A guide to use of the term functional trait

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Abstract

Functional traits are defined such as traits which affect individual fitness. I argue that the use of the term "functional trait" complicates the progress of the field of trait ecology because all traits are potentially linked to fitness. Obviating the potential link of all traits with fitness is related to dismissing (i) the integration of the phenotype, (ii) the spatio-temporal variation of environmental pressures and (iii) the genotype by environment interaction effect on the phenotype. These conceptual gaps could explain the weak predictive power of many functional ecology studies. I develop here some of the reasons why we should consider that all traits are related to fitness -advocating simultaneously for a change in terminology.

A guide to use of the term "functional trait"

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Traits are functional

Trait-based ecology relates individual fitness to ecosystem functioning, an integrated approach that beautifully surpasses traditional discrete levels of organization of life from organs to biomes. One promise of functional ecology is to predict ecosystem functions from values of traits involved directly or indirectly on such functions.

Functional traits are defined as traits that affect individual fitness (Violle et al. 2007), and represent ecological strategies that determine how plants respond to environmental factors, affect other trophic levels, and influence ecosystem properties (Pérez-Harguindeguy et al. 2013). I argue that all traits are potentially linked to fitness. To acknowledge the potential link of all traits to fitness considers *(i)* the integration of the phenotype, *(ii)* the spatio-temporal variation of environmental pressures, and *(iii)* the genotype by environment interaction effect on the phenotype. Here I develop reasons that support the case that all traits are related to fitness, and thus are functional by definition.

Relationships between traits and fitness are complex

The relationships between traits and fitness in a given environment are defined by multiple selective coefficients that shape the evolutionary course of populations. Natural Selection explains much of evolutionary processes that link variation in life expression with success in a given environmental context.

The total selection pressure on a given trait comprises the effects of direct, indirect and correlated selection on that trait. Selection of trait values may be direct, as when the environmental pressures affect the distribution of the values of a trait in the population. Or selection may be indirect, as when distribution of trait values is modified due to correlations with other traits under selection. Indirect selection occurs because phenotypes are an integration of realized multiple trait values within a single individual.

Also, selection may be correlated, as when it acts on particular trait combinations (Lande and Arnold 1983). For example, the combination of fruit size and seed size may be a cue for dispersers about pulp quantity. Thus, a negative correlation between these two traits may be related to higher dispersal success (Sobral et al. 2010). Traits may be pleiotropically correlated because they are related to the same genes and biosynthetic pathways. Other reasons for trait correlations include mechanistic relationships. In these relationships, mechanistic reasons preclude the existence of infinite combinations. An example of a mechanistic relationship would occur when the length of a given organ is correlated with the width. Although these traits could be codified by independent genes, and modified by independent selective pressures, the length and width are mechanistically related. The length of a fruit, for instance, must cohere with the width.

All these kinds of selective pressure can be linear or non-linear—that is, quadratic. (Phillips and Arnold, 1989). Quadratic selection implies a trait has different relationships with fitness. These relationships depend on the trait's own value, which causes non-linear selective curves. These curves may be concave or convex, where bimodal or unimodal distributions of the traits would be selected (Stinchcombe et al 2008). This analysis implies that the fitness-trait relationship is so complex that it may vary depending on the values of the trait itself.

Relationships between traits and fitness are defined within a context, but the context varies continuously

Selection coefficients and gradients measure the slope of the relationship between the realized values of a trait and the relative fitness (that is, individual fitness divided by average population fitness) of each individual within a population. But these trait-fitness relationships, or phenotypic selective pressures, make sense only in a given environmental context.

However, environmental contexts vary endlessly. The environment that affects a trait-fitness relationship is complex and acts at different levels. First, at the within-individual environment level (the phenotypic environment), values of a trait would have different fitness outputs depending on the values of other characters within the integrated phenotypes. These different fitness outputs may occur even when the abiotic and biotic environment is equal. This is due to the existence of indirect and correlated selection, as shown above.

Second, at the population environment level, a single trait may be related to different fitness outputs where trait values can be positive, neutral or negative depending on population parameters such as population density (see for example Yang et al 2018).

Third, at the community level, due to mutualistic and antagonistic interactions between species, the expected effects of traits on community composition loop back to modify the relationships between traits and fitness.

Last, at the ecosystem level, the abiotic and biotic environments continuously vary, spatially and temporally. These variations are particularly important, regarding the potential unpredictable shifts driven by Global Change.

Given all the direct and indirect sources of selection previously described, and because of the complexity laid out here of the selective pressures over the integrated phenotype and the varying environment, it is reasonable to argue that any trait would be related to fitness in at least one of the potential environments. That is, traits would be related to fitness depending on environmental variation. For example, a plant population would undergo strong selection on root traits during a drought year, and the same plant population would undergo strong selection on flower traits during a year with severe limitation of pollinators. Nonetheless, if we study the same population during a year with optimum precipitation levels and plenty of pollinators, we cannot argue that root traits or flower traits in this species are non-functional traits.

If in any one of all possible environments a potential link exists between the distribution of values of a trait and fitness, then all traits are potentially linked to fitness, and thus are functional by definition. Evolution happens through ecology, and the object of study in ecology -diversity at different levels- is the consequence of evolution. We cannot rend one from the other. Rather, ecology and evolutionary biology should be integrated in the study of causes and consequences of trait diversity, a possible start point is to acknowledge that all traits are functional.

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