

reproductive benefits, for example if they have an partner who is infertile, a condition that affects an estimated 6% of all men [10]. Supporting evidence for this adaptive ‘fertility assurance’ hypothesis comes from a study on couples where the husband suffered from male infertility, where 29% of the conceptions following a fertility treatment were found to be derived from extra-pair sexual interactions [11]. If approximately one third of all women with an infertile partner would pursue EPCs as a specific strategy to become pregnant, we would expect this to result in an EPP rate of approximately $6\%/3 = 2\%$, which is in the ballpark of both contemporary and historical EPP rate estimates (Figure 1). Under this hypothesis, EPP rates would be expected to remain approximately constant, and would be largely independent of the reliability of available contraception because the intention of woman in this case would be to become pregnant of an extra-pair mate.

Overall, it is clear that further research will be necessary to conclusively decide between these alternative hypotheses for why EPCs occur in humans, and what the motivation and possible adaptive value could be behind their occurrence.

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Appendix A Supplemental Information

Supplemental Information associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.tree.2016.06.012>.

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Letter

Pushing Past Boundaries for Trait Hypervolumes: A Response to Carmona *et al.*

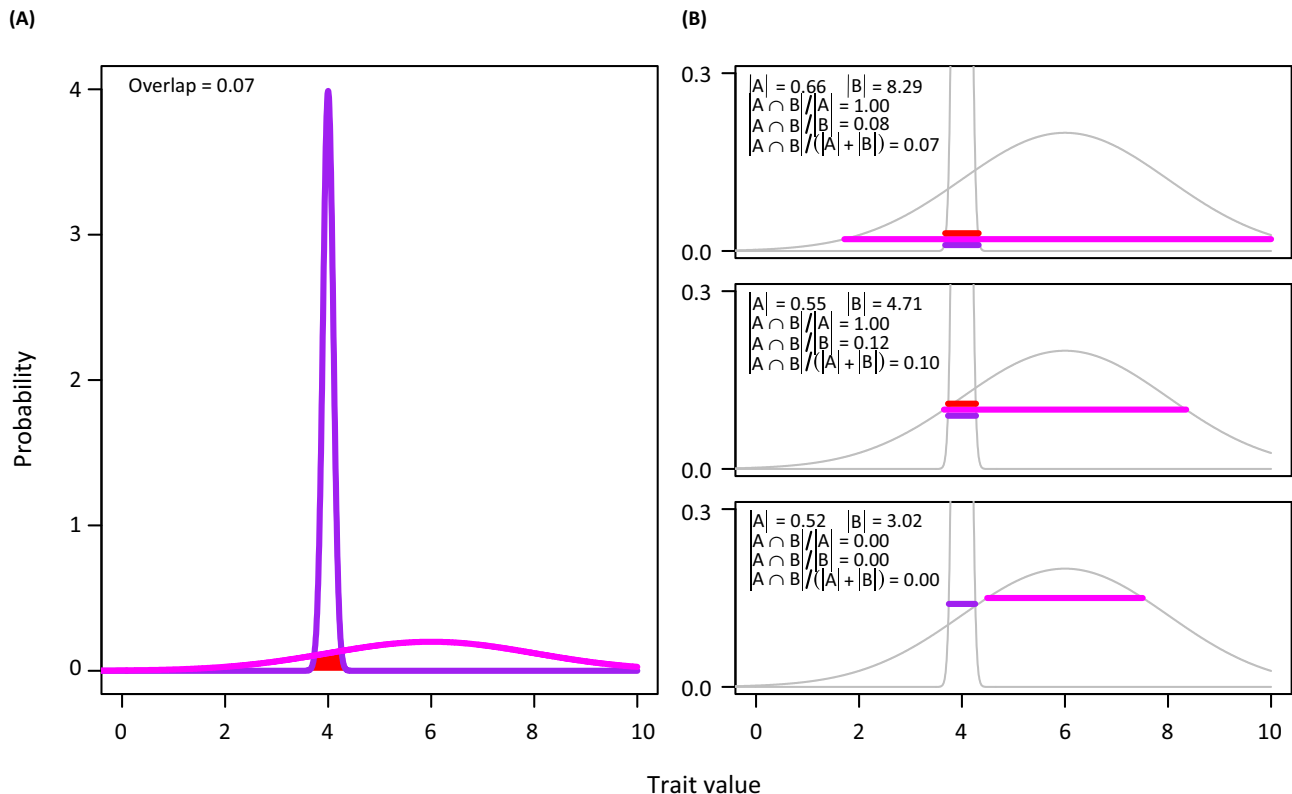
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Functional diversity (FD) has a key role in community assembly [1], biodiversity conservation [2], and ecosystem functioning [3]. Carmona *et al.* [4] recently proposed an approach for quantifying FD across scales using a probability density function (PDF; the distribution of values

along one or more functional trait axes) to better measure functional redundancy, overlap, and dissimilarity. Their work is timely because it builds on a growing interest in making biological inferences from functional traits, and is useful because it unifies functional diversity concepts. However, their approach may lead to inaccurate inferences because of statistical issues around using PDFs to infer trait distribution boundaries, and around transforming data.

Carmona *et al.* propose a fully probabilistic interpretation of trait distributions - that is, one where distributions do not have boundaries (Figure 1A) [4]. However, their illustrations are drawn with boundaries (e.g., their Figure 2 [4]). In general, when using PDFs for statistical inference, distributions are better understood when edges are delineated at a certain probability thresholds (Figure 1B). These edges allow for proper quantification of space within the PDF and, as such, are crucial when using PDFs to estimate FD metrics, such as richness (total space occupied) and redundancy (number of species per unit space occupied). If a threshold is not used to delineate edges, and the probability density estimated with a Gaussian kernel or any other function with non-zero probability density everywhere, then hypervolumes will have infinite boundaries that are not useful for analysis. Thresholds can be chosen either by fixing a value [5] or by using an algorithm [6]. Importantly, the choice of threshold can change the size and shape of the trait distribution, leading to different values of FD metrics and different inferences (e.g., overlap or no overlap) (Figure 1B).

Another issue in working without boundaries via a fully probabilistic assumption is that trait distributions must integrate to one, potentially leading to the biologically unrealistic overlap of multiple traits. Traits with wide ranges are forced into distributions that take very low values over most of their ranges, even if biological performance is high over that range.



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Figure 1. Contrasting Two Approaches for Trait Hypervolumes. The two example trait distributions are shown in purple (A) or magenta (B), with overlap indicated in red. (A) The probabilistic approach proposed by Carmona *et al.* [4] calculates a unique overlap value as the area of intersection between two distributions. When one distribution is much wider than another, this fractional value is always low. Additionally, because both distributions continue to infinite trait values, neither distribution can be assigned a clear boundary, making it difficult to quantify size. (B) The semiprobabilistic approach delineates boundaries at a selectable probability threshold. Depending on the threshold chosen, the size of each distribution ($|A|$ and $|B|$; horizontal colored lines) can differ, with higher thresholds generally leading to smaller sizes. Multiple overlap metrics (e.g., intersection as fraction of A and B or intersection as fraction of either A or B) can be calculated, providing additional insight into the type of overlap that is occurring. For some thresholds, the overlap may decrease to zero, providing a more detailed view of the shape of each distribution.

Overlap metrics will also always be low when one distribution is contained within another (Figure 1). Performing algebraic operations (e.g., weighted means or differences) on trait distributions is better achieved through thresholding distributions on functions that do not sum to one.

Carmona *et al.*'s conceptual approach for measuring functional redundancy can also be made more robust. They propose to count species in trait bins, weighted by the probability of that trait value [4]. Given that they estimate the trait probability density and number of species per bin from the same data source, combining these two quantities produces no more information than using either alone. Data binning also

loses information (as with histograms) and, therefore, functional redundancy can be measured more simply and accurately as the local probability density value at any point in the trait space.

Software tools already exist for estimating probabilistic thresholded n -dimensional hypervolumes for Gaussian distributions [7,8], for Gaussian mixture distributions [9], and for arbitrary geometries [5,10]. These tools scale well in high dimensionalities and permit analysis of large empirical data sets.

The data transformations proposed by Carmona *et al.* could lead to incorrect inferences. In particular, they propose that unscaled continuous data can be used for

analyses [4]. However, doing so would render results incomparable since their framework relies on calculating Euclidean distances and overlaps. Euclidean distance is only defined if all axes have the same units (e.g., meters). Thus, choosing dimensionless or common units is necessary. Data with incomparable units should be rescaled (e.g., via z-transformation) before analysis.

Carmona *et al.* also propose to integrate categorical and ordinal variables by dissimilarity-based ordination [4]. These variables must be handled carefully. Volume, distance, and overlap concepts require a metric distance, that is, one that satisfies the triangle inequality (where the trait distance from species or community A to C is

no greater than the distance from A to B plus the distance from B to C). Without a metric distance, if A and B are similar and B and C are similar, there is no guarantee that A and C will also be similar. In general, basing functional diversity calculations on distances from non-metric dissimilarity coefficients will lead to non-interpretable results. Probabilistic approaches should only be applied to continuous axes or to categorical axes where the triangle inequality is satisfied for distances. Gower dissimilarity has this property [11] and can be used for mixed categorical/continuous data, but many other metrics do not.

In summary, the conceptual framework proposed by Carmona *et al.* proposes a useful and novel research agenda, but is limited by the approaches that have been proposed to implement it. Fortunately, these limitations can all be overcome in the ways outlined above. By building on the robust tools that already exist for addressing this research agenda in a semiprobabilistic framework, trait-based ecology may come closer to reaching its goals [12].

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Letter

The Density Awakens: A Reply to Blonder

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 Jan Lepš^{1,4}

In a recent review [1], we presented a framework to estimate functional diversity (FD) across multiple scales using trait probability distributions (TPD). We are pleased to see that this approach has sparked interest quickly, particularly with Blonder's comment [2] acknowledging its utility. Particularly he raises a series of technicalities which, we agree, need to be considered when applying the framework, but which we did not have space to deal with in our original article. We address these technicalities in this letter.

In our view, the most relevant issues are the definition of 'boundaries' in TPD functions and the effects of trait data scaling and transformation. We recognise the importance of defining probability thresholds to delineate boundaries in TPD functions, an issue that applies to any attempt to estimate some FD metrics, such as functional richness [3]. As far as we are

aware, defining the boundaries of occupied trait space is an arbitrary exercise, with different thresholds and methods possible. Blonder [2] helpfully suggests that our framework could be coupled with multiple boundary definitions to allow a new class of FD-related questions [4]. Thus the availability of multiple possible thresholds can be viewed as much an opportunity as a problem. The main consideration is to clearly explain how boundaries are defined so that analyses are repeatable. In general, to obtain a stable estimate for boundary-dependent metrics, we advise to capture the vast majority (e.g., $\geq 99\%$) of the total TPD. However, the most appropriate threshold might vary depending on the questions addressed and the ecological context. This is an area that could greatly benefit from future research.

We are aware that trait scaling can affect several measures of FD [5] and a variety of standardizations are already available in the literature [6]. It should be noted that in our framework only functional divergence depends on the estimation of distances [1,6]. As such, our framework is, on the whole, scale-invariant (Figure 1). Indeed, we have previously shown that estimates of functional dissimilarity based on TPD overlap are independent of data transformation [7].

Blonder [2] raises concerns on some technicalities of our framework but we do not think they should worry users. We firmly reject his criticism of integrating TPD functions to unity. When trait values are concentrated in a particular portion of its range, then high density values are still possible. For example, the global spectrum of plant form and function [8] shows a highly concentrated occupancy of trait space within the widest possible range along with much less densely occupied areas. We feel it is by far preferable to let the distribution of density be wholly defined by the data rather than allowing it to be influenced by an arbitrary decision on where to place boundaries. We could