

Review

Traits Without Borders: Integrating Functional Diversity Across Scales

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Owing to the conceptual complexity of functional diversity (FD), a multitude of different methods are available for measuring it, with most being operational at only a small range of spatial scales. This causes uncertainty in ecological interpretations and limits the potential to generalize findings across studies or compare patterns across scales. We solve this problem by providing a unified framework expanding on and integrating existing approaches. The framework, based on trait probability density (TPD), is the first to fully implement the Hutchinsonian concept of the niche as a probabilistic hypervolume in estimating FD. This novel approach could revolutionize FD-based research by allowing quantification of the various FD components from organismal to macroecological scales, and allowing seamless transitions between scales.

A Multi-Faceted FD

The responses of species to environmental conditions, disturbance, and biotic interactions, as well as their effects on ecosystem processes, are determined by their **functional traits** (see [Glossary](#)) [1–5]. Consequently, functional trait-based approaches have great potential to address a variety of ecological questions [6], including the impact of global change on biodiversity and ecosystem service delivery [3,7–9], ecological restoration [10], or the assembly of biological communities [4,5,11]. These approaches rely on the adequate characterization of **functional diversity** (FD) [12]. FD is a multifaceted concept encompassing a variety of components [13,14] that can be considered at different scales, from local populations to wide geographical regions [15–17]. The past decade has seen an explosion of methods to quantify the different aspects of FD [18–20], causing much confusion in selecting appropriate methods for specific questions [21]. Further, current approaches generally provide poor continuity between spatial scales. In this review we synthesize existing methods and propose a novel approach that reconciles existing concepts into a single framework. This framework will effectively allow ecologists to navigate the jungle of existing methods, transition seamlessly across multiple scales, and take full advantage of the current increase in trait data availability.

Estimating FD basically consists of summarizing the variation of traits between organisms [12]. The main challenge is that FD can be computed at multiple spatial scales, both within and across different ecological units [15–17,22,23], causing uncertainty in its practical quantification. Traditionally, a great deal of work has been carried out to characterize FD between species in a community. This has generally been done by representing each species by its average trait values [17,24], reflecting the assumption that interspecific variability should be considerably larger than **intraspecific trait variability** (ITV) [25–28]. FD within-communities, thus often assumed to be due mostly to differences between species, can be decomposed into three

Trends

Functional trait diversity, in other words the variation of traits between organisms, can be used to address a great number of pressing ecological questions. Consequently, trait-based approaches are increasingly being used by ecologists.

However, functional diversity comprises several components that can be evaluated at different spatial scales. Because of this conceptual complexity, there is an overabundance of disparate approaches for estimating it, which leads to confusion among users and hampers the comparability of different studies.

A single mathematical framework encompassing different approaches while providing a seamless continuity between spatial scales is needed.

Reconciling the approaches based on the concept of the niche as a hypervolume and those that consider traits in probabilistic terms is the first step towards the foundation of a unified framework.

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primary components (**functional richness**, **functional evenness**, and **functional divergence**) [13,14], each potentially represented by different indices [14,19,20]. In parallel, some of these indices, along with other specific ones [29,30], have been used to characterize FD between communities, similarly to β -diversity in species composition (i.e., β -FD) [31]. The profusion of methods to compute FD at each scale poses a challenge for ecologists and limits the possibility to compare results across multiple studies. On top of this, satisfactory methods are not available for some key biodiversity aspects, such as **functional redundancy** [7,32,33]. To further complicate the study of FD, empirical and theoretical studies are increasingly showing that ITV cannot be neglected in addressing several key ecological questions [34–37]. ITV can explain a substantial portion of total functional trait variability within communities [27,38–41], and has considerable effects on population stability, species coexistence, and ecosystem processes [35,42–44]. As part of the quest to incorporate ITV into FD assessments, recent years have seen the development of methods considering ITV, rather than only species averages [17,24]. However, these new indices are often conceptually different from existing ones [17,45,46], leading to further confusion for users.

TPD: Towards a Scale-Independent FD

If ecologists want to ultimately simplify the labyrinth of methods for quantifying FD, and make results of different studies more readily comparable, they will need to define a single framework that encompasses different approaches while providing the flexibility to move between multiple scales. Below we show that the foundations of such a framework can be found in studies using the concept of the niche as a hypervolume [47,48] and those considering the probabilistic nature of functional traits [45,49,50].

The probabilistic nature of functional traits can be appreciated at different scales. Most notably, the inclusion of ITV into FD calculations requires trait observations to be considered at the individual (or even the within-individual) level [17,24,38]. The notion of individuals of a species spread throughout an area of the **functional trait space** recalls the concept of the niche as a multidimensional hypervolume proposed by Hutchinson [51]. A species could persist at any point within the boundaries of the hypervolume defining its niche, but fitness is not uniform across the whole hypervolume: there is ‘an optimal part of the niche with markedly suboptimal conditions near the boundaries’ [51]. In the past years, given their relation with performance, traits are increasingly being used to quantify the niches of species [36,52]. However, not all the combinations of traits confer equal fitness [36], which implies that trait values within a species [50], community [53], region [54], or even at the global scale [55] are not equally represented across the whole range of possible values (Box 1).

These ideas, while being acknowledged [17,49,51,56], have not been completely implemented so far. Most existing approaches seek to define **functional niches** of species by estimating the boundaries of the region of the functional space that they occupy, using for example the **convex hull** [48] or n -dimensional hypervolume [47] methods. These approaches do allow the expression of FD both within- and between species and communities [16,47], while also allowing the decomposition of β -FD into nestedness and turnover components, in a similar way as for species diversity [29,31]. However, simply characterizing the boundaries of functional niches ignores their probabilistic nature.

Expressing functional niches as probability density functions, for example at the species [25,56,57] and community levels [36,53,56], has been proposed as a suitable approach for incorporating the probabilistic nature of niches in FD calculations. This option has already been adopted by methods using the overlap between the TPD functions of species to estimate their functional differences (Box 1) [45,49]. However, despite its potential and some conceptual attempts at defining probabilistic hypervolumes [58], this approach remains vague and

Glossary

Convex hull: smallest convex volume that contains a set of points. In trait-based ecology, it is used to quantify the functional volume occupied by a species or community, as well as β -FD and its decomposition into nestedness and turnover components. Convex hulls are sensitive to outliers and do not detect gaps in the occupation of functional space.

Ecological unit: any scale at which it is meaningful to estimate FD. Examples are individual organisms, populations, species, communities, metacommunities, geographical regions, and continents.

Functional distinctiveness: the degree to which an ecological unit differs, in terms of functional traits, from other units.

Functional divergence: the degree to which the abundance in functional trait space of the organisms composing an ecological unit is distributed toward the extremes of its functional volume.

Functional diversity (FD): variation of traits between organisms. It is estimated as the variation of traits in the functional space occupied by an ecological unit. Different indices estimating FD attempt to summarize some specific aspect of this variation.

Functional evenness: regularity in the distribution of the abundance in functional trait space of the organisms composing an ecological unit.

Functional niche: region of the functional space containing all the trait combinations displayed by the individuals of a species. Existing FD approaches based on functional niches, such as the convex hull, consider functional niches as uniform features, ignoring the fact that some trait values within the functional niche of a species are more likely than others.

Functional redundancy: two ecological units can be considered to be functionally redundant if they have the same trait values, and hence occupy the same functional space. Communities with high redundancy are expected to be able to lose species without great decreases in ecosystem function.

Functional richness: amount of functional space occupied by the organisms in an ecological unit.

Box 1. Basics of the TPD Framework

TPD functions can be built for any ecological unit. By definition, TPD functions are probability density functions, in other words continuous functions that are defined for the whole functional space. As such, the values of the TPD of an ecological unit (e.g., population, community, or region) are directly proportional to the relative abundance of their corresponding trait values within the unit, and integrate to 1 (Figure 1A).

After building a TPD function for each ecological unit under study, an essential step for putting the framework into action is to estimate the overlap between two different TPD functions (Figure 1B shows examples for single and multiple traits). Let us consider the TPD functions of two ecological units i and j (the following reasoning applies to any scale). The joint density distributions of these two TPD functions can be divided into two different parts. One part corresponds to the overlapping area between the two TPD functions, that is, the volume that is part of the density functions of the two communities (Figure 1B). Logically, the remainder of the joint density distributions is the part that corresponds to differences between units. Because TPD functions integrate to 1, the dissimilarity between the two units (β_0) can be then estimated as 1 minus overlap (Figure 1B) [84]. β_0 is bounded between 0, when two units are functionally identical (overlap = 1), and 1, when there is no functional overlap between them. Considering niches as uniform features, as in the convex hull volume and hypervolume methods [47,48], can result into biased estimates of overlap (overestimates in the examples in Figure 1C).

It should be noted that, to perform operations and combine TPD functions from different species, it is more practical to divide the functional space into a D -dimensional grid (D being the number of traits considered) composed of a great number of equal-sized cells in which TPD is evaluated (Figure 1D). Effectively, this means that the value of the function in each cell corresponds to the probability of randomly extracting an individual with those traits from the population, community, or region in question. Several operations can be performed on a cell-by-cell basis, including, for instance, the weighted sum of the TPD _{i} functions of all the species in a community that are used to calculate TPD _{c} functions.

Functional trait: any morphological, physiological, phenological, or behavioral feature of an organism that can be measured at the individual level and that has an effect on its fitness.

Functional trait space: multidimensional space where the axes are functional traits. Individuals or species are placed in this space in the coordinates given by their functional traits.

Intraspecific trait variability (ITV): variation in functional traits among conspecifics. Although most trait-based approaches consider only a single average trait value for each species to compute FD, it is increasingly clear that the consideration of ITV is crucial for answering a variety of ecological questions.

Trait probability density (TPD): function representing the distribution of probabilities of observing each possible trait value in a given ecological unit.

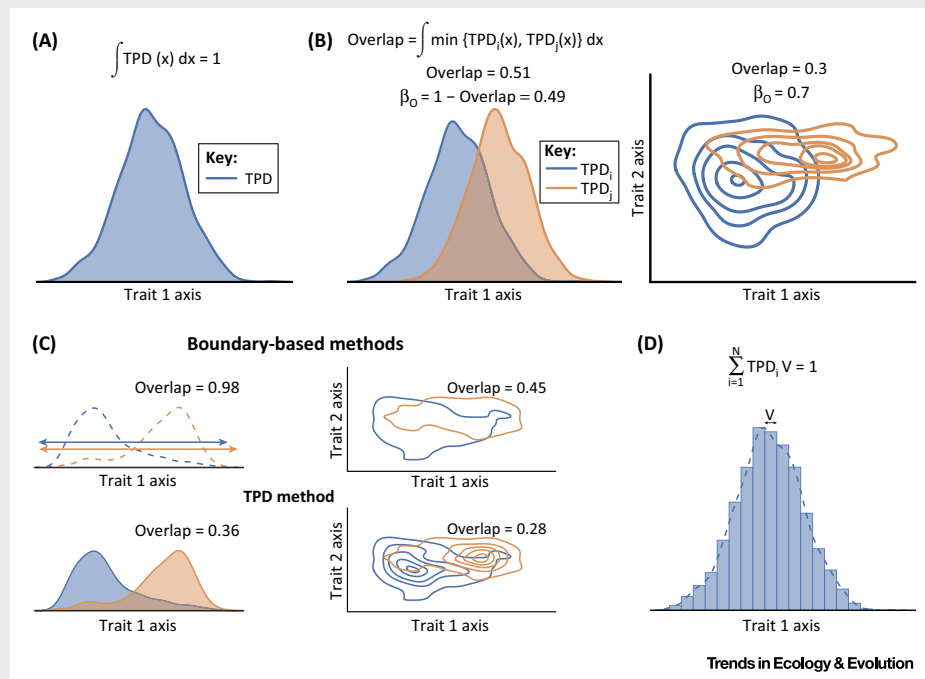
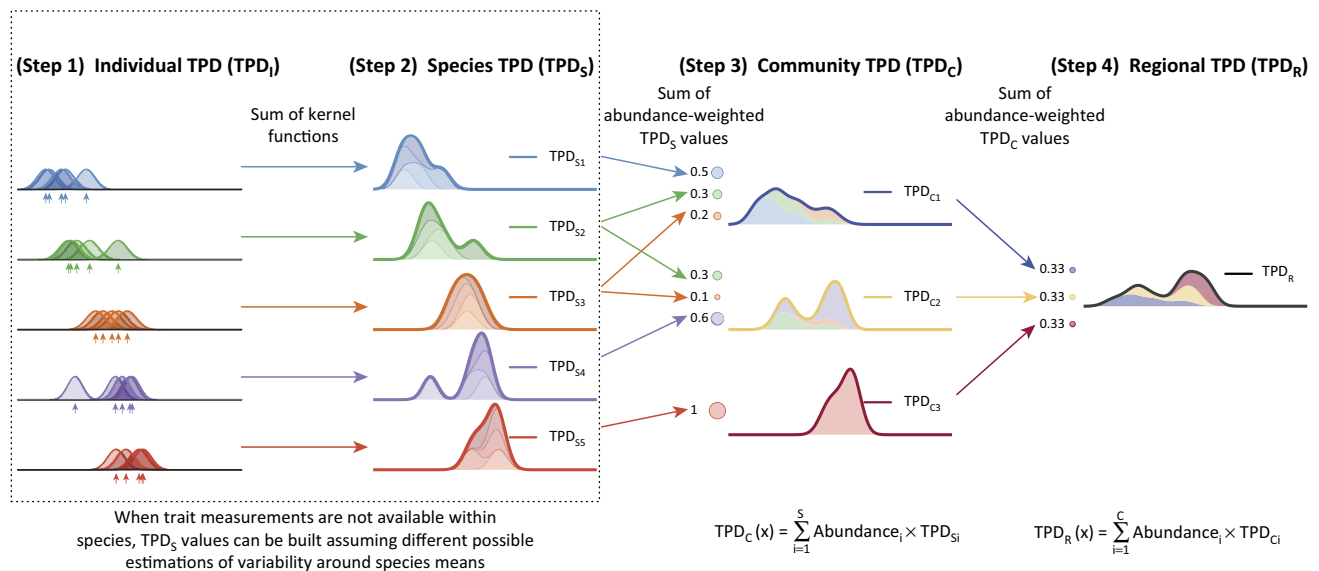


Figure 1. Basics of the Trait Probability Density (TPD) Framework. (A) The TPD of an ecological unit reflects the relative abundance of trait values (x) in that unit, being equivalent to the concept of probability density function. The overlap between two TPD functions (i and j) is calculated as the minimum of the two TPD functions, independently of the dimensionality of the functional space considered (B shows examples for one and two traits). Because TPD functions integrate to 1, the dissimilarity between two ecological units (β_0) can be calculated as 1-overlap. (C) Considering the probabilistic nature of niches can yield results substantially different from methods that only consider the boundaries, particularly when the functional trait space is not homogeneously filled [55]. (D) Although TPD functions are continuous functions (A), to perform operations it is more practical to divide the functional space into a high number (N) of equal-sized cells [with (hyper)volume V], and estimate the value of the TPD function in each cell.

underdeveloped. For instance, although some FD components such as richness, evenness, and divergence were originally conceived using the probability distribution of traits in communities rather than species averages [13], they have apparently never been applied this way. Unfortunately, in the same way as existing methods of accounting for trait hypervolumes do not incorporate the probability density of trait values [47,48], existing methods accounting for probability density of traits have not considered multiple traits [13,45,50], except for some recent preliminary attempts [56,58].

We present a way to integrate the probabilistic nature of trait distributions with the concept of multidimensional hypervolumes. This integration provides a framework for quantifying the different components of FD across multiple scales that unifies existing approaches. Our framework is inspired by the concept of probability density functions which reflect the probability of observing some specific value for a given variable. Because the framework applies to the functional trait space, we refer to these functions as **trait probability densities (TPD, Box 1)**.

The approach for calculating TPD functions using, for example, kernel density estimators (KDE) [59] is based on four steps (summarized in Figure 1). Ideally, TPD functions can be even considered at the individual level (TPD_i; Figure 1, step 1), with various measures within an individual [38]. Because these data are generally unavailable, TPD_i values can be approximated using the measured traits and an estimated variability [47,60]. The TPD_i values of each species



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Figure 1. Illustration of the Steps Necessary To Implement the Trait Probability Density (TPD) Framework at Different Scales. In the example, a kernel density estimator (KDE) [59] is associated with each individual of each species (TPD_i; step 1 shows five individuals for each of the five species, indicated by arrows). The sum of all the TPD_i values of a species yields the trait probability distribution of that species (TPD_s; step 2). Depending on the amount and type of data that are available, other methods such as Gaussian mixture models [85] or multivariate normal distributions [58] could be used to obtain TPD_s functions. The next stage (step 3) involves combining the TPD_s functions of the species present in a given community (in the example, three communities composed of a varying number of species; circle size indicates local relative abundances). Each TPD_s can be rescaled according to the relative abundance of the species in each community, simply by multiplying these factors. After this, and given that relative abundances sum to 1 across all species in a community, the sum of the integrals of all the rescaled TPD_s functions in each community is 1. We can then sum the values of the rescaled functions of all the species in each community, obtaining a function (TPD_c) that represents the probability density function of the whole community (step 3). The integral of any TPD_c equals 1, and its value for each trait value is directly proportional to the relative abundance of that trait value in the community. The final step (4) consists of aggregating the TPD_c functions of the communities from a given region, following a similar procedure to the ones presented in the previous steps, resulting in the TPD of the region (TPD_r; step 4). Biologically, TPD_s, TPD_c, and TPD_r represent the probability of randomly extracting an individual with a given trait value from a species, community, or region, respectively. The framework can be expanded to larger or smaller scales: from using several measurements for one individual [38] to estimate TPD_i, to building TPD functions at any spatial scale (up to the global scale) by combining the TPD functions of lower hierarchical units. Note that multiple traits can be incorporated by using multivariate kernel functions in step 1.

are then summed, yielding a collection of TPD_S functions (Figure 1, step 2) which can be aggregated (with or without considering the abundance of individual species) to form the TPD functions of the communities they occur in (TPD_C ; Figure 1, step 3). Notice that, when trait information for a single species is available at different sites, it is possible to compute a separate TPD_S for each population of that species, thus accounting for phenotypic differences associated with environmental heterogeneity or genotypic differentiation [28,57]. The TPD_C functions can in turn be aggregated to form a TPD for the region (e.g., meta-community) in which they occur (TPD_R ; Figure 1, step 4).

Below we show first how the TPD framework reconciles existing schools of thought in computing FD, while fixing several existing problems with individual indices. We then demonstrate that it provides great flexibility for partitioning FD between scales, and decompose β -FD [29,31] for any type of **ecological unit**. Finally, we illustrate the potential of the framework to advance trait-based ecology by proposing a pure quantitative estimator of functional redundancy [33] at any spatial scale, which is lacking in the literature.

Incorporating Existing Methods into the TPD Framework

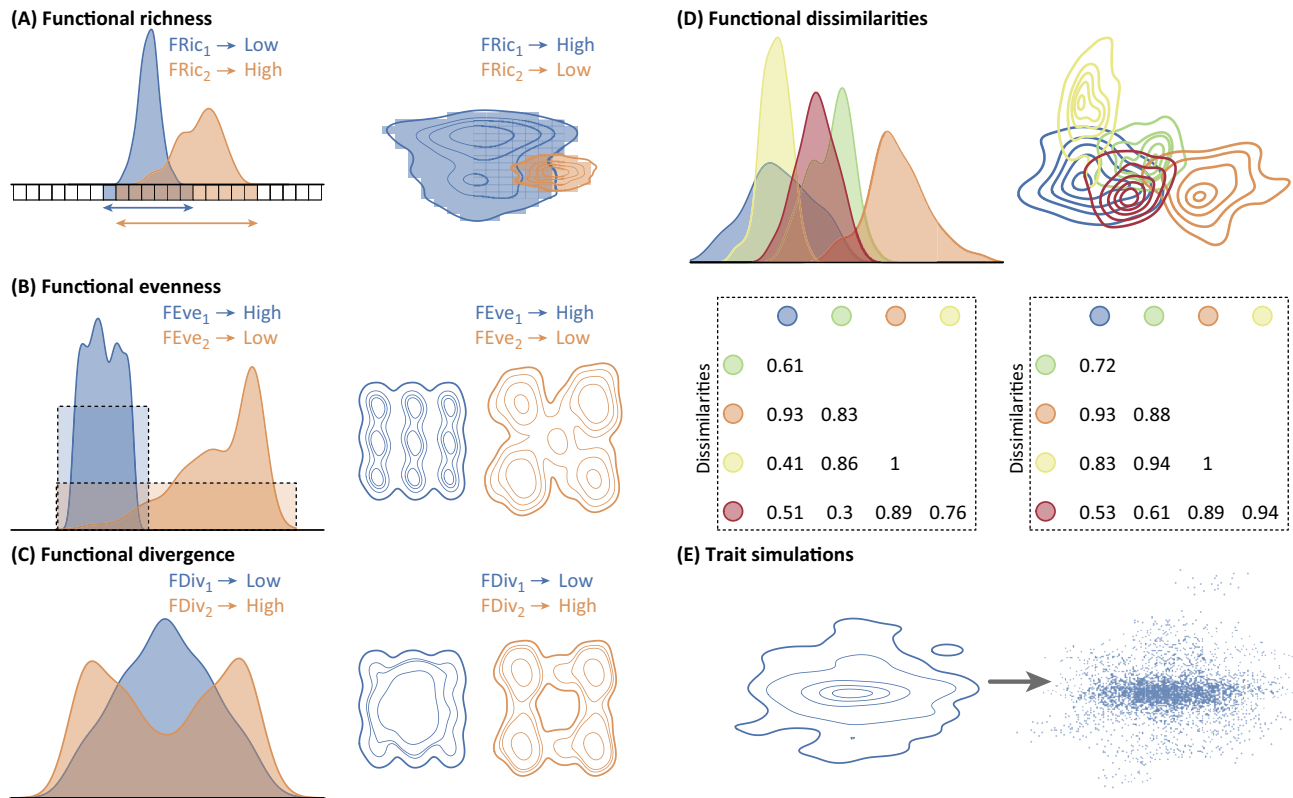
The TPD framework has the potential to unify existing FD approaches into a single and consistent structure, effectively incorporating ITV and the multidimensional nature of functional trait space across scales. In this section we first present corresponding adaptations of weighted mean trait values (TWM) [3], FD components [13], and of any method based on the trait dissimilarity between ecological units [61–65], highlighting when and how these adaptations solve several problems associated with existing approaches. We then provide two examples of novel tools that are possible owing to the development of the TPD framework: simulations for predicting population and community functional structure [53,56,66], and functional redundancy.

FD Components

While the three primary components of FD within communities (richness, evenness, and divergence) were originally described in terms of probability density functions [13], existing methods for calculating them rely on a single average value per species, deviating from the original probabilistic context [14,20]. The use of TPD functions permits a return to the initial conception by providing feasible estimators of these components that incorporate ITV (Figure 2A–C). The TPD-based approach explicitly considers species abundances and ITV, is sensitive to gaps in the functional volume, and is less sensitive to outliers [47], making it preferable to pre-existing methods that use the convex hull volume in the calculation of FRic and FDiv [14]. Moreover, it permits estimation of the amount of functional space occupied by a community even when there are fewer species than trait dimensions. With respect to the hypervolume method [47], FRic has the advantage of being expressed in the same units as the trait data, making directly comparable the results from different studies. In addition, TPD-based FEve can vary independently of evenness in species abundances, being a pure indicator of evenness in the abundance of traits [19], and is also not trivially correlated with FRic [67]. The same applies to FDiv, which in other approximations is also overdependent on abundance differences between species [14].

Dissimilarity-Based Indices

Several indices [61–65] can be incorporated into the TPD framework by using dissimilarities in terms of the overlap between pairs of TPD functions, generally between species, rather than dissimilarities based only on average trait values (Figure 2D). The use of dissimilarities that are not based on overlap generally impedes the consideration of ITV (but see [24]). Moreover, dissimilarities based on average values must be standardized when combined with other traits [30,68], which means that results depend on the species pool considered. By contrast, overlap-based dissimilarities between species yield more context-independent results, which are also more



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Figure 2. Several Existing Approaches Can Be Incorporated into the Trait Probability Density (TPD) Framework. Functional richness (FRic; A) is the amount of functional volume occupied by a TPD, which can be estimated as the sum of the hypervolumes (or range in the single-trait case) of the cells where TPD is greater than 0, and is therefore independent of species abundances. Functional evenness (FEve; B) is an indicator of evenness in the distribution of abundance within occupied functional trait space. Communities where all trait values have a similar probability should have high FEve values, and vice versa. FEve can be estimated as the overlap between the TPD of the considered unit and an imaginary trait distribution occupying the same functional volume with uniform probabilities throughout. Functional divergence (FDiv; C) is an indicator of the distribution of abundances within the functional trait volume. Communities where the most abundant trait values are near the extremes of the functional volume should have high FDiv, and vice versa. The abundance-weighted distance to the center of gravity of the TPD proposed in [14] can be used as an indicator of FDiv, using calculations based on the relative abundance of individual cells within the TPD instead of on species average trait values and species abundances. Dissimilarity between units (D) can be calculated from overlap between their TPD functions. Finally (E), TPD functions can be used to randomly draw trait values consistent with those present in a given unit (e.g., population, community, region).

consistent with biologically expected patterns [50]. Using the TPD approach, it is possible to estimate the average, minimum, maximum, and total overlap between the species in a community [17,50,57], or any other scale (see ‘Diversity Between and Across Ecological Units’ section).

Trait Predictions

Raw TPD functions can also be directly used for applications predicting the functional structure of populations and communities along environmental gradients. For example, the original version of the ‘Traitspace’ model of community assembly [56] uses the probability density distributions of the traits of species (TPD_S) to locate species in functional trait space. Subsequently, the model estimates the probability that simulated trait values along environmental gradients belong to each species, thus providing an estimate of the relative abundances of species along environmental gradients. A subsequent implementation of the model samples TPD_C values to simulate potential trait values consistent with a given set of environmental conditions [53], and thus the potential species pool. In general, any application requiring predictions of trait values from a

given population, community, or region could use TPD functions to randomly draw these values using a simulation approach (Figure 2E).

Functional Redundancy

Recent literature on functional traits has emphasized the importance of functional redundancy within a community as a potential control on community resilience and resistance [69,70]. Basically, two species can be deemed as functionally redundant if they have the same trait values, in other words if they occupy the same portion of the functional space. Although it is unlikely that any two species will be totally redundant in terms of multiple traits [71], partial redundancy between species – species sharing part of their functional niches – is common, and could allow communities to lose some species without losing ecological functions. According to this concept, the removal of a highly functionally-redundant species from a community should not result in a substantial reduction of the functions of the community. Despite the practical and theoretical importance of redundancy, all existing approaches to quantify it have serious shortcomings. Box 2 summarizes these shortcomings and shows a novel way to quantify functional redundancy that can even be applied to specific regions of the functional space corresponding unequivocally with the concept of redundancy.

TWM Values

TWM values provide information about the dominant traits in an ecological unit [72,73]. Estimating TWM is especially relevant in the context of the mass ratio hypothesis [74], which states that the traits of the dominant species in a community are the main determinants of ecosystem functioning [75]. Both in the uni- and multivariate context, TWM is indicated by the center of gravity of the corresponding TPD distribution.

Diversity Between and Across Ecological Units

As anticipated above, the promise of the TPD framework goes well beyond calculations within units. TPD functions can be used to evaluate mechanisms driving the spatial or temporal differences in the functional structure between populations, communities, or regions, that is, β -FD (see [76,77] for reviews on the questions that can be tackled by studying β -diversity). We envisage that the TPD framework will lead to new techniques for estimating diversity across scales, for example quantifying the contribution of individual species to community diversity or how a given habitat type contributes to the diversity of a region.

Decomposing β -FD

Functional differences in the TPD framework can be evaluated through overlap-based dissimilarity at any scale (Box 1) [49]. This comes with the advantage that dissimilarities estimated this way are independent of the considered species pool (see ‘Dissimilarity-Based Indices’ section), which permits the direct comparability of results from different studies. Overlap-based dissimilarity quantifies the differences between pairs of units (e.g., populations, communities, or regions). However, two pairs of units with the same percentage of dissimilarity (the same value of β_D) can have substantial differences in the way in which they differ. Consider for instance the case of two communities that are highly dissimilar because each occupies a part of the functional space that is not occupied by the other. By contrast, another two communities could also be highly dissimilar even when they occupy the same part of the functional space but where traits are present in the two communities with different abundances. This issue was solved for taxonomic dissimilarity by decomposing it into two components: turnover, as a result of species replacement, and nestedness, owing to differences in species richness [31]. The extension to functional dissimilarity considers the overlapping and non-overlapping fractions of the convex hull-based hypervolumes of the considered communities [29,78]. However, as discussed earlier, convex hull volumes ignore the probabilistic nature of FD. The TPD framework allows

Box 2. Functional Redundancy

Functional redundancy should ideally measure the degree to which traits are represented by multiple species in an assemblage. High levels of redundancy imply that loss of a single species should not affect the functionality of the assemblage because other species with similar traits remain [86,87]. Uncertainty exists, however, in estimating this component of FD. Most attempts to quantify functional redundancy use a functional group approach [7,88], involving subjective decisions, such as the number of groups to consider and the classification of species into groups. Moreover, this approximation deems the species in the same group to be totally equivalent, and totally different from those in other groups. Existing methods that do not rely on functional groups generate other complications. For instance, studying redundancy through the patterns of covariation between species richness and FD [89,90] does not yield redundancy values for each individual community, hampering comparability between studies. Finally, with methods based on species dissimilarities calculated using species averages [91], redundancy could potentially increase when a new trait is taken into consideration. Such an outcome is biologically counterintuitive because the proportion of functional space shared by two species cannot increase when extra dimensions are considered [33]. TPD-based redundancy (FRed; Figure 1) overcomes these problems: there is no need to classify species into discrete functional groups, there is a unique and biologically meaningful value of redundancy for each community, and redundancy cannot increase when new traits are added. FRed can be easily estimated by calculating the average number of species in an assemblage that have the same trait values (Figure 1). Moreover, redundancy can be estimated at specific areas of the functional trait space to detect trait combinations that are over- (several species occupying that portion of the space; over-redundancy [92]) or under-represented (Figure 1).

In practical terms, the functioning of communities with highly-redundant species should be more resistant to species extinctions. FRed can be applied in the context of ecological restoration: similar species should compete more strongly for resources than dissimilar species [93]. Therefore, projects aimed at excluding non-native invader species can select combinations of species highly redundant with respect to the invader [10,94]. Further, evaluating the redundancy of individual species at the community or regional pool scales can inform about the importance of each species for different functions, and hence about the vulnerability of such functions [32,82]. This highlights the potential usefulness of the estimation of redundancy at multiple scales. For example, community-level redundancy might be low due to competitive exclusion but, if there is high redundancy at the regional level, then one species lost from a community could be replaced by a functionally similar species from the regional pool.

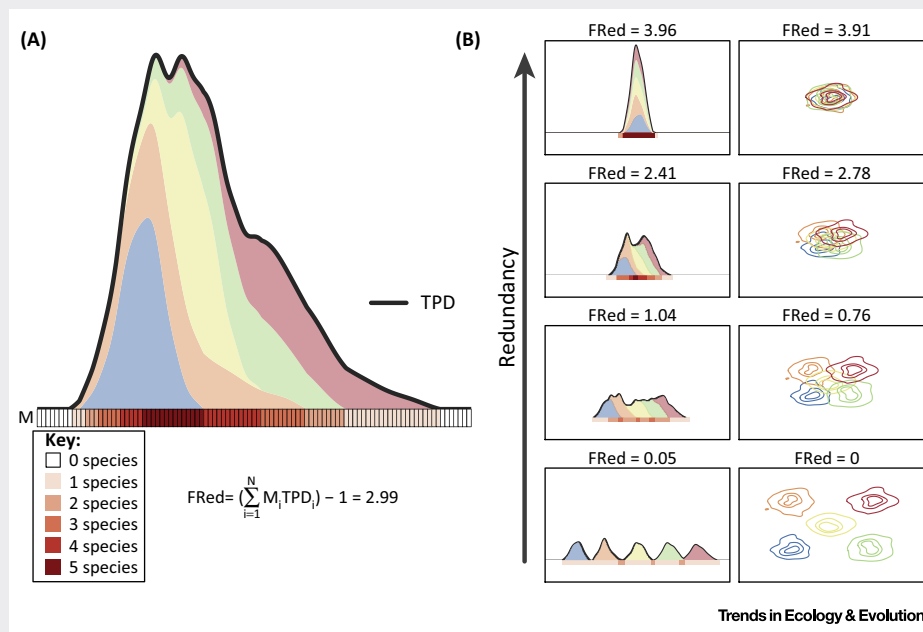
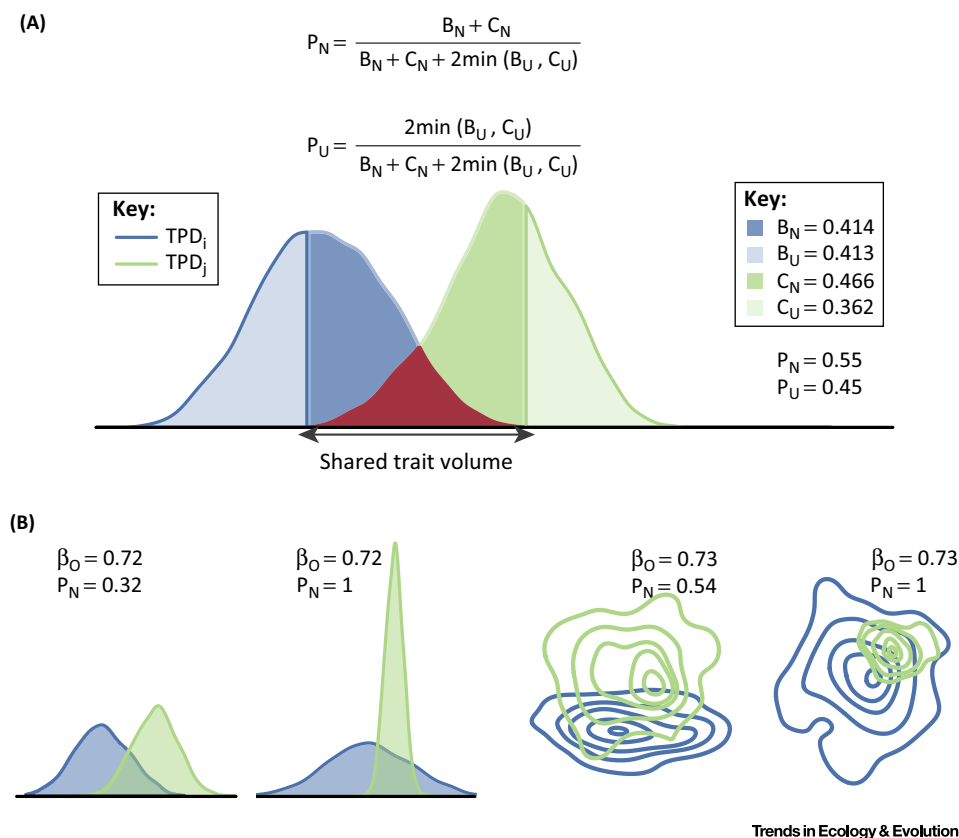


Figure 1. Average Functional Redundancy of a Community. (A) The rationale behind the calculation of functional redundancy (FRed) is simple: for each of the N cells of the grid we can count the number of species (M) that have a trait probability density (TPD) value greater than zero. This method effectively counts how many species display each trait value, and then calculates a weighted average of that number, using the value of TPD_C in the cell as the weighting factor. After subtracting 1, FRed expresses the average number of species (taken across cells) that could be removed from the community without reducing its functional volume (i.e., without losing an occupied cell from the grid). Consequently, FRed will be equal to 0 when all species are functionally unique (bottom panels in B), and equal to $S-1$ in the case in which the S species are totally functionally redundant (top panels in B). Following this approach, redundancy can also be calculated at the regional level (using TPD_R), and also at specific areas of the functional space, revealing vulnerable (i.e., right tail of TPD_C in A) and over-redundant (i.e., central part of TPD_C in A) areas.

decomposition of the functional dissimilarity between ecological units while avoiding the shortcomings of convex hulls.

The decomposition of functional dissimilarity has two complementary components. The first is due to the parts of the functional volume of the joint distribution that are exclusively, or uniquely, occupied by one of the units but not by the other (P_U). The second is due to the dissimilarity in the amount of relative abundance in functional trait space included, or nested, in the joint volume (P_N). The procedure to estimate these components is relatively simple, as shown in Figure 3A. High levels of functional dissimilarity between units of the same hierarchical level can be the result of different processes; the decomposition of β_O helps to disentangle them. For example, when two communities occupy different parts of the functional space, P_U will account for the greatest proportion of dissimilarity. On the other hand, when two communities share the same part of the functional space, P_N will approach 1 (Figure 3B).



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Figure 3. Decomposition of Functional Dissimilarity. Dissimilarity (β_O) can be decomposed into two complementary components: one due to the dissimilarity in the relative abundances of traits shared by the units (P_N), and the other due to the parts of the functional volume that are exclusively occupied by one of the units, but not by the other (P_U). The joint density distributions of two units can be divided into two parts: one corresponding to the overlapping area between the trait probability density (TPD) functions (red color in A), and one corresponding to the dissimilarity, which can be further divided into B (blue tones in A) and C (green tones in A). B (and also C) can be further decomposed into two complementary subparts: ‘B_N’ is the part of B that corresponds to traits shared by the two units (i.e., the part of B that is ‘above’ the overlapping part, indicated by dark tones), and ‘B_U’ is the part of B that corresponds to traits that are present exclusively in unit *i*, but not in unit *j* (indicated by light tones). The examples (B) show, in 1D and 2D, two pairs of communities with the same β_O ; a great part of the dissimilarity in the first pair is due to communities occupying different portions of the functional space, whereas in the second pair the functional volume occupied by one community is a subset of the functional volume occupied by the other. Decomposing β_O into P_N and P_U allows us to discriminate the underlying patterns leading to dissimilarity, which would be undetected otherwise.

Overlap-based dissimilarity, as implemented by the TPD approach, allows a smooth transition across multiple scales (from populations to regions) and provides great flexibility in partitioning functional trait diversity between scales. It has important advantages with respect to existing methods. First, it overcomes the shortcomings of the convex hull volume and hypervolume methods [14,47]. In addition, the decomposition of dissimilarity between P_N and P_U was not possible using dissimilarity-based methods for diversity partitioning [61,62,64]. Lastly, functional dissimilarity in the TPD framework is based on set-theory, which yields comparable estimates of β -diversity and its components across different types of diversity (taxonomical and functional) using a similar framework [31].

Across Scales

One of the greatest advantages of using overlap-based dissimilarities within the TPD framework is that the concept and properties of TPD functions are independent of the scale considered. As we mentioned earlier, different components of FD (richness, evenness and divergence) can be computed at different scales, in other words within populations, within species, within communities, within regions, etc. Each scale can be related to hierarchically superior scales, for example to estimate how FD of local populations contribute to the total FD of a species in a region, or how a species contributes to the FD of a community, or how a community contributes to the FD of a region. By applying this type of approach, existing attempts to partition FD across scales [16,17,79] can be easily accommodated and expanded to new ones.

In addition, it should be noted that β_O can also be calculated between units in different hierarchical levels. For instance, one could calculate the dissimilarities between the TPD_S functions of all the species in a community and the TPD_C of the community (the same could be done at the regional scale, using TPD_R instead of TPD_C). In these cases, individual dissimilarities indicate the amount of functional differentiation of each species with respect to the combination of all the species. As such, the dissimilarity of a single species with respect to the local or regional pool of species (indicated by TPD_C and TPD_R , respectively) is an estimator of the **functional distinctiveness** of that species [32] in the community or region. This information can be used in combination with indicators of species rarity to inform decisions regarding the protection of functionally-unique species or ecosystems [32,80,81], or to estimate the potential impact of species extinctions on ecosystem functioning [82].

Concluding Remarks

Because FD encompasses a variety of concepts and components, a combination of conceptual and mathematical approaches has, to date, been necessary to quantify it comprehensively [1,19,72]. In this paper we have shown how the TPD concept can be applied to individuals, populations, communities, and regions, and we have provided an assortment of methods to estimate several aspects of FD using one or multiple traits within a single framework. The TPD framework implements, for the first time, the Hutchinsonian concept of the niche as a probabilistic hypervolume, overcoming limitations of existing methods for FD quantification. It permits estimation of all aspects of FD at all scales, and can be adapted to different objectives depending on the research question. By adopting a point of view based on trait distributions, and by allowing full comparability between different scales, the TPD framework is specially promising for studying biodiversity–ecosystem function relationships, including invasibility [10], the effects of functional redundancy on the stability of communities [32], and the contribution of species and community trait structure on the functioning of ecosystems [82]. Most importantly, we show that, when applied appropriately (Box 3), these methods encompass the existing classes of approaches to quantifying FD (FD components, dissimilarity-based, and hypervolume-based indices), thus providing a single, consistent, and intuitive framework that embraces the probabilistic, multidimensional, and multiscaled nature of FD.

Box 3. Practical Considerations

There are several alternative procedures for estimating TPD_S . Kernel density estimators (KDE; Figure 1, step 1) [59] are the most widely used for single traits [45,49,57], and share with Gaussian mixture models [56,85] the advantage of being non-parametric, hence allowing for irregular trait distributions. Nevertheless, constructing TPD_S functions with KDE or Gaussian mixture models requires substantial amounts of trait data, and all traits must be measured on the same individuals so as to locate points in the multidimensional functional trait space; this is not always feasible. When lacking a sufficient number of individual measurements, one could estimate TPD_S functions using multivariate normal distributions [58], which only require the trait averages and variances of the species (and ideally covariance between traits [36]). Moreover, when there is no information about the ITV of a species, which is often the case in functional biogeography studies [95], it is also possible to directly estimate TPD_C functions by using species average trait values to construct one kernel function per species, assigning the same degree of ITV to all species (e.g., [16]).

As for all trait-based approaches, trait selection is a crucial point from the biological, computational, and applied points of view. The framework as presented here works with quantitative, continuous data. Nevertheless, when categorical or ordinal variables need to be included, ordination approaches can be used to identify different axes of specialization (e.g., PCoA [96]), using the ordination axis scores for each individual instead of raw trait values. From the computational point of view, the number of cells increases exponentially with the number of traits, complicating the characterization of the functional space when many traits are considered. Further, a high dimensionality requires a high number of individuals to be measured [36], which can make it unfeasible to accurately estimate TPD functions. However, existing evidence shows that, at least for plants, the intrinsic dimensionality of functional space is relatively low [97], meaning that careful trait selection can markedly reduce the number of traits necessary to adequately analyze ecosystem functioning or species coexistence. In this context, the use of procedures to compare and evaluate the quality of different functional spaces [98,99] appears to be a crucial step before using the TPD approach.

In a context of rapid environmental change and associated losses of species, it is essential to predict changes in species composition and ecosystem functioning from local to global levels [32,77]. This involves the development of standardized tools to characterize these impacts, while taking full advantage of the increasing availability of trait data that the field of functional ecology is currently experiencing (see Outstanding Questions). In this sense, graphical representations of the effects of competing hypotheses on the functional structure of ecological units [21] emerge as a powerful way to select the most adequate TPD-based metrics for different ecological questions. We have shown here some examples, but the number of potential applications of the framework is considerable. For example, the potential of the TPD framework to assess community assembly rules or ecosystem functioning can be increased if used in combination with phylogenetic dissimilarities between species, particularly when there are unmeasured and potentially important traits [83]. In this sense, we want to emphasize that we do not consider the TPD framework as a definitive and closed collection of methods, but rather as a first step towards a unified framework to accommodate the probabilistic and multidimensional nature of the functional facet of biodiversity. We hope that the inclusion of these methods in the toolbox of the ecologist will improve their ability to predict and understand the consequences of environmental changes on ecosystems.

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Outstanding Questions

What is the dimensionality of the trait space? How many independent traits do we need to consider to achieve a minimally-adequate estimate of the functional differences between organisms?

What are the most relevant traits to consider in each type of organism? The number of functional traits that can be measured for any organism is vast, but not all traits are equally easy to measure or have the same effect on fitness in a given environment. Characterizing the traits that most importantly impact on fitness and ecosystem functioning, and how these impacts depend on environmental conditions, is badly needed for the advance of trait-based ecology.

What is the optimal method for building TPD functions (KDE, Gaussian mixture models, multivariate normal distribution) according to the amount and quality of trait data available? Is it possible to define general guidance rules or statistical tests for selecting the most adequate approach in each specific case? KDE and mixture models are much more flexible than multivariate distributions, but have higher requirements in terms of the quality and quantity of trait data.

What is the effect of incorporating ITV into trait-based ecology? How does it change across scales? Answering this question requires appropriate trait information at the species level. We make a plea for ecologists publishing or submitting their data to public repositories to opt for the highest possible quality in this information. Primary trait data measured at the individual level (i.e., several traits measured in each individual) allow full incorporation of ITV, including covariation between traits, whereas mean and variance of each species for each trait is the minimum quality that allows consideration of ITV. Keeping in mind that most studies measuring traits *in situ* do it in several individuals per species, the introduction of the TPD framework seems like an ideal opportunity to revisit existing datasets.

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