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# Functional Traits

Charles A Nock, *Faculty of Biology, University of Freiburg, Freiburg, Germany*

Richard J Vogt, *Department of Biology, Trent University, Peterborough, Ontario, Canada*

Beatrix E Beisner, *Department of Biological Sciences, University of Quebec at Montreal, Montreal, Quebec, Canada*

## Advanced article

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**Functional traits are morphological, biochemical, physiological, structural, phenological or behavioural characteristics of organisms that influence performance or fitness. Grouping species by functional characteristics is a long-standing idea, but there has more recently been rapid development in the application of trait-based approaches to diverse topics in ecology. Two common applications of functional traits are to characterise community responses to changes in the environment, including community assembly processes, and to quantify the influence of community shifts on ecosystem processes. Practical decisions include: What types of traits should be considered? How can traits be measured or inferred? Are traits correlated or traded-off? Which, and how many, traits should be assessed? How should trait data be analysed? Functional trait approaches enhance ecological understanding by focusing on the mechanisms that govern interactions between organisms and their environments. Measuring and understanding traits increases our understanding of ecological processes, thus also informing conservation and restoration.**

## Introduction

Biodiversity is important for human well-being and for the provision and resilience of ecosystem services. Terrestrial and aquatic ecosystems provide many key services such as nutrient

cycling, water purification, climate regulation and cultural services. However, global anthropogenic changes are having widespread impacts on ecosystems, potentially reducing their ability to continue to provide these services. As such, there is an urgent and increasing need to accurately assess biodiversity, the factors influencing it and its influence on ecosystem structure and function. In recent years, ecologists have adopted an approach that focuses on the diversity of organismal functional traits. This approach enhances ecological understanding by focusing on characteristics that define how organisms interact with their surrounding physical, chemical and biological environments (reviewed in Hooper *et al.*, 2005). Still the definition of traits is not always straightforward, and functional traits have been viewed and applied in numerous ways in the ecological literature (for biodiversity and ecosystem function see also: [Biodiversity–Threats](#); [Biodiversity and Ecosystem Function of Decomposition](#); [The Role of Biodiversity](#) and for global change see: [Global Change – Contemporary Concerns](#)).

The functional traits at the heart of these approaches serve two goals: to characterise responses to changes in the environment including community assembly (called response traits), or those that quantify the influence that organisms can have on ecosystem processes (effect traits) (Violle *et al.*, 2007; Diaz *et al.*, 2013). Furthermore, traits can be of several types (i.e. continuous, categorical, ordinal, binary) and can result from varying degrees of measurement rigour (i.e. hard vs soft traits). In most cases to date, however, the increased research effort invested into the quantification of functional traits for biodiversity research has resulted in improved understanding of ecological phenomena (Tilman *et al.*, 1997; Diaz and Cabido, 2001; Petchey *et al.*, 2004; Hooper *et al.*, 2005; Vogt *et al.*, 2010).

Comparative studies have shown that biodiversity indicators that are explicitly based on functional traits can lead to a higher proportion of explained variation in ecosystem properties being studied, over more traditional diversity approaches based on species identity (Tilman *et al.*, 1997; Petchey *et al.*, 2004; Cadotte *et al.*, 2011; Weithoff *et al.*, 2015). Moreover, studying the relationships between important organismal traits and higher level ecosystem phenomena often affords deeper mechanistic insight by which diversity can be important in the provision of ecosystem functions or services (Norberg, 2004; Hooper *et al.*,

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2005; Vogt *et al.*, 2010; Weithoff *et al.*, 2015) including resilience (Walker *et al.*, 1999) and redundancy (Petchey and Gaston, 2002). Trait-based data also facilitate comparison of biodiversity effects across ecosystems in contrast to taxon-specific approaches, rendering results more amenable to being incorporated into developing general principles in ecology (McGill *et al.*, 2006).

With rapid recent progress in this area, there remains a considerable degree of variation in how functional traits are characterised and how they are used in understanding community assembly and function as well as ecosystem processes. Here, we provide an introduction to how ecological traits are defined, measured and used in the modern ecological literature.

## What Are Traits?

The functional trait concept has deep roots. We provide here a brief historical overview of some conceptual ‘milestones’ in trait-based approaches (**Table 1**), but note that a more comprehensive overview is beyond the scope of this article. Generally speaking, early developments mostly focused on variations of classifying organisms into functional groups (e.g. Raunkier life-forms; **Table 1**).

More recently, functional traits are at the heart of functional ecology, which focuses on the physiological and anatomical characteristics of species in order to better understand ecological patterns and the processes that generate them, including community assembly (Calow, 1987; Keddy, 1992). Since then, traits have been extended to estimate functional diversity to relate community composition to ecosystem-level processes (Walker *et al.*, 1999; Nalley *et al.*, 2014).

Functional traits have been viewed and defined in a variety of ways (McGill *et al.*, 2006; Violle *et al.*, 2007). In one common definition, a *trait* is ‘a well-defined, measurable property of organisms, usually measured at the individual level and used comparatively across species’. In turn, *functional traits* are recognised as those traits that strongly influence an organism’s performance (McGill *et al.*, 2006). In this case, community assembly processes are the primary focus. A second common definition describes functional traits as ‘morphological, biochemical, physiological, structural, phenological, or behavioural characteristics of organisms that influence how they respond to the environment and/or their effects on ecosystem properties’ (Violle *et al.*, 2007); thus also including the effects of traits on ecosystem

processes. This second definition emphasises not only the types of traits ecologists measure but also the two main *raison d’être* for trait-based approaches: to quantify trait–ecosystem ‘effects’ and trait–environment ‘response’ relationships.

Functional traits commonly characterise organismal physiology (e.g. basal metabolic rate, corporal nutrient concentrations and stoichiometries, frost tolerance, potential photosynthetic rate), morphological (e.g. beak size, seed or egg size, body mass, leaf mass per area (LMA), wood density) or behavioural (e.g. feeding strategy, predator evasion strategies, trophic level) (Weiher *et al.*, 1999; Cornelissen *et al.*, 2003; Poff *et al.*, 2006; Barnett *et al.*, 2007; Litchman and Klausmeier, 2008).

## Effect or Response, or Both?

Effect traits of a species are those that determine its influence on ecosystem properties and, in turn, the services or disservices that human societies derive from them (**Figure 1**). Response traits influence the abilities of species to colonise or thrive in a habitat and to persist in the face of environmental changes (**Figure 1**). In addition, a number of commonly measured functional traits have been studied as both effect and response traits. As an example, consider LMA. Because leaves with more mass per unit area decompose more slowly, nutrient cycling in mixtures of species with high LMA will be slower compared to mixtures with low LMA. In this case, the leaf trait LMA acts as an effect trait – it affects nutrient cycling. However, there are also numerous examples in the literature of LMA representing a response trait, with, for example, trends towards higher LMA with increasing aridity or decreasing fertility (Wright *et al.*, 2002). In the aquatic habitat, it has long been established that body length of plankton communities can respond to predation pressure by gape-limited predators such as macroinvertebrates or young fish: body size acting as a response trait. However, body size can also affect the sinking rate of dead plankton or their faecal pellets in the water column, thereby influencing biogeochemical cycling in pelagic ecosystems (Jiang *et al.*, 2005).

## Soft and Hard Traits

In practice, it is important to measure or obtain trait values on a wide variety of species (e.g. ‘screening’ *sensu* Keddy,

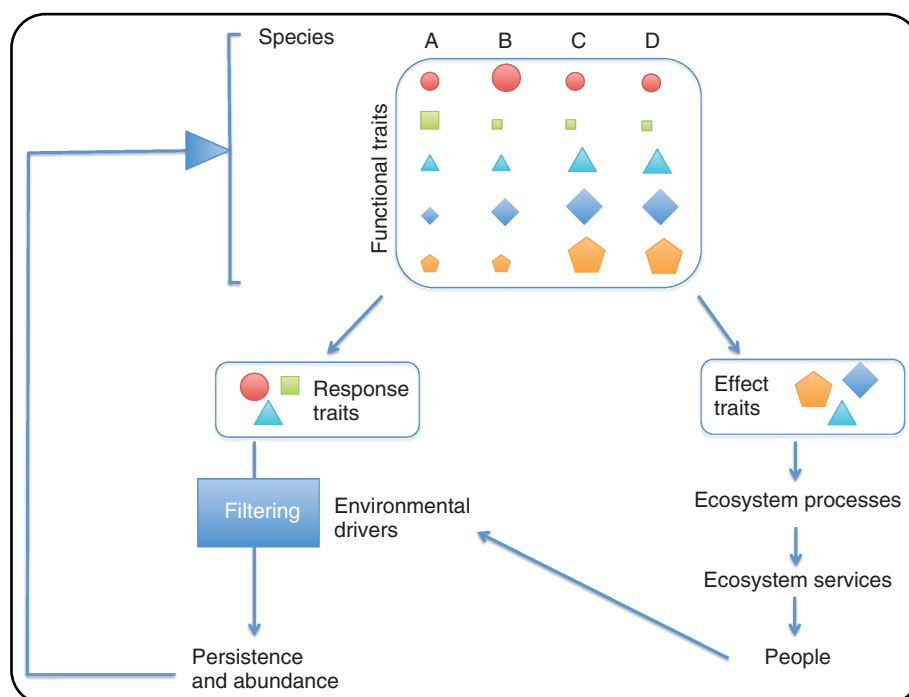
**Table 1** Overview of historical conceptual developments in functional trait approaches

Year	Author	Concept
300 BC	Theophrastus	<sup>a</sup> Functional plant classification by physical characters (plant height, stem density)
c. 1200	Frederick II (1194–1250)	<sup>b</sup> Classification based on physical characters
1859	Darwin, C	<sup>c</sup> Traits influence organism performance (e.g. beak length)
1934	Raunkiaer, CC	Plant functional classification based on life-form (e.g. plant height)
1963	Odum, E	Functional grouping of organisms (producers, consumers, decomposers)
1979	Grime, JP	Plant functional classification based on common strategies

<sup>a</sup>In Weiher *et al.* (1999).

<sup>b</sup>In Cadotte *et al.* (2011).

<sup>c</sup>In Violle *et al.* (2007).



**Figure 1** Overview of organismal functional traits showing how certain traits determine species' responses to the environment, and/or their effects on ecosystem processes, and in turn ecosystem services and people (redrawn from Diaz *et al.*, 2013). Shapes indicate the particular trait variables (e.g. leaf mass per unit area, body size) and the size of the shapes indicate the magnitude of the trait state.

1992), despite the challenge this poses for extremely diverse communities. To enable this, relatively easily and quickly quantified 'soft traits' are often considered (Hodgson *et al.*, 1999; Walker and Langridge, 2002; Cornelissen *et al.*, 2003). Soft traits are less mechanistically correlated with precise functions than are 'hard' traits, but may be used as proxies because their measurement is less labour-intensive. Hard traits are more time-intensive to measure and consequently difficult to quantify for large numbers of species in many regions of the world (Hodgson *et al.*, 1999; Weiher *et al.*, 1999; Lavorel and Garnier, 2002). Here, the rationale for the use of the terms 'soft' and 'hard' is related to the strength of the trait relationship to species effects or responses, with hard traits representing accurate, mechanistic indicators of species functions, responsible for community responses or ecosystem effects (Table 2). Probably the most commonly used soft trait in aquatic environments is body size, which in the plankton is a good indicator of several hard traits such as grazing/nutrient uptake and growth rates. Similarly, in terrestrial plants, the size and shape of seeds is an easily measured soft trait that allows inference of the more difficultly measured hard trait of dispersal rates.

## Types of Traits: Nominal, Ordinal, Interval and Ratio

The multitude of characters which can be described for species (e.g. the character of colour) are defined in ecology as *variables*.

Variables have a set of possible *states* (e.g. brown, green, blue), with a single one representing an *element* (e.g. brown) applied to the entity being described (individual or species). The quality or detail of the information collected determines the *measurement scale* (nominal, ordinal, interval and ratio) of the variables, which in turn dictates the mathematical and statistical methods that can be applied to the data (Schmera *et al.*, 2015).

Functional traits measured on the nominal scale consist of unique states from a set, but which cannot be put into a meaningful order. For example, amongst primary producers, a commonly described state includes the ability to fix nitrogen by phytoplankton or by plant roots. Mode of propagule dispersal is another common nominal variable. Nominal scale variables are limited to tests of equivalence, but ordinal variables permit ranking. For example, the trophic position of zooplankton, describing the degree of herbivory versus omnivory versus carnivory can be ordered (Vogt *et al.*, 2013). However, differences among the ranks cannot be interpreted such that the difference between states *a* and *b* cannot be compared to the difference between states *b* and *c*. This presents a challenge when dealing with ordinal data, so the ordinal scale is often either reduced to the nominal scale, or expanded to the interval scale (Schmera *et al.*, 2015). Interval scale data is characterised by meaningful differences among states (but without a zero point such as temperature measured in °C), so that sums, means and variances can be calculated. However, because interval data does not have a mathematical zero point, ratios are not meaningful (Schmera *et al.*, 2015). Finally, as suggested by its name, ratio operations are meaningful on the ratio scale along with other arithmetic operations. For example, if a species has

**Table 2** Examples of hard and soft traits from terrestrial and aquatic communities

Ecological process	Hard trait	Soft trait
<i>Terrestrial plants</i>		
Dispersal	Dispersal capacity	Seed mass Dispersal mode Seed mass and shape
Competitive ability	Competitive effect and response	Height Above-ground biomass
Disturbance response	Vegetative spread	Clonality
	Phenology	Flowering onset
	Palatability	Leaf mass per area Leaf water content
<i>Aquatic organisms</i>		
Dispersal	Dispersal capacity	Resting stage formation Presence of flying stages Clonality
Competitive ability	Clearance (grazing) rates	Body size Feeding apparatus Setae distances
		Body size
		Size: volume ratio
	Nutrient uptake rates	Body size
	Growth rates	Size: volume ratio

a maximum capacity to conduct photosynthesis at a rate of 100 nmol CO<sub>2</sub> m<sup>-2</sup> of leaf per s, this is 10 times the rate of a species with a maximum photosynthetic capacity of 10 nmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> (**Figure 2a**).

Note that variables measured in the same scale may be referred to using different terms: a nominal variable such as N-fixing (two states; yes or no) may also be referred to as a binary variable; an ordinal variable with ranked states may be referred to as a discrete variable; and a ratio scale variable such as maximum photosynthetic rate may be referred to as continuous (a potentially infinite number of states) (Schmera *et al.*, 2015).

## Functional Traits Enjoy Company: From Single Traits to Trait–Trait Relationships

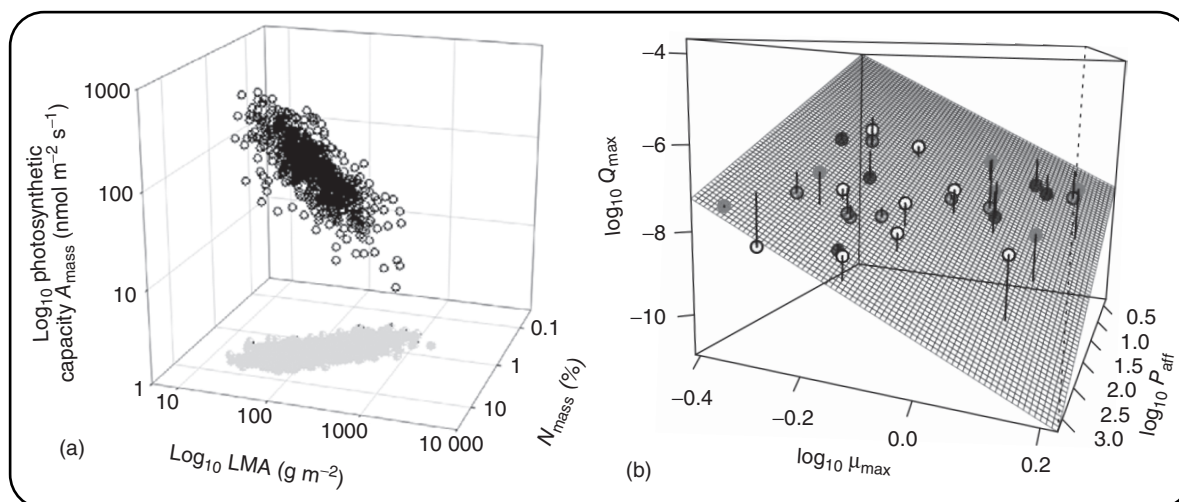
Functional traits can help assess fundamental trade-offs that determine species' ecological roles, potentially enabling biodiversity. Such trade-offs are revealed by examining relationships among traits in multidimensional trait space. In some of the ecological literature, especially related to terrestrial plants, this trait space is referred to as a trait syndrome (Keddy, 1992).

Probably the most classic case of a trait syndrome is the leaf economics spectrum (LES; **Figure 2a**; Wright *et al.*, 2004). This spectrum characterises species with potential for quick returns on investments of nutrients and dry mass in leaves to species with a slower potential rate of return. At the quick-return end are species with high leaf nutrient concentrations, high

rates of photosynthesis and respiration, short leaf lifetimes and low dry-mass investment per leaf area. At the slow-return end are species with long leaf lifetimes, expensive high-LMA leaf construction, low nutrient concentrations and low rates of photosynthesis and respiration. The LES has become a dominant paradigm for ecologists seeking to understand diversity in plant function and its implications for topics as diverse as (1) diversity–biomass relationships in large-scale dynamic global vegetation models (Sakschewski *et al.*, 2015), (2) the relationship between plant traits and life history strategies (Adler *et al.*, 2014) and (3) the response of plant community diversity to land-use change (Nock *et al.*, 2013).

For aquatic organisms, trade-offs amongst traits in phytoplankton (**Figure 2b**) (Litchman and Klausmeier, 2008; Edwards *et al.*, 2013), fish (Winemiller *et al.*, 2015) and lotic insects (Poff *et al.*, 2006) are the best established to date. In the phytoplankton, trade-offs have been found between the growth rate parameters for populations growing according to Michaelis–Menten nutrient uptake combined with a Droop growth model. Generally, there are important trade-offs between the parameters that describe velocity, affinity and storage traits. Specifically, across phytoplankton classes there are predictable trade-offs in the trait for nutrient affinity or uptake ( $P_{\text{aff}}$ ), the storage capacity trait of cells, permitting survival during low nutrient periods ( $Q_{\text{max}}$ ) and the maximum population growth rate or velocity trait ( $\mu_{\text{max}}$ ) (**Figure 2b**). Together these traits permit the prediction of competitive ability of phytoplankton and thus their distribution patterns across nutrient gradients on lake landscapes (Edwards *et al.*, 2013).





**Figure 2** Relationships among key functional traits are central to functional ecology. (a) Photosynthetic rate (a performance currency) is related to SLA (specific leaf area) and nitrogen content. (Reproduced with permission from McGill *et al.*, (2006) © Elsevier.) (b) The affinity-storage-velocity trade-off in phytoplankton traits. (Reproduced with permission from Edwards *et al.*, (2013) © The University of Chicago Press.)

## Prospects for Trait-Based Approaches in Ecology

There are several advantages to the functional trait approach. In some cases, it has been suggested that communities can be characterised largely on the basis of morphological traits that would require less expert taxonomic knowledge (Kruk *et al.*, 2010). The assumption here works especially well for organisms such as phytoplankton for which physiological traits and function are highly linked to body shape and size. However, it can also be useful when considering lotic fish and insect communities for which morphological (soft) traits have proved important for linking species to their trophic or movement (hard) traits (Poff *et al.*, 2006). Also, a trait-based approach can link community patterns to either the processes defining their assembly, or their functioning, permitting the formation of more general and comparable conclusions than a species-by-species approach (Pollard and Yuan, 2010).

The use of traits also presents some challenges. While morphological traits, and some relating to response, can be relatively easily obtained, it can be much more difficult to assemble effect traits because they are often physiologically based and require intense measurement and isolation of individuals, and thus more intense experimental approaches. As a result, there are often a limited number of traits available in the literature for a wide variety of species, which limits large regional studies. There is also the issue of trait convergence through evolutionary means, which indicates that especially for questions related to evolutionary processes, phylogenetic relatedness should be empirically determined *a priori* and accounted for when comparing traits across communities (Losos, 2008; Diniz Filho *et al.*, 2012).

Finally, there can be some degree of intraspecific trait variation such that mean values of interval or ratio scale traits may not always be meaningful, especially if there is significant overlap between the variances of different species. Accounting

for this intraspecific variation is especially relevant in an eco-evolutionary context (Violle *et al.*, 2012), helping to indicate how the populations of a community might show more or less rigidity toward environmental change. With respect to community assembly questions and to the eventual link with ecosystem functioning, intraspecific trait characterisation represents the next frontier, at least with quantitative traits; however, for most organism groups, we are still lacking data that would permit its estimation for more than a few populations at a time.

## Traits and Functional Diversity

Functional measures of biodiversity encapsulate the full range of properties that organisms in a community exhibit and which allow communities to respond to environmental change and influence ecosystem functions and services. The general strategy adopted has been to use analytical techniques to collapse multiple traits into functional diversity indices (Petchey and Gaston, 2002; Podani and Schmera, 2006; Villéger *et al.*, 2008), but these approaches are often sensitive to a great number of methodological choices (Poos *et al.*, 2009), with each metric presenting distinct advantages and disadvantages (Poos *et al.*, 2009; Podani and Schmera, 2011). In recent years, there has been a flurry of activity to develop new functional diversity indicators.

### Which traits?

The selection of traits to include in the calculation of FD needs to be done carefully. While it might seem self-evident, it is important to remember that indices of functional diversity depend on the definition and use of multiple functional traits. In choosing relevant traits, one must consider how each is implicated in the ecosystem function or community response of interest. Different traits will drive different ecosystem functions, so precise

definition of both traits and response variables of interest is important. Similarly, in searching for a community response to environmental change, it is also critical to consider which traits are likely to be most responsive and to remember that some traits might only show a signal under particular circumstances.

On the other hand, by incorporating a suite of traits, the likelihood of capturing diverse responses to environmental stressors, or unique contributions to ecosystem functioning, increases (Lefcheck *et al.*, 2015). Thus, including multiple functional axes by which communities can be differentiated allows for deeper insights into the mechanistic relationships underlying functional diversity–ecosystem functioning relationships (Vogt *et al.*, 2010). In addition, including a diversity of traits that describe a particular class of organism characteristics (e.g. a life history strategy) such as trait syndromes or a suite of soft traits might provide a good approximation of traits that are typically challenging to measure (Lefcheck *et al.*, 2015). Finally, phylogenetic relationships between species have been used in recent years to permit the estimation of unknown traits for suites of species, thereby permitting functional diversity calculations where missing species information would have otherwise precluded it (Guénard *et al.*, 2013).

Phylogenetic considerations may be important in a variety of contexts when it comes to functional traits. With respect to trait selection, it can be important to determine whether phylogenetic relationships exist between species to which traits are attributed. For example, if conservation decisions are to be based on the degree of functional diversity in a community, it is also relevant to consider whether a high degree of phylogenetic diversity will also be favoured by such conservation decisions (Diaz *et al.*, 2013). Phylogenetic relationships have also been the focus of the new subfield of community phylogenetics, which is concerned with which trait combinations coexist in communities (i.e. questions of historical community assembly) and why, but often using phylogenies to infer trait relationships (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2009), instead of traits more directly (Vogt *et al.*, 2013). Whether phylogenies can replace functional traits to address shorter term ecological patterns of community assembly remains an open question.

## How many traits?

The number of traits to include in calculations of functional diversity is another critical consideration. Including fewer traits can increase the probability of detecting functional redundancy (Petchey and Gaston, 2002). On the other hand, when many traits are included, estimations of functional diversity effects will begin to resemble species richness effects with respect to ecosystem processes. For example, using more than eight traits has been shown to lead to diminishing returns when characterising plant communities (Laughlin, 2014).

It is also important to consider interspecific variation when choosing traits to be used in estimating functional diversity. For a trait to be informative, it must vary between species (McGill *et al.*, 2006), with reduced interspecific variability leading to a low estimation of functional diversity. Thus, some traits will be more responsive. In the case of traits associated with the LES (Figure 2a), many of the trait values span two orders of magnitude but variation in most wood functional traits (e.g. density

ranges from 0.1 to 1.5 g cm<sup>-3</sup>) is usually comparatively reduced. In lake plankton communities, phytoplankton body size typically also varies by two orders of magnitude, but the variation amongst crustacean zooplankton is often much less. Sometimes low variability among traits will be unavoidable because a high functional redundancy in an ecological community actually exists. Functional redundancy can, in turn, have important ramifications for community stability (Peterson *et al.*, 1998), and estimations of relative functional trait overlap can thus aid in understanding the importance of biodiversity for how ecosystems function.

Overall, the answer to the question of how many and which traits should be included in any given study is almost certainly likely to vary considerably by organism and ecosystem type. It is useful to make some *a priori* trait selection decisions based on specific ecological knowledge of the system in question (Naeem and Wright, 2003). Such decisions are also governed by important practical considerations such as budget, infrastructure at field sites and available equipment (to name just a few). One of the greatest challenges for functional trait and diversity ecology is the development of techniques to permit differentiation between situations when functional redundancy is a true characteristic of a community, from when it is a consequence of having chosen too few traits. Continued research in a trait-based context will surely enable exciting advancements in community and ecosystem ecology in the years to come.

## References

- Adler PB, Salguero-Gomez R, Compagnoni A, *et al.* (2014) Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences* **111** (2): 740–745.
- Barnett AJ, Finlay K and Beisner BE (2007) Functional diversity of crustacean zooplankton communities: towards a trait-based classification. *Freshwater Biology* **52** (5): 796–813.
- Cadotte MW, Carscadden K and Mirotchnick N (2011a) Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology* **48** (5): 1079–1087.
- Calow P (1987) Towards a definition of functional ecology. *Functional Ecology* **1** (1): 57–61.
- Cavender-Bares J, Kozak KH, Fine PV, *et al.* (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters* **12** (7): 693–715.
- Cornelissen J, Lavorel S, Garnier E, *et al.* (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* **51** (4): 335–380.
- Diaz S and Cabido M (2001) Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution* **16** (11): 646–655.
- Diaz S, Purvis A, Cornelissen JH, *et al.* (2013) Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution* **3** (9): 2958–2975.
- Diniz Filho F, Alexandre J, Rangel TF, *et al.* (2012) Exploring patterns of interspecific variation in quantitative traits using sequential phylogenetic eigenvector regressions. *Evolution* **66** (4): 1079–1090.
- Edwards KF, Klausmeier CA and Litchman E (2013) A three-way trade-off maintains functional diversity under variable resource supply. *American Naturalist* **182** (6): 786–800.

- Grime JP (1979) *Plant Strategies and Vegetation Processes*. Chichester: John Wiley & Sons, Ltd.
- Guénard G, Legendre P and Peres-Neto P (2013a) Phylogenetic eigenvector maps: a framework to model and predict species traits. *Methods in Ecology and Evolution* **4** (12): 1120–1131.
- Hodgson JG, Wilson PJ, Hunt R, *et al.* (1999) Allocating C-S-R plant functional types: a soft approach to a hard problem. *Oikos* **85** (2): 282–294.
- Hooper DU, Chapin FS, Ewel JJ, *et al.* (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* **75**: 3–35.
- Jiang L, Schofield OM and Falkowski PG (2005) Adaptive evolution of phytoplankton cell size. *The American Naturalist* **166** (4): 496–505.
- Keddy PA (1992) A pragmatic approach to functional ecology. *Functional Ecology* **6** (6): 621–626.
- Kruk C, Huszar VLM, Peeters ETHM, *et al.* (2010) A morphological classification capturing functional variation in phytoplankton. *Freshwater Biology* **55** (3): 614–627.
- Laughlin DC (2014) The intrinsic dimensionality of plant traits and its relevance to community assembly. *Journal of Ecology* **102** (1): 186–193.
- Lavelle S and Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* **16** (5): 545–556.
- Lefcheck JS, Bastazini VAG and Griffin JN (2015) Choosing and using multiple traits in functional diversity research. *Environmental Conservation* **42** (2): 104–107.
- Litchman E and Klausmeier CA (2008) Trait-based community ecology of phytoplankton. *Annual Review of Ecology, Evolution, and Systematics* **39**: 615–639.
- Losos JB (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters* **11** (10): 995–1003.
- McGill BJ, Enquist BJ, Weiher E, *et al.* (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* **21** (4): 178–185.
- Naeem S and Wright JP (2003) Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters* **6** (6): 567–579.
- Nalley JO, Stockenreiter M and Litchman E (2014) Community ecology of algal biofuels: complementarity and trait-based approaches. *Industrial Biotechnology* **10** (3): 191–201.
- Nock C, Paquette A, Follett M, *et al.* (2013) Effects of urbanization on tree species functional diversity in eastern North America. *Ecosystems* **16** (8): 1487–1497.
- Norberg J (2004) Biodiversity and ecosystem functioning: a complex adaptive systems approach. *Limnology and Oceanography* **49** (4, Part 2): 1269–1277.
- Odum EP (1963) *Ecology*, Holt, p. 244. New York: Rinehart and Winston.
- Petchey OL and Gaston KJ (2002) Functional diversity (FD), species richness and community composition. *Ecology Letters* **5** (3): 402–411.
- Petchey OL, Hector A and Gaston KJ (2004) How do different measures of functional diversity perform? *Ecology* **85** (3): 847–857.
- Peterson G, Allen CR and Holling CS (1998) Ecological resilience, biodiversity, and scale. *Ecosystems* **1** (1): 6–18.
- Podani J and Schmera D (2006) On dendrogram-based measures of functional diversity. *Oikos* **115** (1): 179–185.
- Podani J and Schmera D (2011) A new conceptual and methodological framework for exploring and explaining pattern in presence-absence data. *Oikos* **120** (11): 1625–1638.
- Poff NL, Olden JD, Vieira NK, *et al.* (2006) Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society* **25** (4): 730–755.
- Pollard A and Yuan L (2010) Assessing the consistency of response metrics of the invertebrate benthos: a comparison of trait- and identity-based measures. *Freshwater Biology* **55** (7): 1420–1429.
- Poos MS, Walker SC and Jackson DA (2009) Functional-diversity indices can be driven by methodological choices and species richness. *Ecology* **90** (2): 341–347.
- Raunkiaer C (1934) *The Life Forms of Plants and Statistical Plant Geography. Begin the Collected Papers of C. Clarendon*, Oxford, UK: Raunkiaer.
- Sakschewski B, von Bloh W, Boit A, *et al.* (2015) Leaf and stem economics spectra drive diversity of functional plant traits in a dynamic global vegetation model. *Global Change Biology* **21** (7): 2711–2725.
- Schmera D, Podani J, Heino J, *et al.* (2015) A proposed unified terminology of species traits in stream ecology. *Freshwater Science* **34** (3): 823–830.
- Tilman D, Knops J, Wedin D, *et al.* (1997) The influence of functional diversity and composition on ecosystem processes. *Science* **277** (5330): 1300–1302.
- Villéger S, Mason NWH and Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **89** (8): 2290–2301.
- Violle C, Navas M-L, Vile D, *et al.* (2007) Let the concept of trait be functional!. *Oikos* **116** (5): 882–892.
- Violle C, Enquist BJ, McGill BJ, *et al.* (2012a) The return of the variance: intraspecific variability in community ecology. *Trends in Ecology and Evolution* **27** (4): 244–252.
- Vogt RJ, Beisner BE and Prairie YT (2010) Functional diversity is positively associated with biomass for lake diatoms. *Freshwater Biology* **55** (8): 1636–1646.
- Vogt RJ, Peres-Neto PR and Beisner BE (2013) Using functional traits to investigate the determinants of crustacean zooplankton community structure. *Oikos* **122** (12): 1700–1709.
- Walker B, Kinzig A and Langridge J (1999) Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* **2** (2): 95–113.
- Walker BH and Langridge JL (2002) Measuring functional diversity in plant communities with mixed life forms: a problem of hard and soft attributes. *Ecosystems* **5** (6): 529–538.
- Webb CO, Ackerly DD, McPeck MA and Donoghue MJ (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics* **33**: 475–505.
- Weiher E, Werf A, Thompson K, *et al.* (1999) Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science* **10** (5): 609–620.
- Weithoff G, Rocha MR and Gaedke U (2015) Comparing seasonal dynamics of functional and taxonomic diversity reveals the driving forces underlying phytoplankton community structure. *Freshwater Biology* **60** (4): 758–767.
- Winemiller KO, Fitzgerald DB, Bower LM, *et al.* (2015) Functional traits, convergent evolution, and periodic tables of niches. *Ecology Letters* **18** (8): 737–751.



- Wright IJ, Westoby M and Reich PB (2002) Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. *Journal of Ecology* **90** (3): 534–543.
- Wright IJ, Reich PB, Westoby M, *et al.* (2004) The worldwide leaf economics spectrum. *Nature* **428** (6985): 821–827.

## Further Reading

### Phylogenetic considerations and traits

- Cavender-Bares J, Ackerly DD and Kozak KH (2012) Integrating ecology and phylogenetics: the footprint of history in modern-day communities. *Ecology* **93** (sp8): S1–S3. Special issue: <http://www.esajournals.org/doi/abs/10.1890/12-0092.1>.
- Díaz S, Purvis A, Cornelissen JHC, *et al.* (2013) Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution* **3** (9): 2958–2975.

### Inferring unknown trait values

- Guénard G, Legendre P and Peres-Neto P (2013b) Phylogenetic eigenvector maps: a framework to model and predict species traits. *Methods in Ecology and Evolution* **4** (12): 1120–1131.

### Intraspecific trait variation

- Albert CH, Thuiller W, Yoccoz NG, *et al.* (2010) Intraspecific functional variability: extent, structure and sources of variation. *Journal of Ecology* **98** (3): 604–613.
- Violle C, Enquist BJ, McGill BJ, *et al.* (2012b) The return of the variance: intraspecific variability in community ecology. *Trends in Ecology and Evolution* **27** (4): 244–252.

### Functional traits, conservation and restoration

- Cadotte MW, Carscadden K and Mirotchnick N (2011b) Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology* **48** (5): 1079–1087.