations contribute differently to the trait space occupied by a population, species or community, or to the differences between populations, species, or communities. Different measures have been developed to reflect the position of an observation in the trait space relative to other observations, including originality, uniqueness, and contribution (Table 3). All these measures quantify in different ways how dissimilar is an observation from all others and hence how much it adds to the group measures. A general method to calculate contribution is to use a leave-one-out approach (Mammola & Cardoso, 2020), whereby the contribution of each observation would be expressed as the difference of a given measure with and without a given observation. This can be applied to richness, divergence, or regularity, allowing to map the different components of functional rarity and commonness (Grenié, Denelle, Tucker, Munoz, & Violle, 2017; Violle et al.,

2017) at different scales of organisation (Carmona, de Bello, Sasaki, Uchida, & Pärtel, 2017). In conservation biology, for example, one can estimate the importance of both common and rare species to the net ecosystem functionality (Chapman, Tunnicliffe, & Bates, 2018) to define species-level conservation priorities (Davic, 2003).

Within groups

Within-group level, often referred to as alpha diversity or simply α, reflects the properties of a group of observations without reference to other groups. Observations add to the occupation of a given trait space that characterizes in different ways a species or community. This is the most intuitive property of groups and by far the most explored level in functional diversity studies.

Between groups

Differences between groups reflect the natural heterogeneity in nature, whereby populations, species, and communities differ in space and time. Also called beta diversity or β, this property was first defined as the extent of change in community composition along gradients (Whittaker, 1960). Since then, the term has expanded its use, although always encompassing some kind of compositional heterogeneity or differentiation (Anderson et al., 2011; Tuomisto, 2010b, 2010a). Importantly, two distinct processes shape species or communities and their functional differences: substitution of trait space and net gain or loss of trait space [see Carvalho & Cardoso (2020) for species and Cardoso et al. (2014) for communities]. When comparing groups, one may understand how niche shifting in space or time relate with competition or ecological release and consequent evolution of traits (Carvalho & Cardoso, 2020), or to explore how trait diversity decays with spatial distance or change through time (Pavoine & Bonsall, 2011).

CONCLUSIONS

We here illustrated the emerging consensus on a few, non-overlapping frameworks for delineating the trait space and measuring its properties. Our hope is that this synthesis, by digesting available concepts (Table 1), methods (Table 2), and metrics (Table 3), will offer a practical overview and workflow for streamlining functional diversity analyses (Figure 2). Four take-home messages emerge from this classification exercise:

i) *Don't mix apples and oranges*. Many studies calculate properties of functional diversity with a cocktail of different methods and metrics. This is the case, for example, of many studies based on the R package `FD`, which estimates richness as the volume of a convex hull, divergence as the distance of the observations to a centroid or center of gravity, and regularity with a minimum spanning tree (Laliberté & Legendre, 2010; Laliberté et al., 2014; Villéger et al., 2008). Whenever possible, we recommend being consistent by choosing a single method for delineating the trait space (e.g., a functional dendrogram or a multivariate space) and sticking to it for exploring its properties in the dimensions of richness, divergence, and regularity. Otherwise, it may be problematic to disentangle the effect of the ecological process(es) of interest from that of the different algorithms used. As a corollary, it must be noted that caution should also be exercised when comparing results from different studies if these were based on different methods and metrics.

ii) *Acknowledge uncertainty*. In an ideal world, by calculating analogous metrics using different methods—e.g., the functional richness calculated with a dendrogram or a convex hull—one would reach the same (or convergent) results. However, as emphasized by a few comparative studies across a selection of methods and metrics (Junker et al., 2016; Mammola & Cardoso, 2020; Mouchet et al., 2010; Wong & Carmona, 2020), this is rarely the case. Discrepancies are partly related to the intrinsic differences of each approach (Table 2), and partly to the scale of analysis and methodological choices on how to handle trait variability (Gentile, Bonelli, & Riva, 2020; Wong & Carmona, 2020). We believe it would be needed to comprehensively analyse properties of the existing methods using either real-world data or simulations based on different combinations of traits, scales of organization, and input parameters. Until then, it is important to acknowledge that often we do not fully understand what each method and metric is exactly measuring.

iii) *Refute parochialism*. There are plenty of functional diversity methods and metrics out there, and many more will likely be developed in the future. While this is certainly disorienting for researchers approaching functional diversity analyses for the first time, choosing between seemingly equally appropriate options remains challenging even for experienced researchers (Cianciaruso, Sobral, & Lees, 2017). Inevitably, most researchers will tend to stick to their 'pet' approach. Yet, it is important to keep in mind that any analytical choice should always be fine-tuned to the ecological question of interest (Figure 2) and the caveats inherent to each method (Table 2), rather than subjective preferences.

iv) *Indulge in the unknown*. The existing breadth of metrics will never allow us to explore all the properties of the distribution of observations in a given trait space and to answer the potentially unlimited number of eco-evolutionary questions. When dealing with novel paradigms and systems, one will often have to develop metrics or functions *de novo*. If one lacks programming skills, there are tools that can facilitate this task. An example is the `dispRity` framework (Guillerme, 2018; Guillerme, Puttick, Marcy, & Weisbecker, 2020), providing a modular architecture to create and test new metrics tailored to specific datasets and questions.

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Author contribution

SM and PC conceived the idea. SM wrote the first draft and prepared figures. PC supervised the work and suggested the framework for Table 3. CPC provided most arguments on trait probability density and entropy-based methods. TG provided arguments for different sections, including terminology (Table 1). All authors contributed ideas, bibliographic suggestions, and with the writing.

Data availability

Data to generate Figure 1 were retrieved from the Web of Science (Clarivate Analytics) on 25 November 2020.

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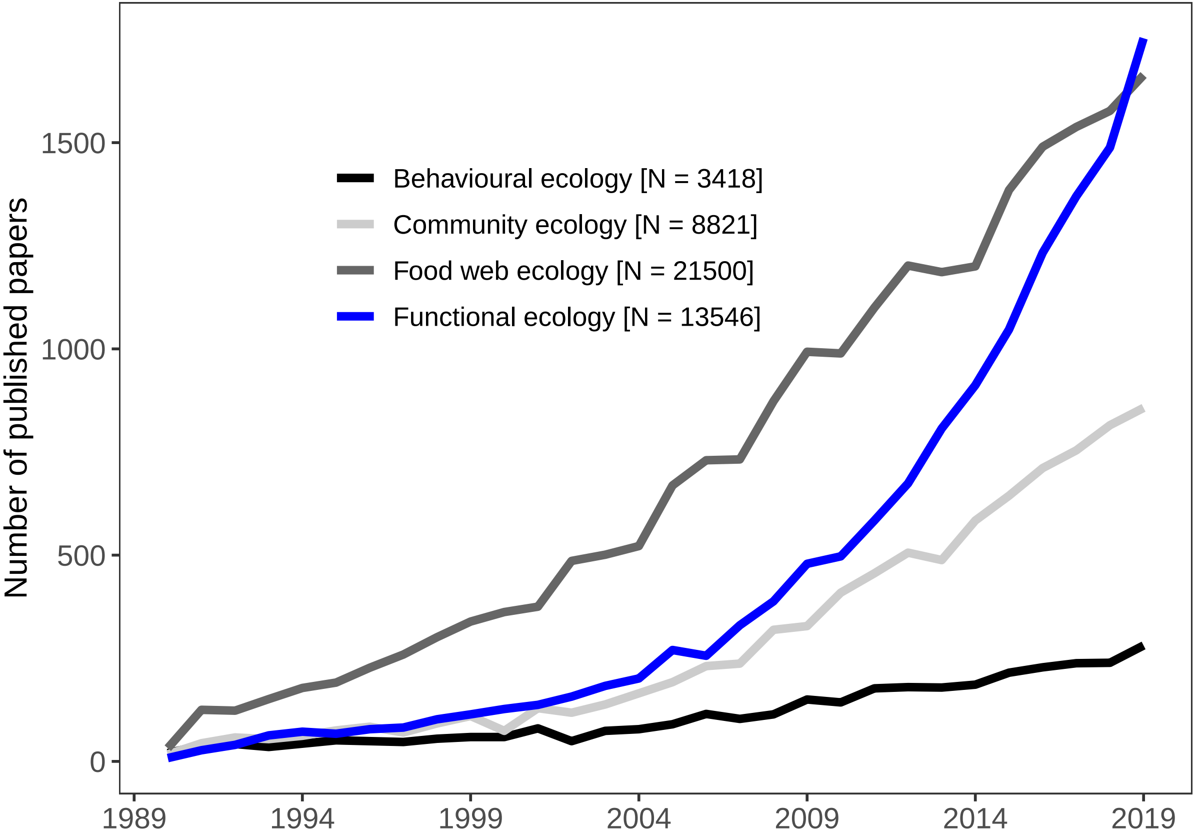
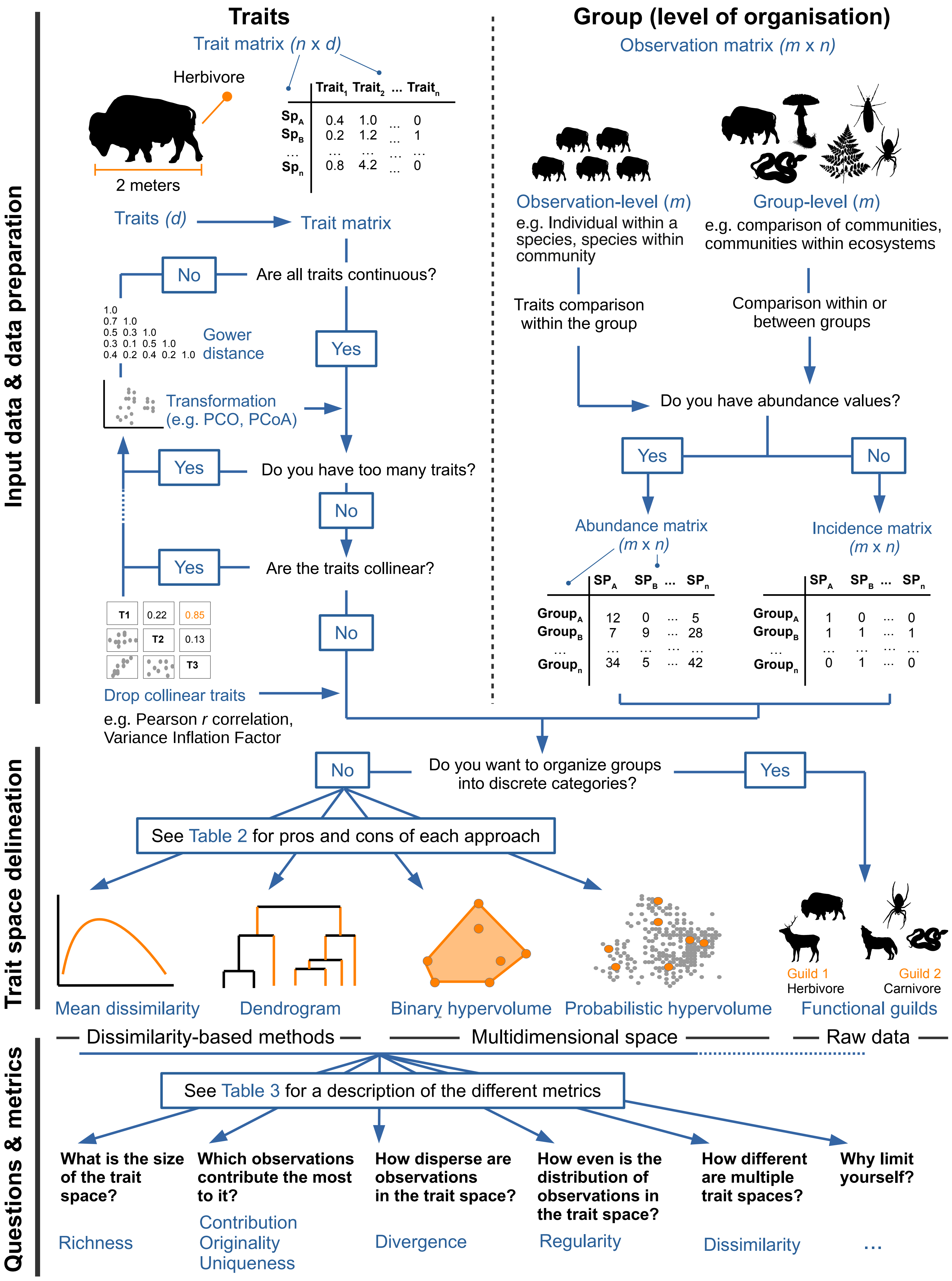
FIGURES CAPTIONS

Figure 1. Growth in functional diversity studies over time. Number of published papers on functional diversity over time, compared to other benchmark disciplines in ecology. The number of papers was sourced from Web of Science (Clarivate Analytics) on 25 November 2020. For functional ecology, we used the query: *TS = ("functional diversity" OR "trait diversity" OR "functional richness" OR "functional trait" OR "trait-based ecology").* For behavioural ecology, the query: *TS=("behavioral ecology" OR "behavioural ecology" OR "ecological ethology" OR "etho-ecology").* For community ecology, the query: *TS = ("meta-communit*" OR "community ecology" OR "metacommunit*" OR "biological communit*")*. For trophic web ecology, the query: *TS = ("trophic web" OR "food-web" OR "food web" OR "ecological network" OR "network ecology").*

Figure 2. A theoretical workflow for functional diversity analyses. The scheme is structured as a decision tree designed to guide the researcher along three consequential steps: i) data preparation; ii) definition of the trait space; and iii) characterization of the properties of the trait space using different metrics to answer different research questions. See Table 1 for a definition of terms used.



Data: Web of Science (WoS)


Input data & data preparation
Traits
Trait matrix (n x d)
Herbivore
2 meters
Trait₁ Trait₂ ... Traitₙ
Sp_A 0.4 1.0 ... 0
Sp_B 0.2 1.2 ... 1
... ...
Sp_n 0.8 4.2 ... 0
Traits (d)
Trait matrix
Are all traits continuous?
No
Yes
1.0
0.7 1.0
0.5 0.3 1.0
0.3 0.1 0.5 1.0
0.4 0.2 0.4 0.2 1.0
Gower distance
Transformation (e.g. PCO, PCoA)
Do you have too many traits?
Yes
No
Are the traits collinear?
Yes
No
T1 0.22 0.85
T2 0.13
T3
Drop collinear traits
e.g. Pearson r correlation, Variance Inflation Factor
Group (level of organisation)
Observation matrix (m x n)
Observation-level (m)
e.g. Individual within a species, species within community
Group-level (m)
e.g. comparison of communities, communities within ecosystems
Traits comparison within the group
Comparison within or between groups
Do you have abundance values?
Yes
No
Abundance matrix (m x n)
Incidence matrix (m x n)
SP_A SP_B ... SP_n
Group_A 12 0 ... 5
Group_B 7 9 ... 28
... ...
Group_n 34 5 ... 42
SP_A SP_B ... SP_n
Group_A 1 0 ... 0
Group_B 1 1 ... 1
... ...
Group_n 0 1 ... 0
Trait space delineation
Do you want to organize groups into discrete categories?
No
Yes
See Table 2 for pros and cons of each approach
Mean dissimilarity
Dendrogram
Binary hypervolume
Probabilistic hypervolume
Guild 1
Herbivore
Guild 2
Carnivore
Functional guilds
Dissimilarity-based methods
Multidimensional space
Raw data
Questions & metrics
See Table 3 for a description of the different metrics
What is the size of the trait space?
Richness
Which observations contribute the most to it?
Contribution
Originality
Uniqueness
How disperse are observations in the trait space?
Divergence
How even is the distribution of observations in the trait space?
Regularity
How different are multiple trait spaces?
Dissimilarity
Why limit yourself?
...

TABLES

Table 1. Glossary of terms. Modified from Guillerme et al. (2020).

Term	**Mathematics**	**Definition**	**Examples in literature**
Trait matrix	Matrix (n x d)	The matrix reporting the traits of the studied system. It reflects the variation of traits in the *trait space* occupied by a certain ecological or evolutionary unit.	Functional space, ecospace, dissimilarity matrix, etc.
Observations	Rows (n)	The units of focus in the study.	Taxa, populations, morphospecies, species, etc.
Traits (= dimensions)	Columns (d)	The number of elements (traits) that were measured for each *Observation* or any transformation thereof (e.g., principal components).	Traits, ordination scores, distances, principal components, etc.
Observation matrix	Matrix (m x n)	Optional matrix that provides attributes for the *Observations* (e.g., abundances, weights) and the subdivision of the *Trait matrix* into relevant *Groups*.	Abundance data, community data, incidence data, biomass data, etc.
Groups	Rows (m)	The meaningful groups of observations for answering the research question(s) of interest.	Communities, ecosystems, species, clades, geological strata, etc.
Trait space	Graphical representation of the *trait matrix.*	Any transformation and/or visualization (graphic representation; usually a 2D or 3D projection) of the *trait matrix*. It represents the space in which *functional metrics* are most often visualized.	Hypervolume, convex hull, functional dendrogram, probability density, etc.
Functional metric	Statistic (i.e., a measure)	The metric is the aspect(s) of interest that attempts to summarize some intrinsic feature of the variation in the *trait space*. This is what is measured (usually at the level of the *group*) to answer the research question(s) of interest.	Functional metric, functional index, functional diversity, functional richness, beta functional diversity, trait dispersion, trait divergence, etc.

Table 2. **Advantages and disadvantages of the existing frameworks for functional diversity**. Main R packages for calculation are given in alphabetic order.

Family	Method	Advantages	Disadvantages	R packages
Raw data	Functional guild or any other raw representation of the traits	- Simplest approach. - Rooted in a milestone ecological concept: the guild. - Easily communicated or visualized, even for the general public.	- Functional guild transforms continuous traits into categories, with consequent loss of information. - Does not provide a direct link with the niche concept. - The selection of the relevant number of groups is often subjective. - The delimitation of groups is subjective.	`stats`
Dissimilarity-based methods	Mean dissimilarity methods	- Allow considering abundances. - Clear biological interpretation. (average dissimilarity between the individuals composing a group). - Clear correspondence with variance, which allows using an analysis of variance framework (De Bello et al., 2011). - Allow for partitioning of diversity across scales (de Bello et al., 2010; Pavoine et al., 2016). - Can be applied to other aspects of diversity (taxonomic, phylogenetic) using a single coherent mathematical framework (Pavoine, Marcon, & Ricotta, 2016).	- There is not a single entropy-based framework to measure richness, divergence and regularity components of the trait matrix. - Does not come with a clear graphical representation of the trait space – although possibilities do exist (Bruelheide et al., 2018; Carmona et al., 2012). - Choice of distance measure is not trivial; should be considered carefully as it may affect results significantly (De Bello, Carmona, Mason, Sebastià, & Lepš, 2013). - Not intuitively linked to the concept of species niche. - Diversity does not necessarily increase when more observations or traits are added (this may also be seen as an advantage, e.g. when calculating redundancy).	`ade4` (Dray & Dufour, 2007); `adiv` * (Pavoine, 2020); `entropart` (Marcon & Hérault, 2015); `funrar` * (Grenié et al., 2017); `FD` * (Laliberté et al., 2014); `picante` (Kembel et al., 2010); `TPD` * (Carmona, 2019)
	Functional dendrogram (= functional tree)	- Intuitive visual presentation, potentially allowing to calculate by hand all functional diversity metrics (easy error checking). - The theoretical understanding of tree objects properties is vast, thanks to a long tradition of phylogenetic studies. - Can be applied to other aspects of diversity (taxonomic, phylogenetic) using a single coherent mathematical framework based on trees (Cardoso et al., 2015).	- Not sensitive to abundances when calculating richness. - Choice of distance measure for tree estimation is not trivial; should be considered carefully as it may affect results significantly (Podani & Schmera, 2006). - Not intuitively linked to the concept of ecological niche.	`adiv` *; `BAT` * (Cardoso et al., 2020); `vegan` (Oksanen et al., 2018)
Multidimensional space	Binary hypervolume (= convex hull)	- Intuitive visual presentation of the trait space (Cornwell et al., 2006). - Conceptually simpler than probabilistic hypervolumes. - Computationally faster than probabilistic hypervolumes.	- Only suitable for exploring the Richness dimension of functional diversity (see Table 3) - Curse of dimensionality (Bellman, 1957): a linear increase in the number of dimensions requires an exponential increase in the number of observations. Also, computation time scales exponentially with the number of dimensions (Blonder, 2016; Guillerme et al., 2020; Mammola, 2019). - Do not allow the existence of variable densities in the trait space – 'convex hull expectation' (Blonder, 2016). - Extremely sensitive to outliers: a single functionally distinct observation may	`BAT` *; `betapart` (Baselga et al., 2018); `FD` *

			significantly affect the estimation of the volume. - Perform poorly with low sample size. - Cannot consider abundances when calculating richness. - Categorical traits are not fully implemented in the calculation – although possibilities do exist (e.g., Carvalho & Cardoso, 2020; Lloyd, 2016, 2018).	
	Probabilistic hypervolume (= continuous hypervolume, n-dimensional hypervolume)	- Stems from a milestone theoretical concept in ecology: the Huntchinsonian niche (Hutchinson, 1957). - Allow considering abundances. - A density-based description of the trait space enhances the possibility to explore areas of higher and lower functional density within the boundaries of the hypervolume (Blonder, 2016; Carmona et al., 2019).	- Curse of dimensionality (see above). - Categorical traits are as yet not fully implemented – although possibilities do exist (see above). - For stochastic hypervolumes, might require to perform iterations and report results using null modeling techniques. - Sensitive to the choice of bandwidth when kernel density estimations are used. - Diversity does not necessarily increase when more observations or traits are added [negative contribution *sensu* Mammola & Cardoso (2020); this may also be seen as an advantage, e.g. when calculating redundancy]. - Time consuming for big or complex datasets.	`BAT` *; `dynRB` (Junker et al., 2016); `hypervolume` (Blonder, 2018); `nicheROVER` (Swanson et al., 2015); `TPD` *

* Packages with a large set of complementary functional metrics to explore the richness, divergence and regularity components of the trait space.

Table 3. A periodic table of functional diversity. The classification is adapted from the Pavoine–Bonsall scheme (Box 1). The row entries distinguish between observation, within groups, and between groups levels; column entries represent the three dimensions of richness, divergence, and regularity under the main frameworks identified in this study. The table is expanded from those proposed in Mammola & Cardoso (2020). Examples of R functions for calculation (ordered alphabetically) are mostly taken from packages fully devoted for functional diversity estimations (see Table 2).

	Dimension:	**RICHNESS (… how much?)**					**DIVERGENCE (… how different?)**					**REGULARITY (… how regularly?)**				
	Framework:	**Raw data**	**Mean dissimilarity**	**Functional dendrogram**	**Binary hypervolume**	**Probabilistic hypervolume**	**Raw data**	**Mean dissimilarity**	**Functional dendrogram**	**Binary hypervolume**	**Probabilistic hypervolume**	**Raw data**	**Mean dissimilarity**	**Functional dendrogram**	**Binary hypervolume**	**Probabilistic hypervolume**
OBSERVATION LEVEL	**Metric:**	**Contribution to richness**					**Originality / Uniqueness**					**Contribution to evenness**				
	Question:	How much does an observation add to the total trait space?					How different is an observation to the others?					How much does an observation increase the regularity?				
	Example calculation:	For each observation is 1 divided by the number of observations with the same combination of traits.	-	Edge length provided by an observation.	Contribution of an observation to the total volume of a convex hull.	Contribution of an observation to the total volume of a probabilistic hypervolume (can be negative)	The distance of each functional observation from the average of the trait itself.	Average distance between an observation and all others (originality) or between an observation and the closest (uniqueness).	Average distance between an observation and all others (originality) or between an observation and the closest (uniqueness) in the tree.	Not applicable: a convex hull, being homogeneous, is equally dispersed throughout.	Average distance between an observation and a sample of random points within the probabilistic hypervolume, or overlap between the TPD function of a single observation and the TPD function of the whole set of observations.	Contribution of an observation to the evenness of a community.	Contribution of an observation to the evenness of a community.	Contribution of each observation to the evenness of the functional dendrogram.	Not applicable: a convex hull, being homogeneous, is even throughout.	Contribution of an observation to the evenness of a probabilistic hypervolume.
	Example R function(s):	n.a.	n.a.	`BAT::contribution`; `vegan::spantree`	`BAT::hull.contribution`	`BAT::kernel.contribution`	n.a.	`funrar::uniqueness`	`BAT::originality`; `BAT::uniqueness`	n.a.	`BAT::kernel.originality`; `TPD::uniqueness`	n.a.	n.a.	`BAT::evenness.contribution`	n.a.	`BAT::kernel.evenness.contribution`
	Metric:	**Richness**					**Divergence**					**Evenness**				
	Question:	What is the size of the trait space?					How disperse is the trait space?					How regular is the trait space?				
	Example calculation:	Number of unique combinations	Number of equivalent observations	Total branch length of the functional tree	Volume of the convex hull or sum of	Volume of the hypervolumes or, in `TPD`,	Standard deviation of functional	Expected dissimilarity between two	Average dissimilarity between any	Not applicable: a convex hull,	Average dissimilarity between any	Regularity of trait values,	Regularity of abundances and distances	Regularity of abundances and	Not applicable: a	Overlap between the hypervolume

WITHIN GROUPS		of traits (or weighted mean of the trait values).	(i.e. maximally dissimilar observations needed to produce the observed diversity)		areas of successive convex hulls (after Fontana, Petchey, & Pomati, 2016)	the sum of cells where trait probability density > 0 (Carmona, de Bello, Mason, & Lepš, 2016a; Carmona et al., 2016b)	observations.	observations randomly taken from the group (De Bello et al., 2011) or average distance of observations to a center of the trait space (Laliberté & Legendre, 2010)	two observations in the tree.	being homogeneous, is equally disperse.	two random points within the boundaries of the hypervolume or the distance between random points and the centroid.	reflecting trait abundances and distances between values. Approximated as the kurtosis of traits (Gross et al., 2017) or weighted evennes of the traits.	along the minimum spanning tree linking all observations (Villéger et al., 2008); or deviation in the uniqueness.	distances between observations in the tree.	convex hull, being homogeneous, is even throughout.	and an imaginary hypervolume where traits are evenly distributed within their possible range (Carmona et al., 2019; Mammola & Cardoso, 2020)
	Example R function(s):	`BAT::cwm;` `FD::sing.sp;` `FD::functcomp`	`div::EqRao; TPD::Rao`	`BAT::alpha`	`BAT::hull.alpha;` `FD::dbFD`	`BAT::kernel.alpha;` `TPD::REND`	`BAT::cwd`	`FD::Fdis;` `TPD::Rao`	`BAT::dispersion`	n.a.	`BAT::kernel.dispersion;` `TPD::REND`	`BAT::cwe`	`FD::feve;` `funrar::uniqueness`	`BAT::evenness`	n.a.	`BAT::kernel.evenness;` `TPD::REND`
BETWEEN GROUPS	**Metric:**	**Beta richness**					**Beta replacement**					**Beta evenness**				
	Question:	How dissimilar is the size of multiple trait spaces?					How distant are multiple trait spaces?					How different is the regularity of multiple trait spaces?				
	Example calculation:	Net difference in the number of distinct functional observations.	Number of equivalent observations estimated at nested scales	Net difference in summed length of edges of functional dendrograms (beta richness sensu Cardoso, Rigal, Carvalho, et al., 2014)	Net difference in amplitude of binary hypervolumes (or nestedness sensu Villéger et al., 2013)	Net difference in amplitude of probabilistic hypervolumes (Carvalho & Cardoso, 2020)	Replacement of distinct functional observations between groups	Divergence among different groups	Replacement of the edges of functional dendrograms (beta replacement *sensu* Cardoso, Rigal, Carvalho, et al., 2014)	Replacement of functional space enclosed by convex hulls (or turnover *sensu* Villéger et al., 2013)	Replacement of functional space enclosed by probabilistic hypervolumes (Carvalho & Cardoso, 2020) or overlap between probability density function	Difference in evenness values between two groups	Difference in evenness values between two groups	Difference in evenness values between two functional dendrograms	Not applicable: a convex hull, being homogeneous, is even throughout.	Difference in evenness values between two probabilistic hypervolumes
	Example R function(s):	n.a.	`adiv::EqRao ;` `TPD::Rao`	`BAT::beta`	`BAT::hull.beta;` `betapart::functional.beta.multi`	`BAT::kernel.beta`	n.a.	`ade4::disc;` `TPD::Rao`	`BAT::beta`	`BAT::hull.beta;` `betapart::functional.beta.multi;`	`BAT::kernel.beta;` `BAT::kernel.similarity;` `TPD::dissim;`	n.a.	n.a.	`BAT::beta.evenness`	n.a.	`BAT::kernel.beta.evenness`

n.a. = No specific function available.