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

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**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 fulfil 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 all six 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 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 moving 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 interpret 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 quantify ITD.

**Key-words:** divergence, evenness, individual-level trait diversity, richness, statistical ecology, trait diversity indices

**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 (Barabás & D’Andrea, 2016; 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).

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 implementation). For example, an index that measures ITD by comparing discrete trait values with a continuous reference trait distribution, or the other way around, is not consistent. Conceptual consistency ensures that the index returns a value that bears a biological meaning.
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  individuals with unique traits, this can be challenging to interpret. Evaluation of trait indices in the literature have mainly 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 variable on ITD do not mistake effects on abundance (sample size) for effects on ITD.

These three criteria generalise the different requirements for trait diversity indices mentioned in the literature. For example, the monotonicity (trait richness should increase with the addition of unique trait combinations) and twinning (trait richness should flatten with the 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, the requirement by Schleuter et al. (2010) 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 using the three above-mentioned criteria. We selected indices based on the criteria laid out in Fontana, Jokela, & Pomati, 2014. The indices include 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, and criteria *ii* and *iii* 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. 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.

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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’squadratic entropy (Rao, 1982) 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 (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.

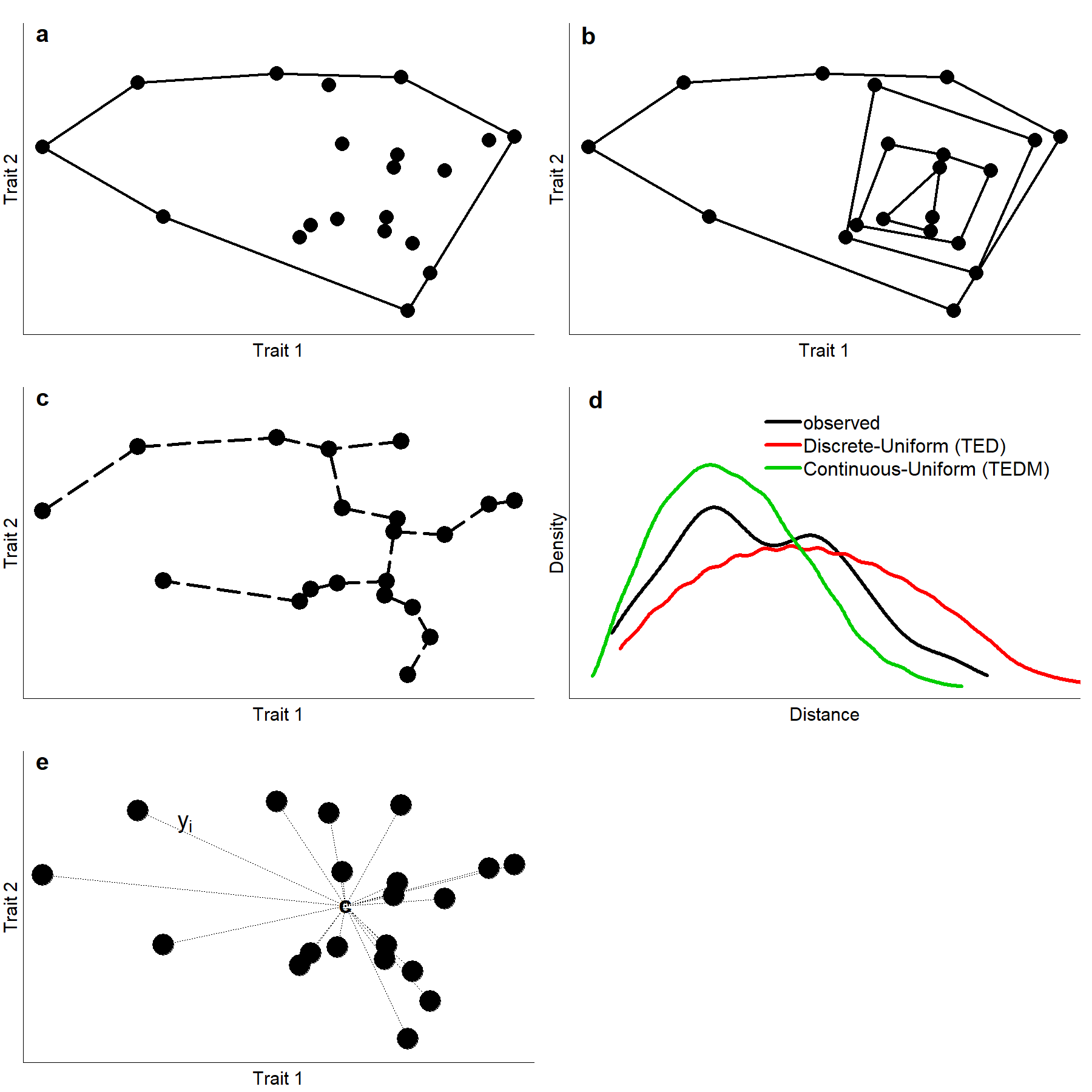
FDis(Laliberte and Legendre, 2010)**,** functional dispersion, measures functional diversity as the average distance of species to the centroid of species in the community. It is developed based on the multivariate dispersion of Anderson et al. 2006:

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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*

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 normally 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

**Figure 1**: A hypothetical population of individuals represented in a two-dimensional trait space. Panel a: The volume of the black polygon (minimum convex-hull encompassing all individuals) gives the FRic. Panel b: TOP is the sum of the area of all peelable convex-hulls (black polygons). Panel c: FEve examines the regularity of the branch length from one individual to the other in the minimum spanning tree (the 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 instead. Panel e: FDis is the average of the , where each is the distance of a trait value of individual *i* to that centre ***c***.

mean value of 5 and 10 on axis and two respectively), and gradually shifted the mean of 20%

(addition of δ = 0.5 to their trait values) along trait axis one till their mean on this axis is twice their initital 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 expected 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 expected an initial increase in evenness because  the points will at some point be more evenly spread across the space than they were initially (panel B in Fig. 2). However, we expected evenness loss 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 makes individuals no longer evenly spread across the trait space (panel E-G in Fig. 2). ). In scenario three,  we believe that a trait index should not change with the 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 evaluated criterion *i* based on the definition, implementation and known mathematical properties of these indices. We evaluated 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 from scenario three. For each

**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 present the expected trends in each scenario.

scenario, we simulated trait values and computed 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. We all the simulations performed using R (R Core Team, 2012), version 3.5.3.

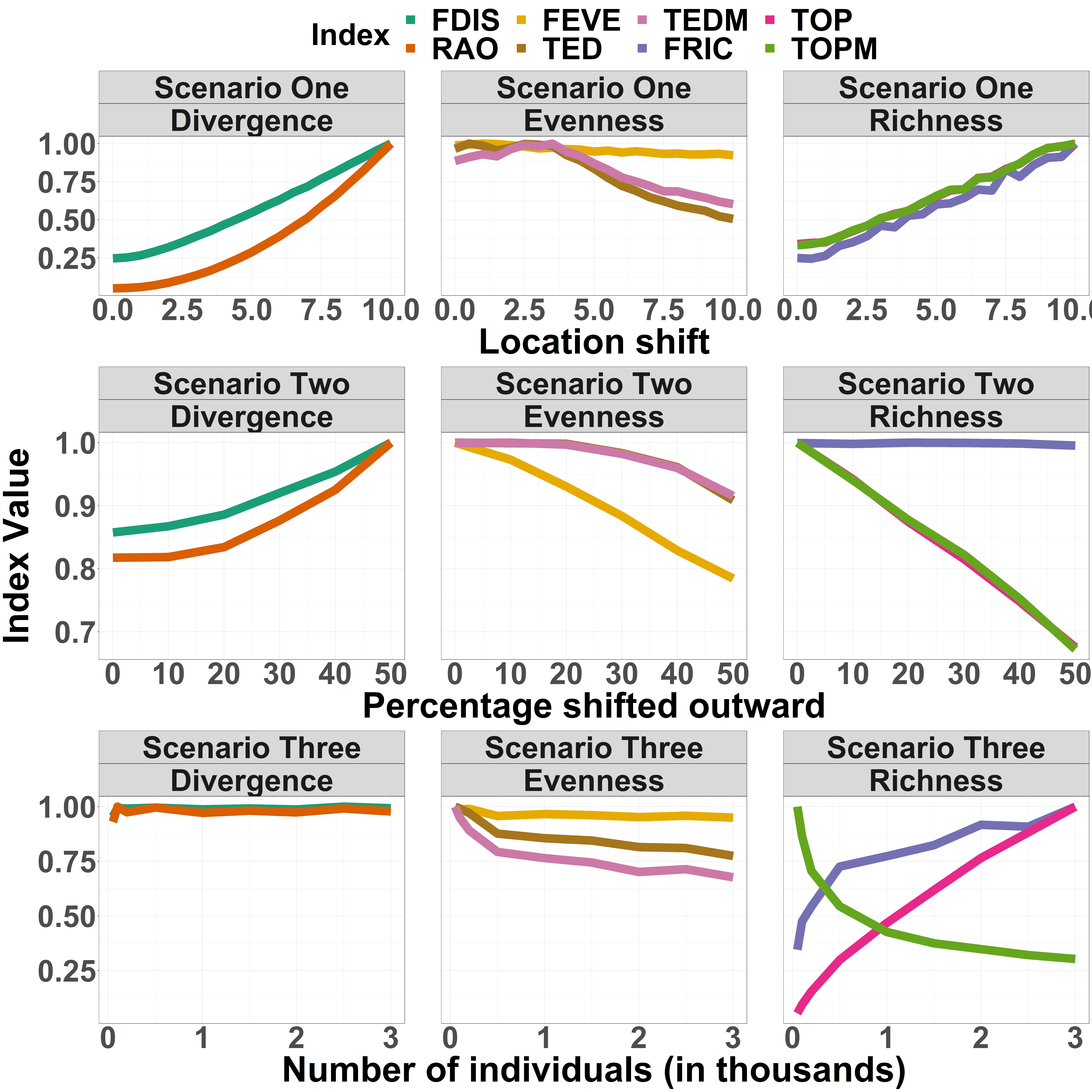
*Calculation of indices and settings*

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 satisfied criterion *i*, while one of the evenness and two of the richness indices failed to meet this criterion. FEve and TEDM are mathematically consistent because the former is an absolute index (with no reference), while the latter compares evenness in continuous traits data with evenness from a simulated continuous data. 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 many experimental and observational studies (Kattge et al., 2011; Litchman, Klausmeier, Schofield, & Falkowski, 2007). FRic satisfies criterion *i* since it is essentially a volume (an absolute measure). As a direct consequence of its definition, i.e. summation of the area of peelable convex-hulls, TOP (TOPM) changed in a discontinuous way when individuals move from one convex hull to another (see appendix A1). Thus, both indices did not satisfy criterion *i*.

Both trait divergence indices considered met criterion *ii*, as they reproduced the desired positive response to trait differentiation in both scenarios (Fig. 3). One or more of the trait evenness indices failed at reproducing the desired trends in either of scenario one or two. In scenario one (disruptive selection), TED and TEDM reproduced the desired 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

 **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. All indices have low variance across the replicates in scenario one and two, while trait divergence indices are more variable than the rest in scenario three. 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.

at the center of the trait space in scenario two, while TED and TEDM responded slowly to this loss. The first response of both TED and TEDM to this loss of trait combinations occurred when at least 30% of the trait combinations at the center were lost (scenario 2 in Fig. 3). All trait richness indices reproduced the desired trends for trait richness in scenario one, but FRic did not for scenario two. From its definition, it becomes clear that 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 reflect 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

**Table 1.** Performance of the examined trait diversity indices under the criterion of interest. **+** = criterion satisfied, **–** = criterion not satisfied, \*criteria will be satisfied if number of individuals is at least three thousand, \*\*criteria will be satisfied if the number of individuals is at least five hundred.

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

the number of individuals in the trait space. Both trait divergence indices did not change with 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 was more pronounced for TED and TEDM, but less so for FEve. Therefore, these indices did not produce the desired trend, thus failing to meet criterion *iii*. Trait richness indices increased with the number of individuals in the trait space, except for TOPM (scenario 3 in Fig. 3). Thus, these indices did not reproduce the desired trend for scenario three.

The variability of the indices in scenario one and two is very low (Appendix 4, Fig A4 in supporting information) compared to scenario three. Trait divergence indices are most variable in scenario three when the number of individuals simulated is below five hundred. In this scenario, we observed that FDis is less variable than Rao, FEve and TEDM are less variable compared to TED, and TOP and TOPM are less variable compared to the FRic.

**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. We found that none of the currently available indices meets all three criteria put forward by us, except for the trait divergence indices.

*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 satisfy this criterion, while two of the richness indices and one of the evenness indices do not.

Fontana et al., 2016 showed that the TOP always increases with the appearance of unique trait combinations in any part of the trait space (monotonicity). However, our analysis shows that TOP, and also our TOPM, are discontinuous functions (Appendix 1, Fig A1 in supporting information). The increasing TOP trend jumps back to the same value at points where the red point joins another convex hull (panel B in Fig A1). At these jumps, the red point has exactly the same trait combinations as one individual in new convex hull it joined. This means that TOP trends discontinues when individuals evolve to have similar trait values. 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. This means that, in case there are many individuals and many hulls, for example of phytoplankton system (Haverkamp et al., 2009), 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, Fig 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.

*Criterion ii: Reflecting established intuition and ideas*

ITD indices should reflect established intuition and ideas to enable proper interpretation of findings about trait evolution. That is, they should produce values or trends that confirm expectation when applied to 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, rather it should instead be defined as a multidimensional range (Fontana et al., 2016; Schleuter et al., 2010). Despite these shortcomings, FRic can be applied in studies that address questions about trait based niche expansion (Pigot, Trisos, & Tobias, 2016), as indicated by our results from scenario one.

FEve will respond to changes in the 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 changes 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 and TEDM were more sensitive to trait expansion. TED and TEDM could not dectect the decreasing evenness because there was no change in the distance distribution of the simulated trait matrix until we have shifted thirty percent of the individuals away from the center of the trait space (Appendix 3 in supporting information). Furthermore, the sensitivity of TED (TEDM) is dependent on the comparison metric used (Fontana et al., 2016). 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 fails to produce desired results.

*Criterion iii: 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, one should be able to separate the effect of this factor on both. 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, an index should ideally approach an asymptote as more individuals enter into the trait space. All three evenness indices and TOPM are clearly approaching an asymptote with increasing number of individuals (Fig. 3). This suggests that from a certain number of individuals onwards (1000 for FEve and 3000 for TED and TEDM), these indices will be independent of the number of individuals. 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 down this dependence. However, this approach could become computationally demanding.

*Recommendations*

Although Fontana et al. (2016) present some arguments for the use of FDis over Rao, we found both satisfying the proposed criteria. Our results do 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 of anticipated minute change in trait evenness that may not lead to a change in the distance distribution (appendix A3). We recommend the use of FEve, if the number of individuals in the study is variable and below three thousand.

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, bootstrapping across samples 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 remains constant. FRic is only recommended in studies about trait expansion.

**Conclusion**

Several studies have carried out simulations to evaluate and understand the performance of ITD indices in 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 approach a step 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.

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**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. Olusoji O. D. wrote the code and manuscript.

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