



Which trait dissimilarity for functional diversity: trait means or trait overlap?

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Abstract

Question: Many functional diversity indices require the calculation of functional trait dissimilarities between species. However, very little is known about how the dissimilarity measure used might affect conclusions about ecological processes drawn from functional diversity.

Methods: We simulated real applications of functional diversity, to illustrate the key properties of the two most common families of dissimilarity measures: (1) 'Gower' distance, using only 'mean trait' value per species and then standardizing each trait, e.g. relative to its range; (2) 'trait overlap' between species, which takes into account within-species trait variability. We then examine how these approaches could affect conclusions about ecological processes commonly assessed with functional diversity. We also propose a new R function ('trova', i.e. TRait OVerlap) which performs computations to estimate species trait dissimilarity with different types of data.

Results: The trait overlap approach generally produces a less context-dependent measure of functional dissimilarity. For example, the results are less dependent on the transformation of trait data (often required in empirical datasets) and on the particular pool of species considered (i.e. trait range, regularity and presence of outliers). The results therefore could be more easily compared across studies and biomes. Further, trait overlap more reliably reproduces patterns expected when niche differentiation structures communities. The Gower approach, on the contrary, more reliably detects environmental filtering effects.

Conclusion: The two approaches imply different conceptions of how species dissimilarities relate to niche differentiation. Trait overlap is suitable for testing the effect of species interactions on functional diversity within local communities, especially when relatively small differences in species traits are linked to different resource acquisition. Gower is better suited to detecting changes in functional diversity along environmental gradients, as greater differences in trait values reflect increased niche differentiation. Combining trait overlap and Gower approaches may provide a novel way to assess the joint effects of environmental filtering and niche complementarity on community assembly. We suggest that attention should be given not only to the index of functional diversity considered but also whether the dissimilarity used is appropriate for the study context.

Introduction

Functional diversity, the extent of trait differences between species, is a key component of biodiversity (Petchey & Gaston 2002; Mason et al. 2005). As for taxonomical and

phylogenetic diversity, many indices have been proposed to estimate functional diversity, each showing different properties (Mouchet et al. 2010; Schleuter et al. 2010; Pavoine & Bonsall 2011). A common requirement for many functional diversity indices is estimating 'trait

differences' between species (Fig. 1). This is generally resolved by computing a pairwise species trait dissimilarity matrix (Pavoine et al. 2009; Laliberté & Legendre 2010), i. e. a matrix which contains the trait dissimilarity for each pair of species in a dataset. This matrix can be based on single traits or on the combination of multiple traits (Botta-Dukat 2005; Leps et al. 2006; Mason et al. 2011). While several studies have explored the behaviour of the existing functional diversity indices (Villegger et al. 2008; Mouchet et al. 2010; Schleuter et al. 2010), quite surprisingly very little is known about how the methods used to compute the trait dissimilarity matrix affect functional diversity values. In particular, it remains unclear how different methods for calculating dissimilarity might influence conclusions about ecological processes drawn from functional diversity (see Mason & de Bello this issue, for the set of ecological processes most commonly assessed with functional diversity).

To our knowledge, there are two main families of approaches for estimating this trait dissimilarity matrix. For illustration, let us consider here the case of a single quantitative trait (we discuss below also cases combining different types of traits). The first family of approaches was described by Botta-Dukat (2005) and Pavoine et al. (2009) and it is based on the popular Gower distance (Gower 1971). This approach, which we will call 'Gower' for simplicity, considers only a single mean trait value per species to estimate trait dissimilarity. For quantitative traits, dissimilarity is simply computed as the difference in mean trait values between species. To allow comparisons across different traits, this difference is standardized between 0 and 1 for each trait. This standardization can be obtained in different ways, but mostly the trait difference between each species is divided by the spread of trait values existing in the dataset. The original Gower distance (Gower 1971) divides, for example, the trait differences by the trait range (Botta-Dukat 2005). This approach is now used in most of

the popular packages to compute functional diversity. Gower distance is quite useful for combining different types of traits (e.g. quantitative, qualitative, semi-quantitative), it can deal with missing trait values, and the importance of individual traits can be weighted differently according to their importance (Pavoine et al. 2009; Laliberté & Legendre 2010).

As mentioned, for a given trait the Gower approach considers only a single mean trait value per species. However, it is increasingly recognized that species present a considerable amount of intraspecific trait variability, both within and across communities (de Bello et al. 2010b; Hulshof & Swenson 2010; Violle et al. 2012). Using only a single mean trait value for species, as with the Gower approach, obviously ignores this intraspecific trait variability (de Bello et al. 2010a; Leps et al. 2011; Albert et al. 2012). Another potential problem of the Gower approach is that different traits vary on different orders of magnitude. For example the range of variation in height and seed mass described in Cornelissen et al. (2003) is 10^{-1} to 10^2 m and 10^{-3} to 10^7 mg respectively. Transformations are, therefore, often required to account for lack of normality of trait values (Westoby 1998). It is unclear what is the effect of trait range variations and potential transformations on describing trait dissimilarity patterns.

The second family of approaches to compute trait dissimilarity, which we call 'Overlap', has been proposed by different authors, although with different algorithms (MacArthur & Levins 1967; Mouillot et al. 2005b; Leps et al. 2006; Mason et al. 2008, 2011; Geange et al. 2011). For a given quantitative trait, the approach estimates the overlap in trait distribution between species, i.e. considering intraspecific trait values (Fig. 1). The dissimilarity is commonly computed as one minus the overlap in trait distribution (given that the area of the density curve of trait distribution is equal to one). The approach was designed to estimate overlap in resource use and acquisition between

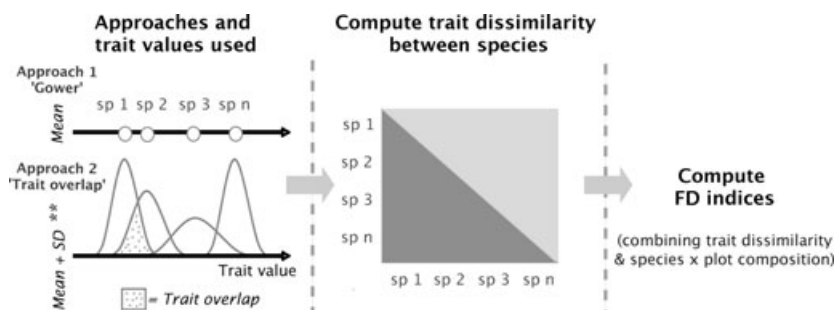


Fig. 1. The trait dissimilarity between species, normally expressed by a triangular or symmetrical matrix, is essential to compute most functional diversity indices. Depending on the data available two families of approaches exist to compute it. The first basically expresses differences between species' mean trait values and standardizes trait values based on trait range (or similar). The second expresses trait overlap between the curves of trait distribution for each pair of species (**Here estimated with mean and standard deviation of trait values, but other calculations are possible, see text).

species, thus providing a means of testing for the effects of interspecific competition on community structure (Mac Arthur & Levins 1967; Mason et al. 2011). There are generally two ways to compute trait overlap. The first assumes trait values to have a normal distribution around the trait mean (Mac Arthur & Levins 1967; Leps et al. 2006). For this approach it is necessary to estimate, for each species, the mean and standard deviation for each trait to build normal trait distribution curves (Fig. 1). The second approach does not assume that trait density curves follow a normal distribution. Rather, it uses kernel density estimators to build trait density curve, which requires no assumptions about curve shape (Mouillot et al. 2005b; Geange et al. 2011; Mason et al. 2011). The second is certainly more realistic but probably requires more field measurements. Our experience suggests these two methods give similar results, particularly relative to the Gower approach, and therefore we do not compare them here.

This study aims at comparing the two existing families of approaches (i.e. 'Gower' vs 'Overlap') to compute trait dissimilarity. We develop several tests, mimicking common applications of functional diversity, to assess and discuss the main properties and applications of these two approaches. For the different tests described below we follow a common approach using simulated trait values for a set of hypothetical species. In the following sections, we first outline each test (summarized in separate figures; i.e. Figs 2–7) and the implications of the results obtained with each test. Then we discuss more generally the applications of these approaches and the biological implications of our findings. We selected a number of tests that, we believe,

illustrate the general behaviour of these methods for several key applications of functional diversity. We claim that no approach is better *a priori* but that users should be aware of their potential advantages and pitfalls. Finally, we considered only one trait but we discuss the implication of our tests for combining multiple traits together.

Test 1: Do Gower and overlap produce analogous dissimilarity values?

Approach

The first test is a simple illustration of the expected distribution of dissimilarity values produced by the Gower and Overlap approaches. This shows what kind of values are generally expected with both methods. We simulated quantitative trait values for 20 species (Fig. 2, left panel). We first defined the mean trait value for each species, with mean values increasing across species. For illustration purposes we only show the case of mean values increasing on a logarithmic scales, but similar patterns were observed when considering log and non-log scales (Test 2). Then we randomly created 20 individuals per species. For each species we randomly selected 20 trait values from a normal distribution, with the standard deviation (SD) proportional to trait mean, so that all the species have similar coefficient of variation (CV, i.e. SD divided by trait mean). The increase of SD values with increased mean is a common pattern in many traits (de Bello et al. 2010b). The CV was fixed at 26%, a value within the range of values most often found for many traits (Cornelissen et al. 2003). For results with other values of CV see Appendix S1. After producing

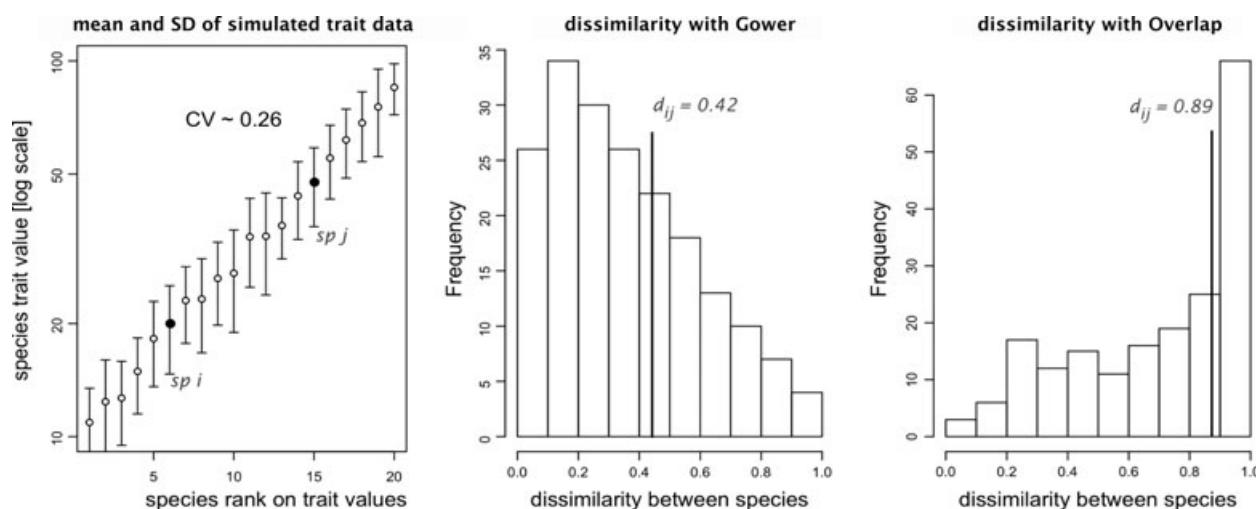


Fig. 2. Left panel: data simulated with 20 species having log-increasing mean trait values and coefficient of variation around the mean of ca. 26%. Central and right panels: typical histograms of trait dissimilarity between species obtained using Gower distance vs trait overlap (central and right panel respectively). Most values are close to zero with trait mean and close to one with trait overlap. For two species *i* and *j* (black circles in the left panel) the corresponding dissimilarity is shown for both methods (central and right panel respectively).

trait values for the 20 individuals per species, and log-transforming these values, we computed a new mean and SD of trait values per each species. Given that the individual values were generated randomly, the final values of CV were not exactly 26% but very close to that quantity. It should be noted also that the trait values within species, which were normally distributed before log-transformation, are slightly right-skewed (i.e. there are more small values and few large ones compared to the mean, Fig. 1; however, this skewness is negligible with a CV of 26%). Then we computed trait dissimilarity between species either using the Gower approach or the Overlap approach (based on mean and SD).

Results

The trait dissimilarity values obtained with the Gower distance were much lower than those obtained with the Overlap approach (i.e. the distribution was skewed towards smaller values; Fig. 2). The patterns observed in this example were also observed in all other examples in this paper and, most importantly, even across most of the real datasets for which we have made this comparison (not shown for simplicity). With the Gower approach there are many more values close to zero and only one single pair of species has dissimilarity equal to 1 (i.e. the combination of species with highest and lowest trait values in the dataset). With Overlap, many species have trait dissimilarity equal, or approaching, to one. Since overlap tends to 0 when species have sufficiently different trait means and small SD, dissimilarity will be close to one. An increase in SD values will result in higher overlap and, therefore, generally lower dissimilarity (Appendix S1).

Test 2: How much do trait transformations affect dissimilarity?

Approach

One common problem when using traits to compute functional diversity is transformation of trait values. Transformation alters the relative distances between species in trait space, i.e. by magnifying distances between some species pairs and 'shrinking' distances between others and their effect will depend on the original spread of trait values. It is unclear to which extent this will affect the results. Therefore, we followed the same approach as for the Test 1, but expanding the test to 65 species. The trait values were either log-transformed (as for Test 1) or not before the calculation of trait mean and SD. It should be noted that transforming trait values increases here also the evenness of species distribution along the trait gradient. Using raw or log-transformed data, therefore, also mimics the case of considering a more, or less, even trait distribution in a dataset.

Results

For the Overlap approach, transformation of trait data had a minimal effect on dissimilarity values (Fig. 3). By contrast, for the Gower approach, dissimilarity values were greatly affected by transformation of the trait data. We expect that they will vary more when the original range of trait values is greater, because the effect of log-transformation on raw trait data is greater when the trait range considered is greater. Comparing Gower vs Overlap values (Fig. 3 lower panels, with and without log-transformation) shows in which conditions the two approaches are comparable. Only after log-transformation and at low levels of dissimilarity (<0.2 in this specific case for the Gower approach) there is a correlation between the distances calculated with the Gower and Overlap methods. With log-transformation, there seems to be a threshold above which values with the Overlap approach tend to 1 and the correlation is disrupted. Without transformation of trait data the two approaches provide rather incomparable dissimilarity values.

Test 3: How do the range of trait values in a pool of species influence dissimilarity?

Approach

Very often researchers compare functional diversity values across different vegetation types or before/after producing some experimental modification (Freschet et al. 2011; Mason & de Bello this issue). This implies comparing functional diversity across pools of species with, for example, different trait ranges. We expected that the results, and consequent biological interpretations, of these comparisons could indeed depend on the way species dissimilarities are estimated. To show this we simulated four scenarios, each with a pool of 65 species but with different trait ranges ('XL', 'L', 'M', 'S'). The trait mean across all 65 species was the same across all four scenarios. Within each scenario, species trait mean values were randomly generated with a normal distribution around this fixed value (i.e. the same in all the four scenarios). The difference across the four scenarios was that the normal distribution of species trait values around this fixed mean was set from larger to smaller (i.e. ('XL', 'L', 'M', 'S' scenarios). We assumed here that the SD of the trait values within species was constant for all species and scenarios (as in the case of log-transformed data in test 1). We did this because we wanted to ensure that species with a given difference in trait means would have the same trait dissimilarity, irrespective of their trait mean, to allow comparisons across different trait ranges. We simulated community samples (20 communities per scenario), by randomly selecting 12–15 species from the whole pool of 65 species (Fig. 4). The assumption

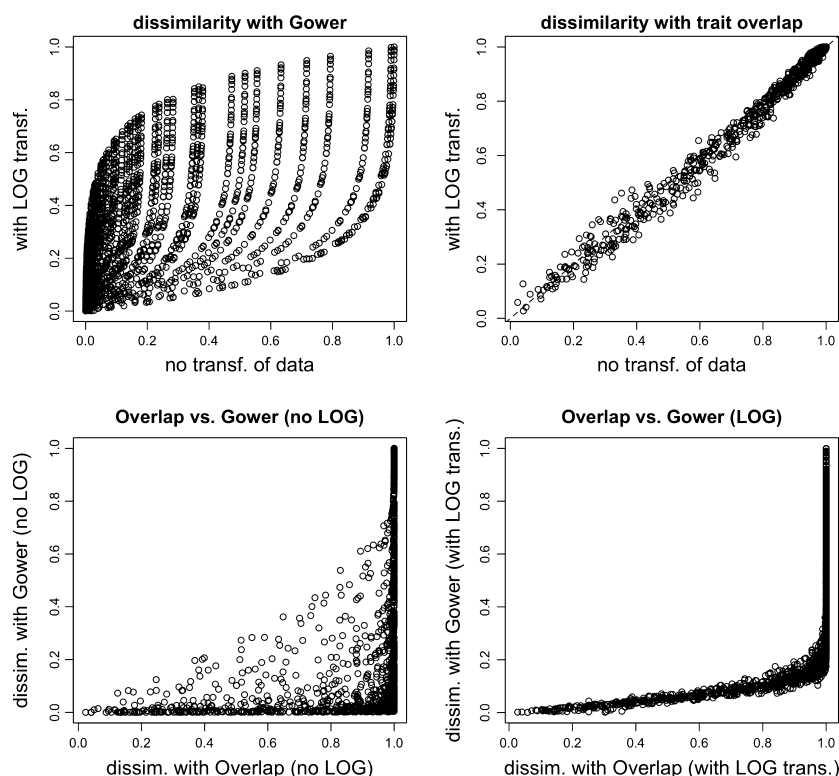


Fig. 3. The dissimilarity with the Gower distance (left-above panel) is much more variable, compared to trait overlap (right-above panel) with and without transformation of the data (here log-transformation). Comparing trait dissimilarities based on trait overlap and Gower distance (lower panels) show some correlation between the methods only at lower values of dissimilarity and only with log-transformed data.

of a reduction in species richness of around 80% from the species pool to the community level was based on field observations (Pärtel et al. 1996). Following this first step, we then added a new species to each of the four scenarios. This species was intended to be an outlier increasing the existing trait range, and was assigned a mean trait value equal to 1.5 times the maximum value in the trait range for each scenario (Fig. 4). We then recalculated trait dissimilarity between species (either with Gower or with Overlap).

We then computed the Rao index of functional diversity (Rao 1982; Botta-Dukat 2005; Leps et al. 2006) for each sample, using the matrices of dissimilarity between species computed using either the Gower approach or the Overlap approach. We used the Rao index expressed in terms of equivalent numbers (de Bello et al. 2010a) but we also discuss results in the context of other indices (see Appendix S2 and Discussion). The Rao index is a key index of functional diversity, which reflects the property of various similar functional diversity indices (Pavoine & Bonsall 2011). It expresses the sum of trait dissimilarities between each pair of species in a sample weighted by species relative abundance (in all our examples with functional diversity, we assume equal abundance of species in a community,

i.e. species relative abundance being equal to $1/\text{species richness}$). As for many existing indices of functional diversity, the trait dissimilarity is an essential parameter for the calculation of the Rao index (Pavoine & Bonsall 2011). For this and the following tests, we also performed calculations using another functional diversity index, the one by Petchey & Gaston (2002). This index is defined as the total branch length in a trait dendrogram connecting all species, and was chosen because it should provide very different results from the Rao index.

Results and implications

This test shows two important patterns, both observed with the Rao index (Fig. 4) and with the index of Petchey & Gaston (2002); Appendix S2). First, Overlap seems better able to detect differences between XL, L, M and S scenarios, with functional diversity decreasing from XL to S. This confirms that Gower distance comparisons across data sets should be done carefully as it depends on the pool of species used for its standardization. For example, consider comparing functional diversity of grasslands and forests with height as a trait. The range of trait values will be clearly lower in grasslands and, intuitively, the functional

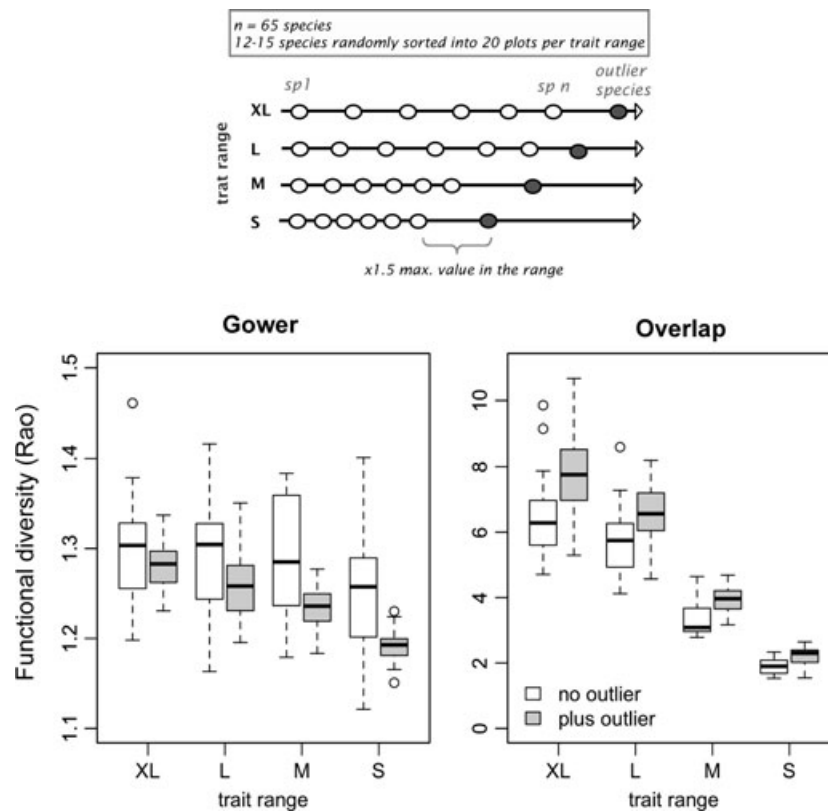


Fig. 4. Functional diversity computed with Gower (left panel) or trait overlap (right panel), depending on the range of trait values considered (from largest 'XL', to smallest 'S') with and without the inclusion of a new species outside this range. The scheme above the results shows the simulation approach, with 65 species equally spaced on a trait range. A total of 20 plots per range were built by adding 12–15 species randomly to each plot. The outlier species was set as having 1.5 times the trait value of the species with highest trait value in a given range.

diversity should be lower. However if the trait standardization is done for each vegetation type separately the values of functional diversity obtained with the Gower distance could be artificially similar across vegetation types (Fig. 4). With the Overlap approach this problem does not seem to exist or, more generally, the range of trait values considered should influence much less the results of functional diversity. As for Test 2, this test shows the context-dependence of dissimilarities values obtained using the Gower approach, because the values depend on the standardization of trait differences. As we show with Test 2, standardizations are not necessary with Overlap.

Second, with the Gower approach the addition of an outlier (or any new species in the dataset having sufficiently different traits from existing species) can produce some counterintuitive results of functional diversity. Consider the case of repeatedly measured of plots invaded by an alien species having extreme trait values relative to existing species. Assuming, for simplicity, that the existing species remained, this should intuitively increase functional diversity in the plots. The Overlap approach shows this pattern, while the opposite is found with Gower. This counterintui-

tive result arises because range-standardised distances between pre-existing species decrease when the observed range of trait values increases. Consequently, outliers strongly affect the mean dissimilarity values obtained with the Gower approach. It also implies that studies considering repeated measures of species composition should carefully consider how to compute the dissimilarity with Gower across repeated measures, if they do not want to artificially affect the variation in functional diversity. Most ecologists, including our selves (Hejda & de Bello this issue), would avoid these problems by considering both invaded and non invaded conditions together when estimating the observed range of trait values.

Test 4: How much do dissimilarity estimations influence the tests on species niche differentiation and coexistence?

Approach

One increasingly common application of functional diversity is the study of niche differentiation within communities (i.e. differences in alpha niches; Silvertown et al.

2006). It is expected that higher functional diversity should indicate communities with higher divergence between species in terms of traits, consistent with the hypothesis of limiting similarity, i.e. in order to coexist species with different traits occupy different niches within a community (Mac Arthur & Levins 1967). Niche differentiation could arise, for a given trait, if species are evenly distributed in trait space (i.e. functional evenness Mason et al. 2005 or functional regularity Moullot et al. 2005b).

Ideally, if we need an index of functional diversity to provide a general indication of niche differentiation between species, it should take higher values in communities with an even trait distribution (all else being equal). While similar tests have been applied to many indices of functional diversity (Mouchet et al. 2010), we further tested if this expectation was met using either Gower or Overlap. Again, as for test 4, we considered for this test the Rao index although we discuss further the implications for considering other functional diversity indices (Appendix S2 and below). We considered the pool of 65 species simulated for Test 2. Then we assembled communities either random or with even-spacing of trait values. With the random scenario, species were randomly selected across the 65 species. With the even-spacing scenario we fixed a minimal distance between species with closest trait values (Fig. 5). This minimal distance was set, with the Gower approach, as to be between 3/65 and 5/65 (in order to produce 13–21 species). We then computed both the Rao index of func-

tional diversity and the Petchey & Gaston (2002) index, either using Gower or Overlap to determine species dissimilarity. Finally, we also assessed the relationship between species richness and functional diversity, both with Rao and Petchey and Gaston indices. In this case, out of the pool of 65 species we randomly selected 1000 communities with richness varying from 3 to 40 species.

Results and implications

Using the Rao index with the Gower approach, the communities in the random assembly scenario wrongly showed the same functional diversity as the community having even-spacing of trait values. By contrast, with the Overlap approach, functional diversity was higher when trait values were evenly distributed. The reason for these patterns is that, as we discussed above (Test 1), the highest values of dissimilarities with the Gower index are only obtained between the species with most different trait values. The same problem, on the other hand, does not apply to the Petchey and Gaston index (Appendix S2). However, it is well known that this index is very strongly influenced by the number of species (which was constrained here). Therefore we claim that, with the Gower approach, various indices of functional diversity similar to Rao (Pavoine & Bonsall 2011) will show the highest values only when species having maximal and minimal trait values in the species pool are included in the community (i.e. functional

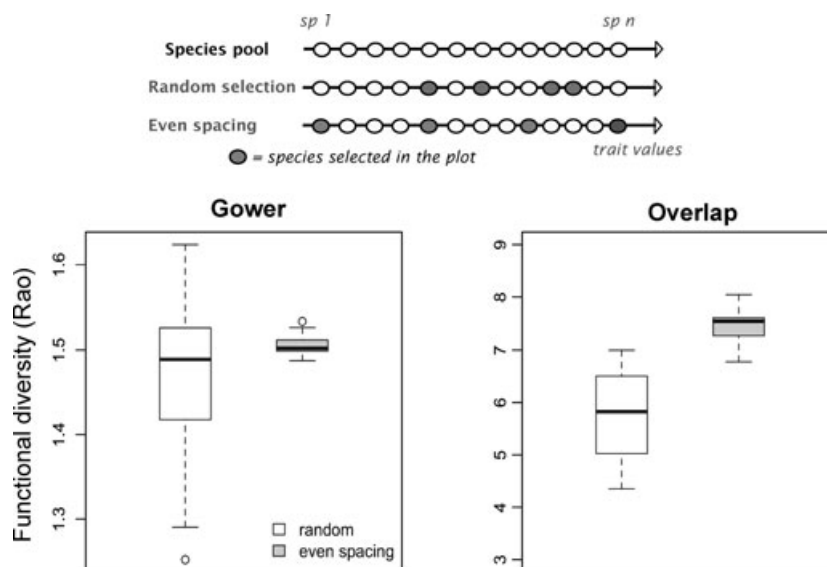


Fig. 5. Functional diversity (with the Rao index) patterns in communities assembled randomly or with even spacing in trait values (20 communities per scenario, each containing 13–21 species out of the 65 in the species pool). Random communities were assembled with species sorted randomly from the species pool. Even spaced communities were assembled by excluding all species too close on a trait gradient. Functional diversity, expressed here as the Rao index, should be higher with even spacing scenario reflecting higher niche differentiation.

diversity will depend, at least partially, on the range of trait values). This example also serves to highlight the problem of interpreting a general index of functional diversity like Rao. We currently lack pure indices of functional evenness that meet all necessary criteria (Mason et al. 2005; Mouillot et al. 2005a). For example, the most commonly used index of functional evenness (Villeger et al. 2008) is affected by the trait range considered (lower trait range having higher chances to detect even-spacing). Other indices could be considered, after validation (Kraft & Ackerly 2010; Thuiller et al. 2010b). Consequently, it remains difficult to isolate functional evenness from other functional diversity components, but the Rao index using trait Overlap could provide an interesting measure of functional evenness.

Another pattern that we detected is a changing relationship between species richness and functional diversity. Using both the Rao index (Fig. 6) and the Petchey & Gaston index (Appendix S2), we detected more linear patterns between species richness and functional diversity with overlap. Most of the dissimilarity values are higher (i.e. many values are close to 1) with overlap and species will be considered functionally different. This means that with overlap there are greater chances to get a positive correlation between species richness and Rao compared to the Gower approach.

Test 5: How much do dissimilarity estimations influence the tests on environmental filtering?

Approach

Another increasingly common application of functional diversity is to quantify the influence of environmental fil-

tering along ecological gradients (Freschet et al. 2011; Mason et al. in revision this issue). Environmental filtering implies that variation across sites in their environmental conditions causes different trait values to be selected for (i.e. the traits conferring greatest fitness vary according to local environmental conditions; Gotzenberger et al. 2012). This gives rise to the often-observed pattern where species occurring at a given site are more similar in their traits than species from different sites (Diaz et al. 1998; Gotzenberger et al. 2012). In addition to this, it has long been theorised that environmental filtering influences species occurrences and abundances more strongly in stressed environments (Weiher & Keddy 1995; Mason et al. 2008; Pakeman 2011). This should lead to lower functional diversity at stressed vs benign environments (Mason et al. 2008; Carmona et al. 2012; Munkemüller et al. 2012).

We tested the behaviour of Rao functional diversity computed with Gower and Overlap to detect these expected patterns. We defined a pool of 300 species having mean trait values regularly spaced between 1 and 300. We then simulated 300 plots having a different mean trait value (i.e. the mean of species trait values) across an environmental gradient. The mean trait value of the plots was set to decrease with the environmental gradient. To simulate environmental filtering, within each plot only a reduced range of trait values, compared to the whole pool of 300 species, was allowed around the plot mean. We then considered two scenarios where the range of trait values around the plot mean was set either (1) to decrease with the gradient (and therefore with the site trait mean) or (2) increase (Fig. 6). This simulates a case where the importance of environmental filtering either increases or decreases along the environmental gradient. Thus, the

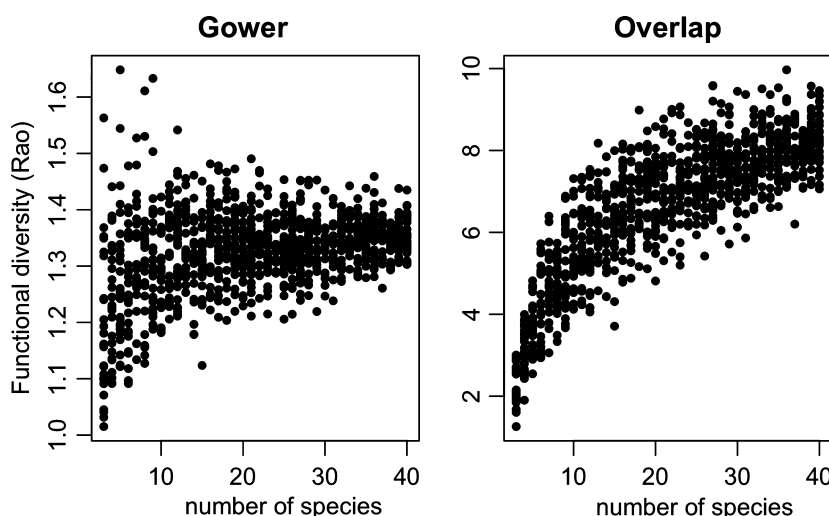


Fig. 6. Relationship between species richness and functional diversity (with the Rao index) in 1000 communities randomly assembly out of the 65 in the species pool used in previous tests. See Appendix S2 for results on other functional diversity indices.

range of trait values allowed within a plot was lower at one extreme of the trait gradient (8% of the trait range of whole pool of species) compared to the other (40%). Our idea was to simulate a large environment gradient, say an altitudinal gradient, in which environmental filtering was increasing, or decreasing, towards one extreme of the gradient. For each plot, a fixed number of species (15) were randomly selected from within the range of trait values allowed.

We then computed trait dissimilarity (either with Gower or Overlap) and functional diversity values (again with the Rao index). For the Gower approach we used either raw or log-transformed trait data (this creates more 'compacted' trait values with increasing trait mean). For the Overlap approach we either considered the SD of trait values for each species to increase with trait mean (i.e. SD = 30% of trait mean) or was considered as fixed (i.e. for all species it was fixed to 10, so that species having a trait difference of 30 would have a dissimilarity around 0.85).

Results and implications

Both the Gower and Overlap approaches generally produced the expected pattern of decreasing functional diversity toward one end of the environmental gradient. However in some specific conditions these patterns were not properly revealed and users should be aware of possible existing limitations. The problem, in this case, seems slightly more serious with the Overlap approach and when both (1) the SD of species trait values increases with species trait means and (2) when this occurs in combination with community samples where the range of trait values decreases with plot trait mean (for example when vegetation with lower species has also a lower range of height values, which is a rather likely scenario; de Bello et al. 2012). In this case, species with greater trait values and greater SD will occur in communities with higher trait range. However, because of increased SD for a given distance between species means, overlap will be greater than at the other extreme of the gradient (where species have lower SD in plots within a lower plot trait range). In this case the Gower approach, which is really proportional to differences in trait means, should better discriminate changes in FD across a gradient. The main risk with the Gower approach occurs in the same scenario (i.e. communities with higher trait mean having higher trait range), and when already normally distributed trait values are unnecessarily log-transformed. In this case, again, functional diversity does not vary along the environmental gradient as expected. This is because when higher trait ranges correspond with higher species mean trait values log-transformation shrinks distances between species in communities with high range values more than in communities with low range values.

These results suggest that even a simple study assessing changes in functional diversity across an environmental gradient should carefully consider various details of trait dissimilarity computation before deriving conclusions about environmental filtering. Users could also consider, before calculations, whether the trait ranges in communities increase with community trait means and whether data transformation is really required.

Discussion

In this study we show that the method used to compute species trait dissimilarity can have profound consequences for the detection of expected ecological patterns assessed using functional diversity. We claim that the two approaches considered (Gower vs Overlap), when applied carefully, are both viable but one should be aware of the assumptions, potential applications and pitfalls (Table 1). We also claim that, for a given trait, the Overlap approach is (1) generally less context dependent for distance-based measures of functional diversity and (2) takes into account intraspecific trait variability of species, which is most often neglected in functional ecology (Albert et al. 2012; Violle et al. 2012).

We also claim that the two approaches (Gower vs Overlap) imply rather different conceptions of the linkage between species dissimilarity and niche differentiation between species and are therefore suited to different applications. The Overlap approach was created mainly to understand differences in terms of niche within a community, i.e. what kind of resources are used by coexisting species and if species compete or not for the same resource (Mac Arthur & Levins 1967; Mouillot et al. 2005b; Leps et al. 2006). This implies that traits, and trait differences, are used to infer the 'alpha' niche of species (Silvertown et al. 2006) and it suggests that trait overlap could help focussing particularly on niche differentiation *within* communities. As such Overlap could help depicting all biotic mechanisms driving the coexistence of species, such as the effect of competition is increasing, or even decreasing, the functional differentiation between species (Mayfield & Levine 2010; Mason et al. 2011).

It should be noted, that the Overlap approach generally assumes that even small differences between species may suggest that they occupy a different niche. This might be reasonable in some occasions but not in others. It might be mostly appropriate when small differences in trait values imply differences in the mode of resource acquisition, or the types of resources used. This applies, for instance, food type for animals in the original concept of niche overlap (May & Mac Arthur 1972). Indeed our examples suggest that species could be functionally more different than assumed using the Gower approach. However, these

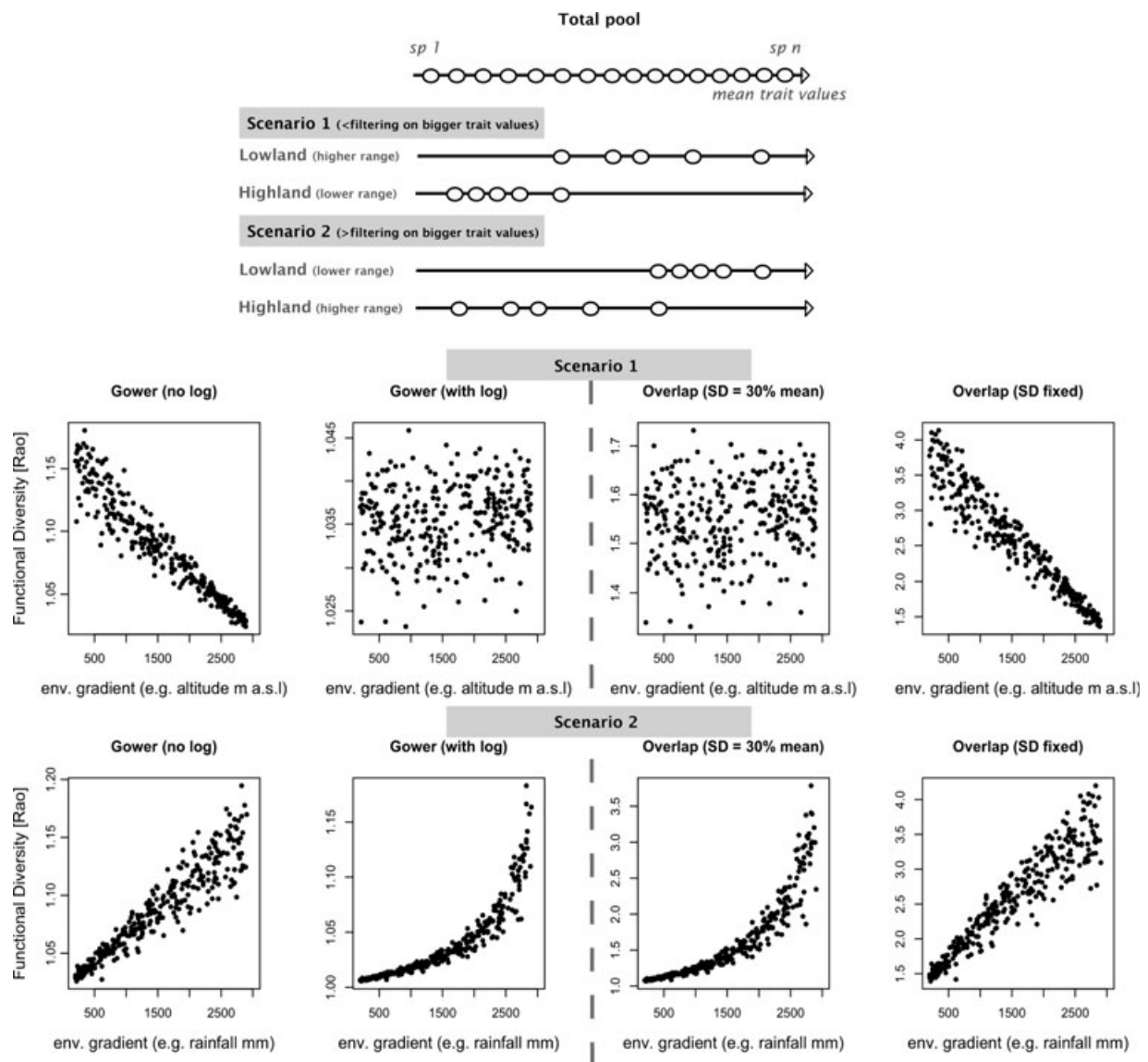


Fig. 7. Simulations to show the application of Gower vs Overlap approaches in studying environmental 'filtering' effects on functional diversity (see Test 5). Out of a pool of 300 species we assembled 300 plots having each 15 species across an environmental gradient, e.g. an altitudinal gradient. At low altitudes we simulated plots as having higher trait values and either higher trait range (scenario 1) or lower (scenario 2). For the Gower approach the trait data, which were normally distributed, were either log-transformed or not. For the Overlap approach we simulated cases where the standard deviation would increase with trait mean or would be similar for all species.

assumptions might not be reasonable when competition between species increases progressively with differences in trait values, as for example in the case of size asymmetrical competition. Consider three herbaceous species, species A, B and C with heights of 10, 50 100 cm respectively, and a fixed SD for height of 5 cm. In this case let us assume that the tallest species (C) is a superior competitor for light to species (B) and B is a superior competitor to the shortest species (A). With the Overlap approach discussed here, however, the dissimilarity between species A and B and A

and C could be, in both cases, close to 1. In this case the Gower approach could be preferred, as greater differences in trait means reflect greater differences in competitive ability. More generally, comparing results from the two approaches may provide a novel way to differentiate between different types of competitive impacts on species distribution in trait space.

It could be argued that Gower approach might be preferable when dealing with niche differences across environmental conditions. In this case niche differentiation is

Table 1. Summary of the tests conducted and the main conclusions obtained.

Tests	Gower	Overlap
1. Dissimilarity values	Lower values, many values approaching zero (distribution skewed towards lower values)	Higher values, many values approaching one (distribution skewed towards one)
2. Trait values transformations	Dissimilarity largely dependent on the transformation of data (stronger effect when the differences between species has more order of magnitudes)	Dissimilarity largely independent on the transformation of data
3. Range of trait values	Dissimilarity largely dependent on the pool of species considered and on the inclusion of outliers, or new species in the pool	Dissimilarity is largely independent on the pool of species considered
4. Testing niche differences within communities	Even trait spacing is not always easily detected Species and functional diversity are less correlated	Even trait spacing is more easily detected Species and functional diversity are more correlated
5. Testing environmental filtering	The response of functional diversity to environmental gradients is detected but care is needed	The response of functional diversity to environmental gradients is detected but care is needed
Conclusion	The results are context dependent The pool of species considered in the calculation should be carefully defined Preferable for testing environmental filtering on large environmental gradients	The results are less context dependent The approach can be used to compare across different pool of species more easily Preferable for testing niche differentiation and niche overlap within communities

expressed as the beta niche of species, i.e. differentiating species with a different optima *between* communities across environmental gradients (Weiher & Keddy 1995; Silvertown et al. 2006). Although even the Overlap approach produced similarly trustable results, in this case it might be easier to use only trait means because the data are available in many existing databases (Kleyer et al. 2008; Klimesova & de Bello 2009). The approach probably requires fulfilling fewer requirements in the type of data available (see Test 5) and less data collection effort. We suggest, anyway, that the species trait mean values used for calculations should be measured, for each species, in different environmental condition (Leps et al. 2011). This requires specific field sampling campaigns or simulations, as discussed by Albert et al. (2012), in order to account for changing trait mean values of species along the considered gradient. When using the Gower approach, however, we recommend special care if using, or not, log-transformations. We suggest particularly to log-transform trait values if SD of species is expected to increase along with trait mean (as in height). Following of this recommendation ensures that FD values calculated with the Gower approach behave similarly to those that would have been calculated using the Overlap approach.

In this study we show some key properties of the Gower and Overlap approaches based on single traits. Similar recommendations should be valid when combining multiple traits. Combining different traits together, both with Gower and Overlap, in fact, implies combining trait dissimilarities matrices for single traits. This can be done by averaging the trait dissimilarity across all single traits, or calculating Euclidean distance (i.e. summing the squares of distances and then doing a square root of the result or all

dissimilarity matrices; see Botta-Dukat 2005; Leps et al. 2006 and Pavoine et al. 2009). The new R function provided in the supplementary material include all these options, for both the Gower and Overlap approach (for the Overlap approach both normal and kernel trait distributions are allowed). It should be noted that combining trait dissimilarities from multiple traits with the Gower and Overlap have, however, a different logic. With Gower, the relative weight of individual traits will be affected by spread and distribution of trait value within each trait (de Bello et al. 2010b). For example, the relative weight of height and specific leaf area (SLA) on functional diversity values in meadows will depend on whether some forest species are in the data set (or if the whole range of trait values existing is used for the standardization). If forest species are included, the effect of height will be down-weighted in the meadows – because by including forests, the range of heights will increase by more than an order of magnitude, whereas no such change will happen for SLA. Therefore, in meadows, species differences in height will have practically no influence on functional diversity calculated using two traits (i.e. height and SLA) if tree species are used for Gower standardization (Appendix S3). Thus, it might appear that one community is more functionally diverse in terms of one trait, while these patterns depend only on the mathematical properties of the approach (de Bello et al. 2010b). Moreover, the influence of each trait on functional diversity calculated with multiple traits will depend on which species are used for standardization. This is not an issue when distances are calculated using the Overlap approach.

Finally, in this paper we dealt mostly with cases of computing functional diversity within communities (alpha

diversity). It is well known that applying functional diversity indices for measuring functional diversity among communities (i.e. beta diversity) further requires that a set properties of trait dissimilarity are fulfilled (Ricotta 2005). Here, we show that alpha functional diversity, which is essential for understanding patterns in niche differentiation within and across communities, can be computed with two main families of approaches (Gower and Overlap) and that in some cases one approach could be prove more useful than another (Table 1).

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Further results of the Test 1.

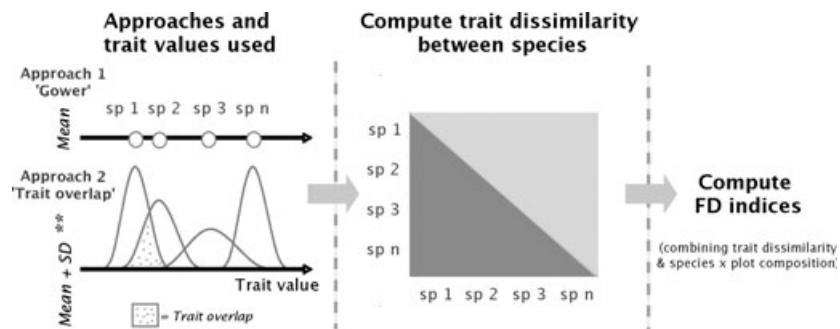
Appendix S2. Test 3 and 4 using the index of functional diversity of Petchey & Gaston (2002).

Appendix S3. Effect of combining two traits for computing functional diversity with the Gower approach.

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Graphical Abstract

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A common requirement for computing most functional diversity indices is estimating trait differences between species. Using simulations we compared the two main approaches to compute trait differences: the Gower distance (using only species trait averages) and trait overlap (using intraspecific trait values). We discuss the major properties of these two approaches and provide guidelines for their applications.