**COMMENT**

**Choosing and using multiple traits in functional diversity research**

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**Defining functional traits**

Over the past several decades, the definition of functional traits (FTs) has become conflated and increasingly specialized. Here, we briefly summarize the history of the term, followed by the definition we have chosen to use for this Comment and why.

The FT concept appears to have evolved within the rich history of comparative plant ecology. By the mid-1990s, FTs were increasingly considered by researchers interested in understanding the relationship between plant morphological traits and key ecosystem processes (e.g., Hooper *et al.* 2005). This practice led to a widely-cited definition of FTs (Tilman 2001): ‘the range and value of species and organismal traits that influence ecosystem functioning.’ McGill *et al.* (2006) also made the distinction between traits writ large, or well-defined attributes used to compare across species, and FTs specifically, used to indicate organismal performance.

Lavorel & Garnier (2002) co-opted the performance-based definition under the guise of ‘effect traits,’ as opposed to ‘response traits,’ which define how organisms respond to, rather than shape, their environment. Violle *et al.* (2007) brought further specialization by proposing 10 separate categorizations for traits, only one of which they considered functional: ‘any trait which impacts fitness indirectly via its effects on [individual] growth, reproduction and survival.’ They argued that lumping together traits operating at different levels of organization (i.e., individuals, populations, ecosystems) could obscure the underlying mechanisms controlling community structure and functioning. Instead, they proposed the integration of traits into a hierarchy that represents how individual responses to environmental conditions translate to changes in individual performance, and ultimately influence community- and ecosystem-level properties.

While Violle *et al.* (2007) propose a sound framework for (functional) traits, we find it restricted by its elaborate complexity. For instance, consider plant tolerance to grazing. They argue that it should not be considered a FT, as it requires that one invoke external forces (i.e., grazers) in its definition. Rather, grazing tolerance is a function of individual characteristics, such as plant lifespan, height, and the presence of certain anatomical features, all of which fit their definition of FTs. Yet, if the goal of the analysis is to consider FTs within the context of primary production, the use of individual traits should lead to the same conclusion as the response trait defined by external factors. Thus, for many applications, it should not matter precisely where in the hierarchy traits fall, as long as we recognize that they have some explanatory relationship to the pattern or process under investigation. As a result, we have provided a broad definition based on the one found in Díaz *et al.* (2013) in the main text.

**Simulation study**

To understand the relationship between the number of traits, their degree of correlation, and species richness, we performed a simple simulation. We randomly generated data for 2-9 traits from a normal distribution N0,1 while varying the correlations among all traits from *r* = 0.01 to 0.99, using the function *mvrnorm* in the *MASS* package (Venables & Ripley 2002). We then repeated this analysis for a given number of species, from 10 to 100 in increments of 10. We set equal abundances for all species. We then calculated functional richness, evenness, and divergence (Villéger *et al.* 2008), functional dispersion (Laliberté & Legendre 2010), and Rao’s Q (Botta-Dukát 2005) from the trait data, using the default settings for the *dbFD* function in the *FD* package (Laliberté & Legendre 2010) in R version 3.1.0 (R Development Core Team 2014), with the exception of Rao’s Q. *dbFD* draws on the *divc* function in the *ade4* package, which calculates the square of the pairwise distances (as in Champely & Chessel 2002). While this transformation ensures the distance matrix is always Euclidean, we chose instead to follow the original definition as presented in Rao (1982), which does not square the pairwise distances. We provide the full R code as a supplement.

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**Figure S1** The relationship between five common indices of FD and the degree of correlation among traits using simulated data. Shading indicates the number of traits included in the analysis. Panels indicate increasing species richness from left to right, from 10-100 species in increments of 10. FDis = functional dispersion, FDiv = functional divergence, FEve = functional evenness, FRic = functional richness, RaoQ = Rao’s Q.

Functional dispersion and evenness were largely unaffected by correlations among traits (Fig. S1), as they both estimate the distribution of species in multidimensional trait space irrespective of its volume (Laliberté & Legendre 2010). However, we chose to fix species abundances to 1. It is possible that uneven distribution of individuals whose traits highly covary may cause functional evenness and dispersion to shrink. However, this clustering can represent a legitimate ecological phenomenon (e.g., environmental filtering, weak competitor exclusion), and we agree with Villéger *et al.* (2008) that it makes sense to retain traits in this context. Oppositely, functional richness and dispersion converge on small values irrespective of relative abundances (Fig. S1). Indeed, functional richness by design independent of abundance (Cornwell *et al.* 2006). Thus, we recommend careful consideration of trait correlations when using these indices. Rao Q showed no trend with increasing correlations, although this could also be a consequence of our choice to equalize species abundances (Botta-Dukát 2005). We recommend further simulations to understand whether there is any bias in these indices as a consequence of the uneven distribution of individuals in functional space.

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