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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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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., ≥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

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Figure 1. Scale Invariance of FD Indices Using the TPD Approach. We used trait information on plant height (cm) and specific leaf area (mm² mg⁻¹) from 40 annual plant communities [12]. We estimated a bidimensional TPD_C of those communities considering these two traits, using either the traits in their original scale or zscored rescaled (converting traits to zero mean and unit variance), and used them to estimate the indices presented in [1]. Functional richness units (A) depend on the scale of the traits used, but there is perfect correlation among the two sets of traits. Functional evenness (B), functional divergence (C), dissimilarity between communities (D) and its nested component (E), and functional redundancy (F) are totally scale-invariant. Using the original trait scale eases interpretation and permits direct comparison of functional richness values between different studies, which is not possible when the transformed values depend on the range or standard deviation of values in the study dataset (i.e., when z-scores are used).

not see any justification in Blonder's statement that 'Performing algebraic operations (...) on trait distributions is better achieved through thresholding distributions on functions that do not sum to one.'

We also fail to see any substance in Blonder's criticisms of our functional redundancy estimator that might bring its validity into question. Our proposal to use binning is simply a way to make computations possible, especially considering that probabilities must be calculated under some range, not at individual points. Furthermore, the ecological concept of redundancy is inherently connected to species. Consequently, expressing it only in terms of probabilities, as Blonder

suggests, would not match what a measure of redundancy is expected to offer.

We still maintain that Principal Coordinates Analysis (PCoA) is a good solution for including categorical and ordinal variables and reducing dimensionality. Indeed, the scores on PCoA axes are classical quantitative variables. The problem of nonmetric dissimilarity measures in PCoA is a wellknown one, and there are solutions available [9,10]. Usually only a few PCoA axes are used, representing a high proportion of the dissimilarity structure of the data. Consequently, in practice the problem of negative eigenvalues and imaginary parts of the scores will not be of concern for users. Finally, we were indeed aware of (and cited vide ecologists with greater confidence in

in the original paper) existing software tools while preparing our framework [3,11]. However, we considered that our integrative proposal exceeds the scope of these tools. These and other technical aspects relating to the use of our framework will be covered soon when we release a new R package implementing it.

In summary, we do not feel that any of Blonder's concerns call in to question the utility and technical feasibility of the framework proposed by Carmona et al. [1]. Rather, we view this reply as an opportunity to address certain technical details that we were not able to cover in the original article. We hope that this will pro-

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applying our framework and embracing the fact that trait values are not uniformly distributed within hypervolumes; after all, the earth is round, like an orange.

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