**Measuring individual-level trait diversity: a critical assessment of methods**

**Olusoji O. D.1,2** [**oluwafemi.olusoji@uhasselt.be**](mailto:oluwafemi.olusoji@uhasselt.be)**,** [**oluwafemi.olusoji@unamur.be**](mailto:oluwafemi.olusoji@unamur.be)

**Spaak J. W.2** [**jurg.spaak@unamur.be**](mailto:jurg.spaak@unamur.be)

**Neyens T.1** [**thomas.neyens@uhasselt.be**](mailto:thomas.neyens@uhasselt.be)

**Fontana S.3** [**Simone.Fontana@wsl.ch**](mailto:Simone.Fontana@wsl.ch)

**Aerts M.1** [**marc.aerts@uhasselt.be**](mailto:marc.aerts@uhasselt.be)

**De Laender F.2** [**frederik.delaender@unamur.be**](mailto:frederik.delaender@unamur.be)

**1Data Science Institute, Hasselt University.**

**2Research Unit in Environmental and Evolutionary Biology (URBE), Institute of Life-Earth-Environment (ILEE), Namur Institute for Complex Systems (NAXYS), Universite de Namur.**

**3Swiss Federal Institute for Forest, Snow and Landscape Research.**

**Abstract**

1. Individual-level trait diversity (ITD) has been identified as an essential component of functional diversity and is hypothesised to influence community assembly and structure. Measuring ITD requires specialised indices that should satisfy specific criteria: (i) mathematical and conceptual consistency (ii) intuitive interpretation, and (iii) independent of sample size.
2. We tested if six commonly used ITD indices fulfilled these criteria. We also proposed two modified indices in an attempt to account for some suspected limitations. We examined criterion (i) via the mathematical definition of these indices. We examined criterion (ii) and (iii) by simulating the removal or addition of individuals in a 2-dimensional trait space, and computing these indices.
3. ITD indices measuring trait divergence are the only indices that satisfy the three criteria. One of the indices measuring trait evenness violated criterion (i) because the index compares continuous trait values to discrete trait values. Furthermore, all three trait evenness indices were strongly related to sample size. Finally, two of the three indices measuring trait richness violated criterion (i) because of discontinuity. One of these richness indices did not change when removing individuals not at the edge of the trait space, thus violating criterion (ii). All three richness indices were related to sample size, thus violating criterion (iii).
4. In summary, applying commonly used ITD indices to quantify anything else than trait divergence can lead to results that are challenging to interprete and potentially misleading due to their dependence on the number of individuals, as the effects of some experimental treatment on population size can be mistaken for effects on ITD. These results argue for the development of new indices, the modification of existing ones, or moving away from the use of single indices to measure ITD.

**Introduction**

Quantifying biodiversity is crucial because of its effect on ecosystem functions and services (Cardinale et al., 2012). While there are multiple facets of biodiversity, trait diversity, i.e. variation in phenotypic features of organisms, is of prime interest because it connects structure to functioning (Cardinale et al., 2012; Gagic et al., 2015; Hillebrand & Matthiessen, 2009; Reiss, Bridle, Montoya, & Woodward, 2009; Tilman et al., 1997) and co-determines ecosystem responses to environmental change (Baert, Jaspers, Janssen, De Laender, & Aerts, 2017; de Bello et al., 2010; De Laender et al., 2016; Gross et al., 2017; Lavorel & Garnier, 2002; Naeem & Wright, 2003; Violle et al., 2007).

Individual-level trait diversity (ITD), defined as variation of traits amongst individuals, is an aspect of biodiversity that is increasingly considered (Bolnick et al., 2011; Carmona, de Bello, Mason, & Lepš, 2016; De Laender et al., 2014; Fontana, Thomas, Moldoveanu, Spaak, & Pomati, 2018; Wohlrab, Tillmann, Cembella, & John, 2016). ITD has three primary components: divergence, evenness and richness. Individual-level trait divergence measures  absolute trait differentiation among individuals (Fontana, Petchey, & Pomati, 2016; Mason, Mouillot, Lee, & Wilson, 2005; Schleuter, Daufresne, Massol, & Argillier, 2010); trait evenness measures how evenly these individuals fill up the trait space; richness is the amount of trait space occupied by individuals in that trait space (Fontana et al., 2016; Mason et al., 2005; Schleuter et al., 2010). Intraspecific trait evenness entails how evenly these individuals fill-up the trait space;.

Measuring ITD requires specialised indices that can reflect variation among individual-level measured trait values. Since every individual is a unique combination of traits, each individual must contribute to ITD computation (Fontana et al., 2016). Additionally, we argue that an ITD index needs to fulfil three requirements: *(i)* it is mathematically and conceptually consistent *(ii)* it reflects intuition, and *(iii)* it does not depend on the number of sampled individuals. The reasons for each of these requirements are as follows:

1. The proposed index should be mathematically and conceptually consistent (in both definition and implmentation) such that it returns a value that bears a biological meaning. For example, an index comparing discrete trait values to continuous trait values is not consistent..
2. The second requirement ensures interpretation of observed ITD changes along environmental gradients is possible. This is important because ITD indices are often applied in comparative studies to ask how ITD responds to some experimental treatment or environmental gradient (Craven, Hall, Berlyn, Ashton, & van Breugel, 2018; Kusumoto et al., 2015; Oliveira, Baumgartner, Gomes, Dias, & Agostinho, 2018; Sfair, Rosado, & Tabarelli, 2016). For example, when a richness index increases following removal of  unique individuals, this can be challenging to interpret. Evaluation of trait indices in literature have majorly been in terms of this criteria (Fontana et al., 2016; Legras, Loiseau, & Gaertner, 2018; Schleuter et al., 2010).
3. The third requirement is needed to ensure that experimental studies aimed at testing the effect of some environmental gradient on ITD do not mistake effects on abundance (sample size) for effects on ITD. However, individual-level trait richness should increase with increasing number of unique individuals, but this should approach an asymptote as more individuals are sampled (at some pont, newly sampled individuals will be much more similar to individuals that were already sampled).

Any ITD index that satisfies these three criteria would be fit for use under any study scheme. Furthermore, testing ITD indices in light of these criteria can help identify situations where some indices are useful regardless of their flaws. For example, the third criterion requires the presence of factors that could potentially influence both sample size and ITD. Therefore, an index satisfying the first and second criteria but not the third can still be interpreted properly. The three criteria also generalise the different requirements for trait diversity indices mentioned in the literature. For example, the monotonicity (trait richness should increase with addition of unique trait combinations) and twinning (trait richness should flatten with addition of redundant trait combinations) criteria of Ricotta (2005) for trait richness indices fits into requirement *ii*, because one would expect trait richness to initially increase with the observation of new trait combinations, but to saturate  as similar trait combinations start being added. Also, Schleuter et al. (2010) requirement that diversity indices “should measure exactly what the user wants to describe” fits into criterion *i*.

In this article, we test six individual-level multi-trait indices (indices chosen based on criteria laid out in Fontana, Jokela, & Pomati, 2014) using the three above-mentioned criteria. We included two divergence indices (FDis, Functional Dispersion; Rao, Rao’s quadratic entropy), two evenness indices (FEve, Functional Evenness; TED, Trait Even Distribution and two richness indices (FRic, Functional Richness; TOP, Trait Onion Peeling). We examined criterion *i* by examining the mathematical definition of these indices, while criteria *ii* and *iii* were examined using individual-level data simulated from a 2-dimensional (2D) trait space. We also propose and evaluate a modified version of the TOP(TOPM) and TED (TEDM) to account for some of the suspected limitations of these indices.

**Materials and Methods**

Richness Indices

FRic (Cornwell, Schwilk, & Ackerly, 2006) measures trait richness as the (hyper-) volume or area covered by individuals in a trait space (see panel a in Fig. 1), which is measured by computing the volume of the smallest convex-hull covering all individuals in the population.

TOP (Fontana et al., 2016) is computed by summing areas of convex-hulls peeled off from the individuals in the trait space (see panel b in Fig. 1). It measures trait richness by considering successive areas of trait space covered by all members of the population. It is conceptually similar to the FRic, but it is sensitive to changes in individuals across the whole trait space since all individuals in the trait space are involved in the computation of trait richness.

TOPM: In anticipation of a potential influence of population size (Fontana et al., 2016), we introduce a modified TOP (TOPM) which corrects for the number of individuals in the trait space.

,

N = number of individuals in the trait space

Evenness Indices

FEve (Villéger, Mason, & Mouillot, 2008) measures evenness by considering the regularity with which individuals of a species fill up a trait space (as each single individual has abundance equal to 1):

where , and is the branch length of a minimum spanning tree (see panel c in fig. 1) between individual *i* and any other individual *j*.

TED (Fontana et al., 2016) is a relative comparison between the distribution of Euclidean distances among individuals in an observed trait space to that of a hypothetical or reference trait space filled with evenly distributed individuals (discrete regular grid). TED is essentially a measure of how close the observed Euclidean distance distribution is to that of the reference distribution.

We also introduce TEDM, whichis similar in concept and definition to the TED index with two modifications. The first modification involves replacing the even distribution based on a discrete, regular grid, with simulated trait values from a continuous uniform distribution since it better characterises the definition of trait evenness. The second modification involves limiting the comparison in evenness to the space covered by the observed trait values. This modification ensures that the comparison does not include trait values outside those in the observed trait space (see appendix A2 for more on these modifications).

Divergence Indices

Rao’s(Rao, 1982) quadratic entropy expresses intraspecific divergence as the average difference between individuals. It is computed by weighing the total distances between individuals in the trait space by their relative abundances:

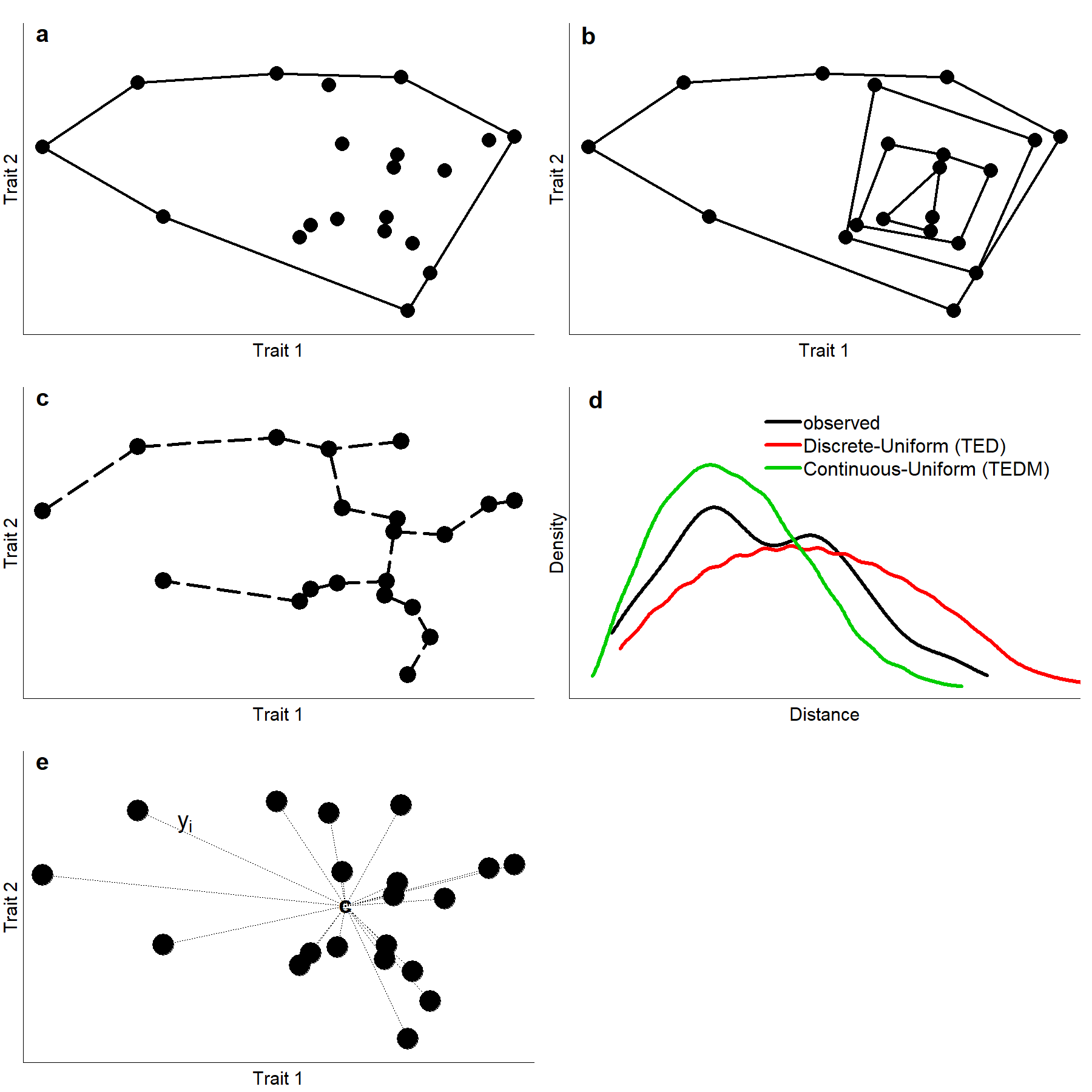
*D* is a matrix of Euclidean distances between individuals and *w*is a vector of relative abundances, (since each individual has an abundance of 1 relative to the total number of individuals in the trait space)*,* where *N* is the number of individuals in the trait space.

FDis(Laliberte and Legendre, 2010)**,** functional dispersion, measures functional diversity as the average distance of species to the centroid of species in the community. Developed based on the multivariate dispersion of Anderson et al. 2006:

,

whereis a vector representing the position of the individual in the trait space, is the trait value of the individual and ***c*** is a vector containing the centroid of the trait.

Simulation Framework

**Figure 1**: A hypothetical population of individuals represented in a two-dimensional trait space. Panel a: The volume of the red polygon (minimum convex-hull encompassing all individuals) gives the FRic. Panel b: TOP is the sum of the area of all peelable convex-hull (black polygons). Panel c: FEve examines the regularity of the branch length from one individual to the other in the minimum spanning tree (dotted line connecting all individuals). Panel d: TED compares the density distribution of Euclidean distances of the observed trait data with density distribution of Euclidean distances from a discrete uniform, and TEDM does the same but it uses a continuous uniform distribution. Panel e: FDis is the average of the , where each is the distance of a trait value of individual *i* to that centre ***c***.

To evaluate these indices for the criteria (*i*) – (*iii*) listed above, we simulated populations

composed of individuals located in a 2D trait space. We sampled continuous trait values from a bivariate trait space that was assumed normal or uniformly distributed. We considered three scenarios. Scenario one involves shifts of the trait values of one part of the population, akin to disruptive selection leading to a speciation event, i.e. the formation of a second cluster in trait space. To simulate this, we started with a bivariate normal trait space (2 traits spread around a mean value of 5 and 10 on axis one and two, respectively), and gradually  shifted the mean of 20% of the individuals in the trait space (addition of 0.5 to their trait values) along trait axis one till their mean on this axis is twice the starting mean. Scenario two involves shifting 10%-50% of individuals closest to the centre of a bivariate uniform trait space trait space away from the center. This scenario represents selection against trait combinations located in the center of trait space. Scenario three involves adding more individuals randomly to a bivariate normal trait space with the same means as in scenario one. We kept the properties of the trait space constant while individuals randomly enter into the trait space such that its size grows from 50 to 3000 individuals.

Desired trends from the three scenarios

In scenario one, trait richness and divergence should increase, but trait evenness should decrease after an initial increase. We expect these trends because shifting a percentage (20%) of the individuals in the trait space to another part of the trait space results in increasing trait differentiation (divergence) and trait space expansion (richness). Furthermore, we expect an initial increase in evenness because  the points are at some point be more evenly spread across the space than initially (panel B in fig. 2). However, one loses evenness as soon as clusters start forming (panel C in fig. 2). In scenario two, trait divergence should increase while trait richness and evenness decrease. We expect these trends because the loss of trait combinations at the centre of the trait space; increases trait differentiation (divergence), makes the trait space less rich, and individuals are no longer evenly spread across the trait space (panel E-G in fig. 2). In

**Figure 2**: An example of three cases arising from each simulation scenario and the expected trend for each ITD component. Panel D, H and M presents the expected trends in each scenario.

scenario three,  we believe that a trait index measuring trait diversity should not reveal any pattern along the gradient of sample size (number of individuals in the trait space). Therefore, we demanded the indices to not change with the number of individuals (panel I-K in fig. 2).

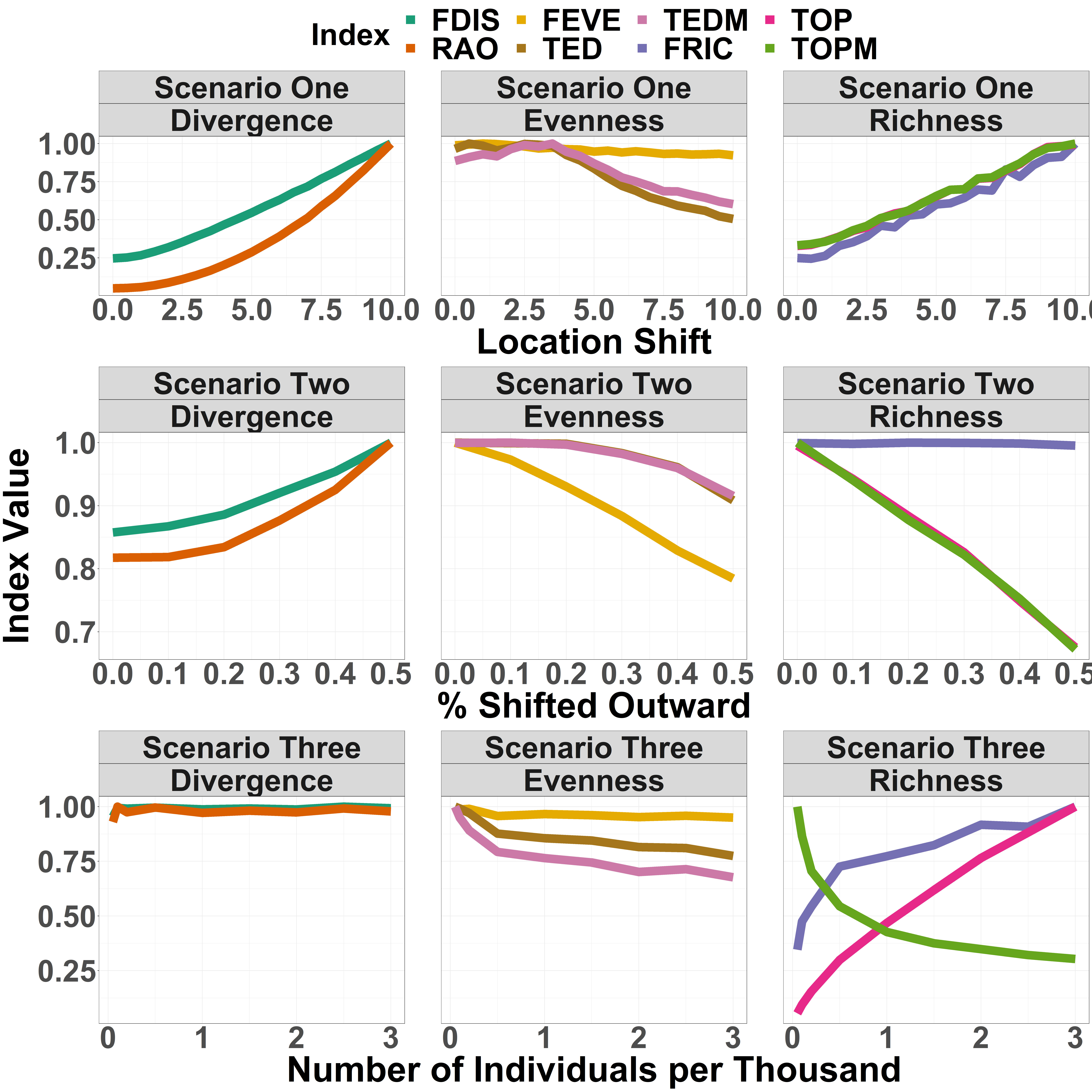
We evaluate criterion *i* based on the definition, implementation and known mathematical properties of these indices. We evaluate criterion *ii* based on whether  these indices matched the desired  trends in scenarios one and two, and we assess criterion *iii* from the results obtained in scenario three. For each scenario, we simulate trait values and compute the indices five times (because of computational time), making five replicates which allow us to examine the variability of these indices in all scenarios considered. All simulations were performed using R (R Core Team, 2012), version 3.5.3.

Calculation of indices and settings

We used the *dmvnorm* function in the mvtnorm package (Mi, Miwa, & Hothorn, 2009) to simulate trait values in the bivariate normal case, and the *runif* function in base R to simulate trait values for the bivariate uniform case. To compute the TED, we simulated the reference trait matrix from a 2-dimensional square using the *geozoo* package (Schloerke, Wickham, Cook, & Hofmann, 2016). For TEDM, we simulated the reference trait matrix using the *runif* function. We used the FD package (Laliberté & Legendre, 2010) to compute FEve, FRic, FDis and Rao, and the *geometry* package (Barber et al., 2015) to compute convex-hulls for TOP, TEDM and TOPM.

**Results**

The trait divergence indices considered satisfies criteria *i*, while one of the evenness and two of the richness indices fail to meet this criteria. FEve and TEDM are mathematically consistent because the former is an absolute index, while the latter compares evenness in continuous traits data with evenness from a simulated continuous data, i.e. like for like. TED is not consistent, and thus violates criterion *i* because the reference trait matrix obtained from the *geozoo* package is discrete (see appendix A2), while many trait data represent continuous traits, as is the case in this article and arguably in most experimental and observational studies **(put some refs here**). Therefore, TED is comparing evenness in continuous traits data with evenness in simulated discrete traits data. FRic also satisfies criterion *i* since it is also an absolute measure. As a direct consequence of its definition, i.e. summation of the area of peelable

**Figure 3**: Observed trends for each scenario. The plots are obtained by averaging the computed indices across the five replicates and rescaling the results to the 0-1 interval. For scenario one and two, the TOPM line covers much of the TOP line because they had similar values after rescaling. We expected this since TOPM is TOP scaled by the number of individuals in the trait space.

convex-hulls, TOP (TOPM) changes in a discontinuous way when individuals move from one convex hull to another (see appendix A1). Thus both fail to satisfy criterion *i*.

In terms of criterion *ii*, both trait divergence indices considered gave expected trends for trait divergence. They increased with increasing trait differentiation in both scenarios (figure 3). One or more of the trait evenness indices failed at producing the desired trends in either of scenario one or two. In scenario one (disruptive selection), TED and TEDM captured the initial increase in trait evenness while FEve did not. Furthermore, FEve responded slowly to decrease in trait evenness afterwards. In scenario two, FEve responded quickly to the loss of trait combinations at the center of the trait space in scenario two, while TED and TEDM responded slowly to this loss. The first reaction of both TED and TEDM to this loss of trait combinations came after almost 30% of the trait combinations at the center were lost (scenario 2 in figure 3). All trait richness indices produced the expected trends for trait richness in scenario one, but FRic failed at producing the desired trend in scenario two. From its definition, it becomes clear the FRic will only be sensitive to changes in individuals at the edges of the trait space. Thus, it remained constant despite the loss of trait combinations at the center of the trait space, and did not capture the decreasing trait richness in scenario two.

For criterion *iii*, trait divergence indices were not sensitive to the number of individuals in the trait space in scenario three, while trait evenness and richness indices were sensitive to

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  |  | Criterion 1 | Criterion 2 | | Criterion 3 |
| Facets | Index |  | S1 | S2 |  |
| Richness | FRic | **+** | **+** | **-** | **-** |
|  | TOP | **-** | **+** | **+** | **-** |
|  | TOPM | **-** | **+** | **+** | **+\*** |
| Evenness | FEve | **+** | **-** | **+** | **+\*** |
|  | TED | **-** | **+** | **+\*** | **-** |
|  | TEDM | **+** | **+** | **+\*** | **-** |
| Divergence | FDis | **+** | **+** | **+** | **+** |
|  | Rao | **+** | **+** | **+** | **+** |

**Table 1.** Performance of the examined trait diversity indices under the criterion of interest. **+** = satisfactory, **+\*** = less satisfactory, **–** = unsatisfactory. S1 describes disruptive selection and trait expansion, and S2 describes selection against trait combinations at the center of the trait space.

the number of individuals in the trait space. Both trait divergence indices considered remained constant relative to the number of individuals in the trait space (scenario 3 in fig. 3), thereby satisfying criterion *iii*. Trait evenness indices decreased with increasing number of individuals. This decrease is more pronounced in TED and TEDM, but less so in FEve. Therefore, these indices did not produce the desired trend, thus failing to meet criterion *iii*.Trait richness indices increased with increasing number of individuals in the trait space except for TOPM (scenario 3 in fig. 3). Thus, these indices did not produce the desired trend for scenario three.

**Discussion**

Empirical and theoretical ecologists often use trait diversity indices such as those evaluated in this study to develop and test theories about - or to understand the effects of environmental factors on - components of trait diversity (Botta-Dukát & Czúcz, 2016; Craven, Hall, Berlyn, Ashton, & van Breugel, 2018; Fontana et al., 2018). Thus, a proper understanding of their properties and limitations is crucial for their application.

*Criterion i: Acceptability, logic and consistency*

Criterion *i* requires that ITD indices  are consistent with the logic underpinning their creation and, if based on comparisons between reference and sampled trait data, that such comparisons are  valid. Our results show that all the divergence indices, while two of the richness indices and one of the evenness indices do not satisfy this criterion.

Fontana et al., 2016 showed that the TOP (by extension TOPM) always increases with the appearance of unique trait combinations in any part of the trait space (monotonicity). However, our analysis show both of them to be discontinuous functions at some points (Appendix 1, figure A1 in supporting information). We observe an increasing TOP trend that always reset back to the same value at point where the red point becomes a part of another convex hull (the red point has exactly the same values as one individual in that convex hull). This means that the increasing trends discontinues when individuals end up with the same trait. This makes them unsuitable for studying trends in individual-level trait richness if individuals. It is important that we state that the discontinuity is proportional to the distance between the convex hulls, so if you have many individuals and many hulls (which is probably often the case) then these discontinuities will not be large.

TED violates criterion *i* because, it involves the use of reference trait values from a trait space that is arguably dissimilar to the observed one (Appendix 2, figure A2 in supporting information). However, our results do not show this to be of significant concern when TED is applied since it performed similarly as its modified version in all the scenarios considered. Therefore, the use of distance distribution from either a discrete or continuous uniform distribution trait space as reference does not influence TED performance as a measure of trait evenness. However, TEDM is more appropriate to use as pointed out in appendix 2.

*Established Intuition and ideas*

ITD indices should reflect established intuition and ideas to enable proper interpretation of findings about trait evolution, i.e. they should produce values or trends that conform to expectation in well understood ecological scenarios.

It is known that FRic remains unchanged when unique trait combinations appear within the edges of the trait space, and it is very sensitive to extreme trait values (Cornwell & Ackerly, 2009; Fontana et al., 2016; Legras et al., 2018; Schleuter et al., 2010). This makes it unsuitable for measuring individual-level trait richness. This index should instead be defined as a multidimensional range and is not a proper measure of trait richness as it is commonly defined (Fontana et al., 2016; Schleuter et al., 2010). Also, FRic does not embody the concept of trait richness when the edges of the trait space are unaffected since it totally ignores trait values that are not at the edge of the trait space. Despite these shortcomings, FRic can be applied in studies about trait space expansion as indicated by our results from scenario one.

FEve will respond to changes in regularity of the distaces (branch length) between individuals in the trait space (Schleuter et al., 2010; Villéger et al., 2008), while TED (TEDM) will respond to change in distance distributions (Fontana et al., 2016). This explains the performance of these indicies in scenario one and two. Our results showed FEve to be more sensitive to loss of trait combinations at the centre of the trait space, while TED (TEDM) were more sensitive to increase in evenness due to trait expansion. One could miss some deviations between distance distributions used for TED (TEDM), if the comparion metric used is not sensitive. Thus, the sensitivity of TED (TEDM) to changes in trait evenness is dependent on the comparison metric used (Fontana et al., 2016). Both index could not dectect the decreasing evenness because the comparison metric (Kullback-Leibler divergence, Joyce, 2011) only identified a difference between the two distance distributions after loss of thirty percent of the traits at the center. FEve not capturing the initial increase caused by the trait expansion in scenario one is due to its lack of an even reference. FEve’s dependence on regularity of branch length makes it more sensitive to removal of branches altogether (scenario two). Fontana et al. ( 2016) and Schleuter et al. (2010) already identified other situations where the FEve is not accurate.

*Independence from the number of individuals*

For studies involving a factor that could affect both the number of individuals in the trait space and ITD, the effect of the factor on both should be separated. Our results show that only the divergence indices satisfy this criterion, while none of the evenness and richness indices satisfy this criterion. We must point out that it is difficult to think of an individual-level trait richness index (and possibly others) that will be entirely independent of the number of individuals. However, as earlier pointed out in the introduction, the ideal index should approach an asymptote. All three evenness indices and TOPM are clearly approaching an asymptote with increasing number of individuals (fig. 3). This suggests that given a certain number of individuals (< 1000 for FEve and > 3000), these indices will be independent of the number of individuals used in computing them. Fontana et al. (2016) already pointed out the dependence between TOP and the number of individuals in the trait space. They suggested a bootstrap across different samples to break this dependence. However, this approach could become computationally demanding.

Recommendations

Although, Fontana et al. (2016) presents some arguments for the use of FDis over Rao, we discovered no issues with the use of either in measuring individual-level trait divergence. Both of them satisfy the proposed criteria, and our results does not show any advantage of using one over the other. Furthermore, we recommend the use of TEDM or TED over FEve for measuring trait evenness except in cases where the comparison metric used is not sensitive. However, if the number of individuals in the study is below three thousand and computational resources are limited, FEve is preferred. Finally, we recommend the use of TOPM for measuring trait richness over TOP and FRic, if the number of individuals is at least three thousand. In this case, bootstrapping across sample will still be required for TOP, but not for TOPM. Either TOPM or TOP can be used if the number of individuals in the study is not of concern. FRic is only recommended in studies about trait expansion.

In general, we recommend examining proposed ITD indices in the light of the proposed criteria, because doing this informs the proper use despite their pitfalls.

**Conclusion**

Several studies have carried out simulations to evaluate and understand the performance of ITD indices under different contexts (Botta-Dukát & Czúcz, 2016; Carmona et al., 2016; Fontana et al., 2016; Grün & Leisch, 2007; Lefcheck, Bastazini, & Griffin, 2015; McPherson, Yeager, & Baum, 2018; Ricotta, 2005; Schleuter et al., 2010). Our work takes this further by proposing a set of unified criteria to assess these indices. We also showed that application of these indices, except for the divergence indices, can result in misleading results and conclusions based on some of the pitfalls identified in this study. Furthermore, we identified situations where researchers can still apply these indices despite their shortcomings.

**Acknowledgements**

Olusoji O. D. received funding support from the Bijzonder Onderzoeksfonds (BOF) co-operation between Hasselt University and Université de Namur through the application prepared by Aerts M., De Laender F. and Neyens T. F. De Laender acknowledges funding from the Special Research Fund’s Concerted Research Action (ARC) DIVERCE.

**Authors’ contributions**

Aerts M., De Laender F., Fontana S., Neyens T. and Spaak J. W. edited the manuscript. De Laender F., Aerts M., Fontana S. and Olusoji O. D. developed the simulation scenarios. Spaak J. W. developed part of the motivation for TOPM and the evaluation of TOP. Olusoji O. D. wrote the code and manuscript.

**References**

Baert, J. M., Jaspers, S., Janssen, C. R., De Laender, F., & Aerts, M. (2017). Nonlinear partitioning of biodiversity effects on ecosystem functioning. *Methods in Ecology and Evolution*, *8*(10), 1233–1240. https://doi.org/10.1111/2041-210X.12804

Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., … Vasseur, D. A. (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology and Evolution*. https://doi.org/10.1016/j.tree.2011.01.009

Botta-Dukát, Z., & Czúcz, B. (2016). Testing the ability of functional diversity indices to detect trait convergence and divergence using individual-based simulation. *Methods in Ecology and Evolution*. https://doi.org/10.1111/2041-210X.12450

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., … Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*. https://doi.org/10.1038/nature11148

Carmona, C. P., de Bello, F., Mason, N. W. H., & Lepš, J. (2016). Traits Without Borders: Integrating Functional Diversity Across Scales. *Trends in Ecology and Evolution*. https://doi.org/10.1016/j.tree.2016.02.003

Cornwell, W. K., & Ackerly, D. D. (2009). Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*. https://doi.org/10.1890/07-1134.1

Cornwell, W. K., Schwilk, D. W., & Ackerly, D. D. (2006). A trait-based test for habitat filtering: Convex hull volume. *Ecology*. https://doi.org/10.1890/0012-9658(2006)87[1465:ATTFHF]2.0.CO;2

Craven, D., Hall, J. S., Berlyn, G. P., Ashton, M. S., & van Breugel, M. (2018). Environmental filtering limits functional diversity during succession in a seasonally wet tropical secondary forest. *Journal of Vegetation Science*. https://doi.org/10.1111/jvs.12632

de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J. H. C., Bardgett, R. D., … Harrison, P. A. (2010). Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation*. https://doi.org/10.1007/s10531-010-9850-9

De Laender, F., Melian, C. J., Bindler, R., Van den Brink, P. J., Daam, M., Roussel, H., … Janssen, C. R. (2014). The contribution of intra- and interspecific tolerance variability to biodiversity changes along toxicity gradients. *Ecology Letters*, *17*(1), 72–81. https://doi.org/10.1111/ele.12210

De Laender, F., Rohr, J. R., Ashauer, R., Baird, D. J., Berger, U., Eisenhauer, N., … Van den Brink, P. J. (2016). Reintroducing Environmental Change Drivers in Biodiversity–Ecosystem Functioning Research. *Trends in Ecology and Evolution*, *31*(12), 905–915. https://doi.org/10.1016/j.tree.2016.09.007

Fontana, S., Jokela, J., & Pomati, F. (2014). Opportunities and challenges in deriving phytoplankton diversity measures from individual trait-based data obtained by scanning flow-cytometry. *Frontiers in Microbiology*. https://doi.org/10.3389/fmicb.2014.00324

Fontana, S., Petchey, O. L., & Pomati, F. (2016). Individual-level trait diversity concepts and indices to comprehensively describe community change in multidimensional trait space. *Functional Ecology*, *30*(5), 808–818. https://doi.org/10.1111/1365-2435.12551

Fontana, S., Thomas, M. K., Moldoveanu, M., Spaak, P., & Pomati, F. (2018). Individual-level trait diversity predicts phytoplankton community properties better than species richness or evenness. *ISME Journal*, *12*(2), 356–366. https://doi.org/10.1038/ismej.2017.160

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., … Bommarco, R. (2015). Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1801). https://doi.org/10.1098/rspb.2014.2620

Gross, N., Bagousse-Pinguet, Y. Le, Liancourt, P., Berdugo, M., Gotelli, N. J., & Maestre, F. T. (2017). Functional trait diversity maximizes ecosystem multifunctionality. *Nature Ecology and Evolution*. https://doi.org/10.1038/s41559-017-0132

Grün, B., & Leisch, F. (2007). FlexMix: An R package for finite mixture modelling. *R News*.

Hillebrand, H., & Matthiessen, B. (2009). Biodiversity in a complex world: Consolidation and progress in functional biodiversity research. *Ecology Letters*. https://doi.org/10.1111/j.1461-0248.2009.01388.x

Joyce, J. M. (2011). Kullback-Leibler Divergence. In *International Encyclopedia of Statistical Science*. https://doi.org/10.1007/978-3-642-04898-2\_327

Kusumoto, B., Shiono, T., Miyoshi, M., Maeshiro, R., Fujii, S. jiro, Kuuluvainen, T., & Kubota, Y. (2015). Functional response of plant communities to clearcutting: Management impacts differ between forest vegetation zones. *Journal of Applied Ecology*. https://doi.org/10.1111/1365-2664.12367

Laliberte, E., Legendre, P., Ecology, S., & January, N. (2010). A distance-based framework for measuring functional diversity from multiple traits A distance-based framework for measuring from multiple traits functional diversity. *Ecology*. https://doi.org/10.1890/08-2244.1

Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Lefcheck, J. S., Bastazini, V. A. G., & Griffin, J. N. (2015). Choosing and using multiple traits in functional diversity research. *Environmental Conservation*. https://doi.org/10.1017/S0376892914000307

Legras, G., Loiseau, N., & Gaertner, J. C. (2018). Functional richness: Overview of indices and underlying concepts. *Acta Oecologica*. https://doi.org/10.1016/j.actao.2018.02.007

Mason, N. W. H., Mouillot, D., Lee, W. G., & Wilson, J. B. (2005). Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos*. https://doi.org/10.1111/j.0030-1299.2005.13886.x

McPherson, J. M., Yeager, L. A., & Baum, J. K. (2018). A simulation tool to scrutinise the behaviour of functional diversity metrics. *Methods in Ecology and Evolution*. https://doi.org/10.1111/2041-210X.12855

Naeem, S., & Wright, J. P. (2003). Disentangling biodoversity effects on ecosystem functioning: deriving solutions to a seemingly insormountable problem. *Ecology Letters*. https://doi.org/10.1046/j.1461-0248.2003.00471.x

Oliveira, A. G., Baumgartner, M. T., Gomes, L. C., Dias, R. M., & Agostinho, A. A. (2018). Long-term effects of flow regulation by dams simplify fish functional diversity. *Freshwater Biology*. https://doi.org/10.1111/fwb.13064

Rao, C. R. (1982). Diversity and dissimilarity coefficients: A unified approach. *Theoretical Population Biology*. https://doi.org/10.1016/0040-5809(82)90004-1

Reiss, J., Bridle, J. R., Montoya, J. M., & Woodward, G. (2009). Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology and Evolution*. https://doi.org/10.1016/j.tree.2009.03.018

Ricotta, C. (2005). A note on functional diversity measures. *Basic and Applied Ecology*. https://doi.org/10.1016/j.baae.2005.02.008

Schleuter, D., Daufresne, M., Massol, F., & Argillier, C. (2010). A user’s guide to functional diversity indices. *Ecological Monographs*. https://doi.org/10.1890/08-2225.1

Sfair, J. C., Rosado, B. H. P., & Tabarelli, M. (2016). The effects of environmental constraints on plant community organization depend on which traits are measured. *Journal of Vegetation Science*. https://doi.org/10.1111/jvs.12453

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., & Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science*. https://doi.org/10.1126/science.277.5330.1300

Villéger, S., Mason, N. W. H., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*. https://doi.org/10.1890/07-1206.1

Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Wohlrab, S., Tillmann, U., Cembella, A., & John, U. (2016). Trait changes induced by species interactions in two phenotypically distinct strains of a marine dinoflagellate. *ISME Journal*, *10*(11), 2658–2668. https://doi.org/10.1038/ismej.2016.57