

Functional Diversity: An Epistemic Roadmap

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Functional diversity holds the promise of understanding ecosystems in ways unattainable by taxonomic diversity studies. Underlying this promise is the intuition that investigating the diversity of what organisms actually do (i.e., their functional traits) within ecosystems will generate more reliable insights into the ways these ecosystems behave, compared to considering only species diversity. But this promise also rests on several conceptual and methodological (i.e., epistemic) assumptions that cut across various theories and domains of ecology. These assumptions should be clearly addressed, notably for the sake of an effective comparison and integration across domains, and for assessing whether or not to use functional diversity approaches for developing ecological management strategies. The objective of this contribution is to identify and critically analyze the most salient of these assumptions. To this aim, we provide an epistemic roadmap that pinpoints these assumptions along a set of historical, conceptual, empirical, theoretical, and normative dimensions.

Keywords: functional trait, biodiversity, ecosystem function, community assembly, functional diversity

Research on functional diversity in ecology has increased from a few dozen publications per year in the 1980s to thousands of publications in recent years. A search on Google Scholar with the keywords *functional diversity AND ecology* revealed over 8000 articles in 2017 compared with just over 300 in 1997—a 25-fold increase. A similar trend was also observed in the Scopus database, although with smaller absolute numbers because of a narrower journal base. When relativized to articles found with the keyword *ecology*, the percentage goes from about 0.1% in 1997 to about 1% in 2017—hence a tenfold increase in functional diversity articles within ecology-related articles. Although the notion of functional diversity was initially developed in the domain of plant ecology, it is now more broadly extended to ecology and biodiversity studies and applied to an increasing number of organisms, including fish (Mims et al. 2010), birds (Meynard et al. 2011), arthropods (Poff et al. 2006, Brousseau et al. 2018a), zooplankton (Hébert et al. 2016), protists (Venail 2017) and ciliates (Weisse 2017), as well as bacteria (Ortiz-Álvarez et al. 2018) and even viruses (Hurwitz et al. 2015). We have reached a point at which this functional approach has developed into a framework that not only investigates ecosystems through the lens of organismal functional traits, but rests on a number of epistemic assumptions, be they conceptual or methodological, that play a foundational role in how

one assesses these functional traits in practice and how one develops ecological models. Our analyses have focused on elaborating an epistemic roadmap that precisely aims at clarifying these assumptions and related issues that bear on the foundation and justification of knowledge in this particular approach to ecology. Recognizing these assumptions and addressing related challenges matter for comparing and integrating functional diversity studies within the different domains of ecology but also—and more significantly—across domains, as is required by the complexity of ecosystems and the interdependencies among organisms at all scales of the tree of life.

This epistemic roadmap identifies and explicates select key underpinning postulates of the functional diversity framework in its use across disparate research questions in ecology (see figure 1). We first show how a historical perspective on functional diversity research and its genealogy sheds light on the anchorage of the framework within specific domains of ecology. We explicate the diverse meanings of the concept of function, and analyze how these meanings interact in the concept of a functional trait. We then turn to how these concepts empirically connect with the real world; we map out empirical challenges of functional trait identification and measurement, and we address the necessity and feasibility of significantly expanding the functional diversity framework beyond the domains in which it is chiefly applied.

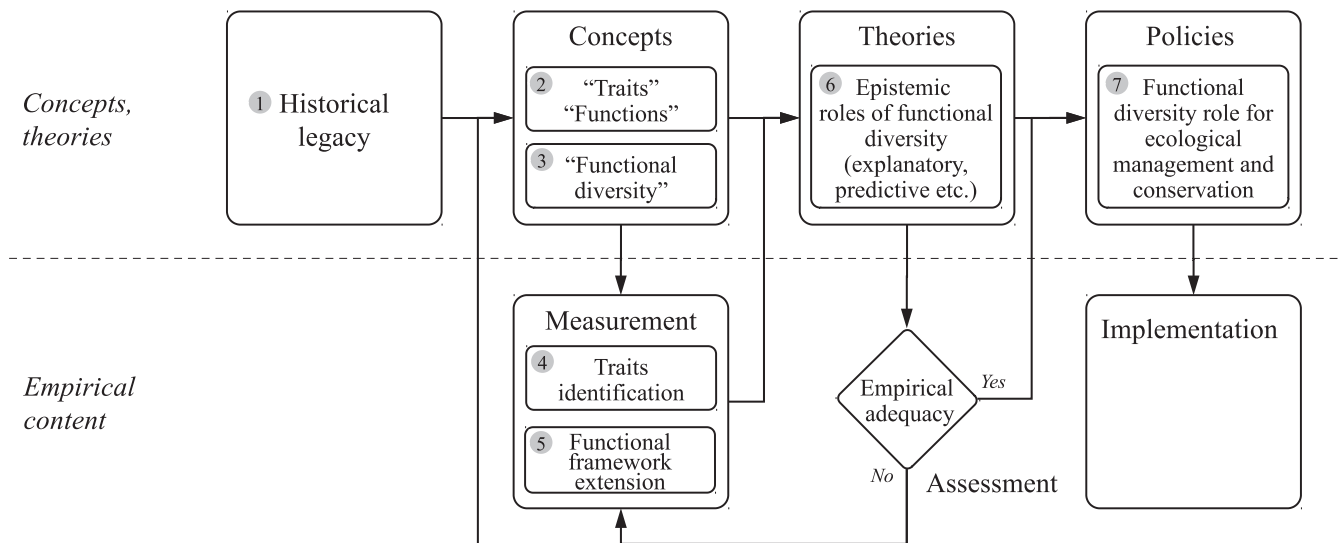


Figure 1. Epistemic roadmap that highlights the main foundational assumptions of the functional diversity framework in ecology, including conceptual, methodological (measurement) and theoretical challenges that may ultimately affect environmental decision-making.

We investigate how such empirical questions affect the epistemic roles that functional diversity is expected to fulfill, be they in terms of explanation, prediction or theoretical integration. Finally, we discuss the ways in which the functional diversity framework—and its accompanying assumptions and challenges—result in a number of very concrete issues when it comes to elaborating ecosystem management and conservation policies.

Our characterization of the rich epistemic landscape underlying the functional diversity framework contributes to making sense of the successes but also the difficulties that it encounters in specific domains of ecology. The benefits are to map out crucial conceptual and epistemic differences that must be overcome to enable comparisons across disparate functional diversity studies while highlighting the different dimensions along which broader integration is sought. The roadmap also reveals the complex set of epistemic assumptions that accompany the functional diversity framework in any of its applications to ecological management and conservation issues.

Biodiversity functionalism in historical perspective

Thinking functionally about living entities has deep historical roots that still strongly affect the conceptual tools used in the investigation of functional diversity today. This way of thinking engages in the characterization and classification of entities by focusing on what they *do* instead of what they are made of. Aristotle (384–322 BCE) already classified animals according to their modes of subsistence—for example, as aquatic or terrestrial and as carnivorous, graminivorous, omnivorous, or special (Lundgren 2009). And one of his disciples, Theophrastus (371–287 BCE), proposed the first functional groupings of plants, on the basis of their height and woodiness, reflecting different resource-use strategies

(Weiher et al. 1999). Thinking in terms of functions also contributes to the view that living entities exist not by themselves but in interaction with other entities and with their environment and can therefore be seen as fulfilling certain *roles* within higher levels of organization such as communities or ecosystems. The naturalist Carl von Linnaeus (1707–1778)—who conceived of living entities as being fitted to one another’s use (Pearce 2010)—was an early proponent of this view. The work of nineteenth century plant geographers, such as Alexander von Humboldt (1769–1859), August Grisebach (1814–1879) and Eugenius Warming (1841–1924), who aimed to capture the relationship between environmental conditions and geographical plant distribution patterns, is another important historical influence on taxonomic classifications based on function (Duckworth et al. 2000). This work was at the origin of subsequent functional classifications linking the traits of plants to their environmental requirements—for instance, by Christen Raunkiaer (1860–1938) or Leonty Ramenskii (1884–1953), culminating in John Philip Grime’s (1935–) still widely used C–S–R classification of plants (as competitive, stress tolerant, and ruderal; Garnier et al. 2016).

Functional classifications used in *animal* ecology are also central to the genealogy of the contemporary functional diversity studies. These functional views derive from a line of research that spans from Charles Elton’s (1900–1991) trophic-focused niche concept, to George Evelyn Hutchinson’s (1903–1991) view of linking species coexistence to resource use (Blondel 2003) and to the research tradition centered around the concept of guild, expression coined by Richard Root (1937–2006) to designate groups of animals that use similar resources in similar ways and are therefore more likely to compete (Simberloff and Dayan 1991). The concept has therefore been central in the search for assembly rules of

ecological communities (Simberloff and Dayan 1991, Keddy 1992, Blondel 2003). Elton's niche concept has also played a significant role in thinking about organisms according to their position within food webs and their contributions to ecosystem-level nutrient and energy flows in ecosystem ecology and functional ecology (Cummins 1974, Naeem 2002b).

These historical streams of research are key to explaining the emergence, at the end of the twentieth century, of a functional framework, initially used in plant ecology and now in many spheres of ecology (Naeem 2002a, Loreau 2010). They are also key to putting into perspective the institutionalization of functional ecology as a subdiscipline of ecology in the late 1980s—when its eponymous journal *Functional Ecology* was founded by the British Ecological Society—and to understanding its foundational concepts.

Traits and functions

The functional ecology framework presupposes the identification of functional traits of entities that compose ecological communities and participate in ecological processes. Therefore, the twofold conceptual challenge of defining a *trait* and explaining why that trait is termed *functional*. Although a recognized definition of trait is any morphological, physiological, phenological, or behavioral feature measured at the level of the individual (Violle et al. 2007, Pey et al. 2014, Garnier et al. 2016), what makes a trait functional varies depending on the perspective one adopts on the term *function*.

In order to clarify the sense in which organismal traits are understood as functional, it is helpful to draw a distinction between concepts of functional response and effect traits on the one hand, and analyses of the concept of *function* by philosophers of biology on the other. One standard philosophical analysis of function in biology is the *selected effect* account, according to which the function(s) of the parts or traits of biological entities are the effects for which those entities were favored under past natural selection (Millikan 1989, Neander 1991). This account therefore equates the concept of function with that of *adaptation*, as it is understood in evolutionary biology, and accordingly emphasizes the contrast between functions and evolutionary by-products (Williams 1966).

Although some discussions in functional ecology associate the concept of function with that of adaptation—and so implicitly cast them as selected effects (Calow 1987, Laureto et al. 2015)—it seems unclear whether all actual uses of *functional* in ecology agree with the selected effect account. In particular, functional ecology typically characterizes traits as either *functional response traits* or *effect traits* (Lavorel and Garnier 2002, Jax 2005). *Functional response traits* are organismal features that determine organisms' responses to changes in environmental conditions (Lavorel and Garnier 2002, Violle et al. 2007). Functional response traits are termed functional insofar as they affect the survival and reproductive success of an organism in an environment. In

contrast, *functional effect traits* are features of organisms that contribute to ecosystem processes (e.g., primary productivity, litter decomposition). These traits are deemed functional insofar as they explain or predict possible roles of organisms in the overall functioning of the ecosystem.

Functional response traits—in that they are usually defined in relation to organismal fitness (e.g., McGill et al. 2006, Violle et al. 2007)—seem to conceivably accord with the selected effect account of function. However, an influential alternative to the selected effect account of function, which also links functions to fitness, is the *dispositional* or *contribution to fitness* account of function (Bigelow and Pargetter 1987, Walsh 1996). Somehow amending the selected effect account—which is focused exclusively on a trait's *past* contributions to fitness and how this contribution explains why an organism has this trait—the contribution to fitness account attributes functional roles to traits on the basis of their contribution to the current propensity of an organism to survive and reproduce (therefore on the basis of their contribution to the organism's current fitness). Whereas the selected effect account is specifically *backward-looking* (i.e., defines function in relation to fitness in past environments), the contribution to fitness account has been termed *forward-looking* in that it defines functionality in relation to expected survival and reproduction in current environment. Of course, *forward-looking*, in the present article, does not imply a view of traits as evolving in anticipation of future events, only that traits should be considered functional to the extent that they increase an organism's propensity to survive and reproduce. In some important respects, *functional response traits* as used in functional ecology better align with the contribution to fitness account. Indeed, when traits are characterized as functional response traits, the primary aim is to predict community assembly and community response to environmental changes on the basis of how specific traits suit the organisms that exhibit them to fare well in such environmental contexts (Keddy 1992). For this purpose, what matters is how an organism's traits affect its ability to survive and reproduce in a given environment, not whether the organism has its traits because they were advantageous in its ancestor's past environment. If the environment changes, a trait that served some particular fitness use in the ancestor's environment can serve a different fitness use in the offspring's environment (as in the case of exaptations; Gould and Vrba 1982), and a trait that possibly served no fitness use at all in its ancestors' environment can end up serving one (as in the case of evolutionary by-products). However, given that the characterization of traits as response traits is often justified in terms of past contributions of these traits, the use of functional response traits also seems to partly accord with the selected effect account. Moreover, it must be recognized that the selected effect and contribution to fitness accounts will converge in cases in which the focus is on recent selection and in which predicted future or hypothetical selection pressures resemble historical ones (Godfrey-Smith 1994).

The notion of functional effect traits seems to accord less with the selected effect account of function. Conceiving of functional effect traits as selected effect functions would entail a view of organisms and their traits as being shaped by natural selection for their roles in ecosystem processes. This would require defending the claim that natural selection customarily operates at the level of ecosystems, contrary to the standard view that natural selection mainly operates at organismal or gene levels (Maclaurin and Sterelny 2008, Odenbaugh 2010). The use of functional effect traits in functional ecology, however, does not seem committed to such claims (Dussault 2018). This suggests that functional effect traits better accord with philosophical theories of function that do not draw connections between functions and evolutionary concepts of fitness and selection (though see Dussault and Bouchard 2017). Accordingly, several philosophers of ecology (e.g., Maclaurin and Sterelny 2008, Odenbaugh 2010) have argued that functional effect traits should be interpreted through the lens of the causal role account of function (Cummins 1975), arguably the most influential nonselectionist account of function developed in the philosophy of biology. The causal role account defines functions as contributions of the parts of a system to a higher-level capacity of that system. In ecology, this capacity may refer to various dimensions of ecosystem functioning (e.g., primary productivity, litter decomposition).

There is a third notion of function that is distinct from—but related to—the previous notions, namely functions as ecosystem services (Jax 2005, Kareiva et al. 2011). An ecosystem service can be defined as a contribution of an ecosystem in part or as a whole to the well-being of humans (Costanza et al. 1997, Daily 1997). In this case, the (fitness-related) functional response traits and the (causal role) functional effect traits of organisms are considered from the perspective of how they indirectly are useful to humans. For example, insects pollinate flowers, mangrove trees can mitigate the effects of sea level rise, bacteria decompose waste, etc. Each of these improves human lives and accomplishes something we would otherwise have to do at great expense. In this respect, ecosystem services are distinct from other notions of function in that other notions of function are not indexed to the contribution of single species well-being. This also adds a value component, which is not necessarily found in other notions of functions. Therefore, because it is also concerned with the responses and effects of organisms as pertaining to the well-being of humans, the notion of ecosystem service is related to—but distinct from—the previous selected effects and causal role accounts of function.

The current discussion indicates that the basis on which a trait is termed functional can be diverse. Functional attributions are intimately linked to the research questions pursued, whether they are assembly or ecosystem focused. Clearly defining what we mean by *functional trait* is therefore important to ensure a consistent conceptual grounding in functional ecology that makes it possible to understand, compare, and aggregate findings across multiple studies.

Functional diversity

Functional diversity can be understood as representing one of the many dimensions of biodiversity. Although biodiversity can loosely be defined as the diversity of life at all its levels of organization, from genes to whole ecosystems (Wilson 1992, Harper and Hawksworth 1995, Gaston and Spicer 2004), functional diversity offers a characterization of this diversity of life in terms of a diversity of functions. Identifying and listing these functions, sorting them out into functional groups and categories, measuring and quantifying them through indices of functional diversity, all of these provide perspectives on biodiversity that are complementary to existing ones, be they genetic, taxonomic or ecosystemic. Functional diversity can therefore be thought as providing a novel vantage point of biodiversity, apprehending the diversity of life in terms of a diversity of organismal functional traits, complementing diversity framed, for instance, in terms of species, genes or ecosystems. In this way, the concept contributes to broadening our understanding of the multiple facets of biodiversity, thereby supplementing taxonomic approaches and revealing another dimension of the complexity of life.

But the concept of functional diversity is more than just a way of depicting the diversity of life; it also enables different predictions and explanations of the ways in which the diversity of life interacts, evolves and responds to change. Indeed, functional diversity perspectives allegedly offer a deeper mechanistic and more integrated perspective onto biodiversity than traditional taxonomic approaches (Norberg 2004, Petchey and Gaston 2006, Gagic et al. 2015), including the degree to which community constituents are redundant or complementary in their functional contributions (Micheli and Halpern 2005, Bracken et al. 2008). Such a perspective is possible by focusing on the different interactions of living forms and the ways in which these interactions are mediated via the functional traits observed. In particular, trait values represented within communities—and their mean and distribution among other statistical measures—can provide complementary insights into ecosystem processes, including the productivity of focal trophic levels and adjacent ones, as well as nutrient cycling (Litchman and Klausmeier 2008, Handa et al. 2014, Hébert et al. 2017). Estimates of community functional diversity and examination of the most responsive traits can also reflect both selective pressures and changes in the biotic and abiotic environment (Vogt et al. 2013).

One such perspective on community functional diversity is that of functional structure, which is described by the community weighted mean of functional traits (CWM, using species abundances in a given community as weights for the trait values exhibited by these species). Another perspective is that of functional diversity, which is used to describe trait value variability in terms of richness, evenness and divergence (Mouillot et al. 2011), richness referring to the extent of the trait value distribution (i.e., the difference between maximum and minimum values) and evenness

and divergence to the regularity or the inequalities in distribution along the axis of trait values, respectively (Garnier et al. 2016). These two perspectives (structure and diversity) underlie the two main hypotheses relating community structure and ecosystem processes, that is the importance of dominance of particular species and traits that control function (importance measured in terms of biomass hypothesis, evaluated by CWM) versus the importance of complementarity, evaluated by trait value variability or divergence (Grime 1998, Tilman 1999). They also underlie investigations of the roles played by keystone and rare species and their specific traits, of trait redundancy (e.g., Jain et al. 2014) and questions about determinants of community assembly (Nock et al. 2016), the community being seen as the result of different filters that exclude those phenotypes that do not have adequate trait values (Keddy 1992).

An epistemic challenge comes from the plurality of indices that have been developed, on the basis of different types of functional data and different mathematical expressions that can be sensitive to context. In this respect, Garnier and colleagues (2016) suggested that one option might be to consistently apply more simple measures of trait distributions (means, standard deviation, skewness, kurtosis), that have well understood mathematical properties. The quantification of functional diversity—with specific metrics and indices that aggregate raw measurements—remains an area in which more work is needed; in particular, the standardization of statistical approaches could contribute to overcome current difficulties for comparing and integrating across different studies.

Empirical challenges: Identifying and measuring functional traits

The epistemic role of functional traits depends on their clear identification and measurement in the field. This, however, is not straightforward. A first challenge consists in identifying the relevant functional traits with regard to the phenomena to be explained. Because organismal traits are extremely numerous, researchers must find ways to focus on those traits that matter for explaining or predicting the target features of the ecological phenomena under investigation. For instance, over the last decades, numerous studies have attempted to explain community structure and dynamics as affected by specific environmental conditions through changes in response traits—traits that respond to abiotic, biotic, and disturbance filters (Lavorel and Garnier 2002, Barnett and Beisner 2007). In this case, the focus is on organismal traits that are related to constraining environmental or biotic variables. For example, an abiotic filter linked to low nutrient availability will result in a restricted range of plant trait values linked to the physiological tolerance to low fertility (traits related to nutrient conservation). In this case, the distribution of community plant traits would converge, corresponding to species that respond similarly to these conditions. When the objective of the study is to relate traits to ecosystem processes, the traits are selected on the basis of

their role in the underlying mechanisms of those processes (such traits are referred to as effect traits in that they have an effect onto ecosystem processes). Although these effect traits are harder to assess in practice because they require singling out—within an extremely large set of possibilities—the most significant activities of organisms that might affect ecosystem processes, experimental approaches have been developed, as in the case of zooplankton or arthropods (Hébert et al. 2017, Brousseau et al. 2018a). For plants, one of the most studied ecosystem processes in relation to leaf traits is that of decomposition. A number of effect traits, both morphological and chemical, have been related to decomposition, but in many studies, the trait of leaf dry matter content seems to be the single trait that explains the most variation in leaf decomposition rate (Garnier et al. 2016). Needless to say, still only a few of all potentially relevant organismal functional traits are known today.

A second challenge concerns the level and granularity at which functional traits should be defined and measured (McGill et al. 2006). In particular, should such traits be considered at the level of species? Should intraspecific genetic variation also be considered? Or should functional traits be aggregated at a higher granularity level of species functional groups or of other evolutionary taxa (e.g., family, order)? For instance, plant trait information is available in data banks such as TRY (Kattge et al. 2011), measured at the level of individual species; whether this is aggregated at another level will depend on the purpose and the particular questions of the study. For example, global vegetation models integrate information at the much higher level of plant functional type, and new approaches are being tested to integrate and aggregate the species-level trait data in these models (Verheijen et al. 2016). The importance of trait variation at the level of the individual can be addressed by questions about intraspecific variability, which represents a current frontier gaining importance in the context of adaptation to global change (Violle et al. 2014). A number of studies indicate that intraspecific variability is most important in systems with lower species richness, such as boreal ecosystems (Kumordzi et al. 2014), and the importance varies with scale, being more important at more local scales (Albert et al. 2011). However, measuring traits at a coarse granularity may be the only viable option for studies that span trophic levels, involving large numbers of taxa whose traits are difficult to measure at the species level, such as plankton or microbial species (Torsvik and Øvreås 2002, Krause et al. 2014).

A third and related challenge concerns the practical measurability of certain functional traits and their substitution by easier-to-measure proxy traits. For example, in plant functional ecology, certain easy-to-measure traits are used and also widely accepted as proxies of traits that are more difficult to assess. A good example is that of leaf dry matter content (LDMC) which is considered a good proxy for both leaf tissue density (Garnier et al. 2001), and also for flammability of plant tissue (Garnier et al. 2004). The fact that it is very easy to measure (two masses—saturated fresh mass

and dry mass) makes it subject to lower error than is likely the case for the measures that it substitutes. In the case of microbial communities, species or taxa are often taken as a proxy for microbial traits that appear to be phylogenetically constrained (e.g., salinity preference, methanogenesis). However, other traits (e.g., phosphate use, phage resistance) appear to be fast evolving and poorly correlated with phylogeny (Martiny et al. 2015). In such cases, assessing their diversity through taxonomic proxies will fail, which leaves open the question of their measurement in practice. More generally, it is important to be aware that, because proxies are less directly linked to ecosystem processes than the traits they replace, their use in practice may be significantly limited. Microbial ecologists are increasingly turning to shotgun metagenomics rather than purely taxonomic surveys to provide a read-out of gene functions present in an environment (Sunagawa et al. 2015, Quince et al. 2017). The extent to which microbial taxa are good proxies for traits (understood as gene functions) is currently an active area of debate (Galand et al. 2018, Louca et al. 2018) and it appears that functional redundancy may be a feature of broad metabolic traits, but not of finer-grained traits related to biotic interactions.

A fourth challenge to measuring functional traits in the field stems from their spatiotemporal variability; measured traits may vary intraspecifically depending on environmental or regional differences to which individuals have been exposed. For instance, in the case of evergreen needle chemistry, studies have found that intraspecific plasticity contributed to significant differences in forest productivity and carbon cycles—and therefore ecosystem functioning (Reich et al. 2014). Note that intraspecific genetic variability often adds to this plasticity, the two not being distinguished in most studies. Although some studies identify at which scales and under which conditions intraspecific variability matters—notably alongside environmental gradients—(Auger and Shipley 2013, Kumordzi et al. 2014, Siefert et al. 2015), measurement at the scale of the individual adds another dimension to functional diversity empirical approaches. In addition, many traits can show variability over time as an organism develops—such as changes in leaf traits, leaf and wood chemistry—as observed, for instance, by Martin and Thomas (2013) for tropical trees of various life stages. In aquatic phytoplankton, rapid generation times and large overall variation in traits have led to a different approach to the spatiotemporal variability challenge: examination of the adaptation of the community composition as a whole—as represented by the constituent traits observed, such as coloniality, cell size (surface-area-to-volume ratio, as an indicator of nutrient uptake and protection against predators), motility and nutritional mode—to local or regional environmental differences (e.g., Leonilde et al. 2017), with consequences for ecosystem processes (e.g., Follows et al. 2007). This approach considers that trait variation conforms to the ubiquity hypothesis according to which “everything is everywhere, and the local environment selects” for microbes

(Baas-Becking 1934). Trait variation across regions then occurs via selection of organisms best adapted to prevailing temperature, mixing, light, ice cover or predation regimes (e.g., Schwaderer et al. 2011, Acevedo-Trejos et al. 2015, Özkundakci et al. 2016, Thomas et al. 2016).

Empirical challenges: Extending the domain of functional diversity studies

Functional diversity studies have—so far—only addressed a very limited spectrum of the biosphere’s total biological diversity and biomass. Underrepresented but vastly abundant and diverse organisms include, in particular, arthropods and microbial organisms—such as protists, fungi, bacteria, and viruses—that have been largely ignored as compared to plants, birds, stream insects, fish and plankton communities as the focus of functional diversity studies (Devictor et al. 2008, Nock et al. 2016). Evidently, these organisms interact with plants and with each other to influence ecosystem functioning. A key empirical question for future research is the degree to which the functional framework initially developed for some macroscopic species can be applied to other kinds of organisms. This includes both the question of which functional traits can and should be measured across the whole range of living organisms, and to what extent the general concept of function will need to be modified.

For instance, microorganisms such as bacteria and archaea present significant challenges owing to limited morphological differences among microorganisms and because most microbial life cannot easily be grown in culture and observed in controlled settings (Martiny et al. 2006, Green et al. 2008, Malaterre 2016). The identification of microbial functional traits has largely focused on two types of traits (Martiny et al. 2015): traits that can be measured directly on microbial organisms in the laboratory (e.g., ability to fix nitrogen or growth rate in culture) and traits that can be inferred on the basis of the presence or expression of genes in an organism or in the metagenome or metatranscriptome of a microbial community (e.g., presence of genes for nitrogen fixation in a metagenomic sample). Several empirical challenges remain: the potential disconnection between the presence of a gene in a genome or community and the expression of that gene due to microbial dormancy (Lennon and Jones 2011); the assumptions associated with inferring functions from phylogenetic relatedness when relative abundances of microbial taxa are estimated only using barcoding approaches, such as sequencing of the bacterial 16S gene to detect the presence of microbial taxa in a sample instead of direct observations of individual organisms and their functions; the difficulty of inferring function from gene sequences, especially for complex or polygenic traits such as behavior and environmental niche tolerances (Keeling and Campo 2017); and the lack of empirical data to identify correlations among microbial functional traits and between traits and ecosystem functions (Fierer et al. 2014).

To take another example that concerns arthropods, empirical challenges have included accounting for strong

sexual dimorphism or highly distinct juvenile and adult life forms within a single species (Brousseau et al. 2018a) and identifying a core set of traits across the staggering diversity of morphologies, life histories, resource acquisition and predator avoidance strategies (Moretti et al. 2017). Although progress has been made, a majority of existing studies lack clear hypotheses associated with environmental filters, traits or functions, limiting the capacity to use the existing conceptual framework predictively (Brousseau et al. 2018a).

Considering traits of organisms of newly studied communities opens the door to the emerging field of interaction ecology. The challenge in this case is to acknowledge the complexity of interactions and incorporate all their different consequences on ecosystem functioning. For example, viruses as free entities may be considered functionally inert, because they have no metabolism and gene expression outside of their host, but, through strain-specific lysis, they influence community structure and are major players in nutrient cycling (Suttle 2007). Moreover, metabolic pathways in viruses can be distributed across many individuals rather than constrained to a single genome (Hurwitz et al. 2013), further complicating the relationship between traits and functions. Another use of traits in the study of interactions is to match traits of consumers to that of their resources in order to predict trophic interactions (Bartomeus et al. 2016). Trait matching of predatory traits (e.g., mandible strength of a carabid beetle) to prey traits (toughness of prey) has been successfully used to predict feeding interactions, providing a technique useful to anticipate consequences of novel communities and ecosystems (Brousseau et al. 2018b). But needless to say, much remains to be investigated.

Epistemic roles of functional diversity

The concept of functional diversity and its empirical assessment fulfill diverse epistemic roles in ecological research. Disentangling these roles sheds light on the various ways by which knowledge is produced and justified in this domain of ecology. As alluded to above (in the “Functional diversity” section), functional traits and their measures of diversity can first be used as *explanatory* factors in models that aim at explaining why and how certain ecosystem processes and properties obtain. For instance, ecosystem productivity measured in terms of biomass can be well explained by models on the basis of functional trait diversity (e.g., Paquette and Messier 2011 for temperate to boreal forests, or, Finegan et al. 2015 for tropical forests). Conversely, functional diversity can also be conceptualized as the element that requires *explaining*. For instance, this is the case when modeling diversity in functional traits as a function of certain environmental gradients (e.g., variation in plant leaf size as a function of environmental water availability and temperature; Wright et al. 2017). This dual role of functional diversity—as something that explains and as something that needs explaining—shows notably in the distinction made by ecologists between functional effect traits and functional response traits.

The explanatory role of functional diversity is often linked to a *predictive* role. For instance, identifying trait values that favor survival in a given environment makes it possible to predict which species have better chances of persisting or are more at risk of becoming extinct given specific environmental changes (Frenette-Dussault et al. 2013). Functional diversity also facilitates the development of testable predictions of broader ecological hypotheses. For example, in asking whether assembly of plant communities was mostly driven by environmental filtering or by competitive interaction, Weiher and Keddy (1995) predicted the former should lead to low variance in the functional traits of a plant community, whereas the latter should lead to a more even distribution of traits around the community trait mean. Such predictions were indeed corroborated in field studies (e.g., Cornwell and Ackerly 2009). Similar questions concern microbial community structure in which environmental filtering also appears to be an important driver (Horner-Devine and Bohannan 2006, Silverman et al. 2017), although the relative importance of environmental filtering and competitive effects varies by trait (Martiny et al. 2015, Trosas et al. 2018). Another instance in which predictions from functional diversity models can inform broader ecological hypotheses concerns the unified neutral theory of biodiversity—that postulates that functional differences among species are unimportant in generating and maintaining the diversity of communities (Hubbell 2004). The neutral theory provides a starting point from which the importance of non-neutral processes might be investigated (O'Dwyer and Cornell 2018). In specific cases in which the neutral theory alone could not account for the empirical data, dual approaches incorporating also functional diversity have been shown to provide more accurate predictions (e.g., Gravel et al. 2006, Yildirim et al. 2018). Interestingly, the neutral theory has also pushed functional ecologists to seek to demonstrate the importance of functional differences instead of simply assuming their importance (e.g., Gotelli and McGill 2006, Rosindell et al. 2011).

Functional diversity can also play a role in further enabling greater *generalization* and *unification* in ecology. Indeed, this may be achieved through the pragmatic operationalization of ecology by the use of a common and reduced set of functional traits representing major resource-use strategies within a given taxon or trophic level. As well, by facilitating the scaling of ecological observations across levels of biological organization, functional diversity may also contribute to the conceptual and methodological unification of fields such as population, community and ecosystem ecology, a major epistemic ideal according to some authors (Pickett et al. 2010, Vellend et al. 2014).

Finally, functional diversity plays a *heuristic* role in the current development of ecological theory. Although functional generalizations in ecology remain limited by the small number of studies conducted using a shared set of traits with standard measurement methodologies, several subfields of ecology have been fruitfully guided by the functional diversity framework (Krause et al. 2014, Moretti et al. 2017). For

example, functional approaches can facilitate the description and study of complex adaptive patterns (Peters 1991, Odenbaugh 2005) so as to focus on specific variables and relations—such as traits that can be linked to functions—over other variables—for example, traits without function—and by shaping the ways ecological hypotheses and models are developed.

The role of functional diversity in ecological management

Research on functional diversity is often considered relevant for ecological management (Cadotte et al. 2011). For instance, the knowledge that functional redundancy and response diversity within functional groups affect ecosystem resilience (Gunderson 2000, Walker and Salt 2012, Desjardins et al. 2015), or that certain traits covary with the presence of some ecosystem properties (de Bello et al. 2010), could be used to influence ecosystems by intervening on functional trait assemblages. Intervening on functional effect traits could therefore be a way to influence ecosystem processes—for instance, to optimize specific functions and services (Isbell et al. 2017), or even promote targeted aspects of biodiversity (Walker 1992, Tilman et al. 2017). Conversely, changes in ecosystemic properties—including changes in spatial and temporal heterogeneity or habitat connectivity—known to affect species diversity in some contexts (Tews et al. 2004, Fahrig et al. 2011) could be sought to induce specific changes on some selected characteristics of functional trait diversity.

Nonetheless, inquiries on the relationships between functional diversity and ecosystem functioning and services are yet to provide clear and well corroborated answers as to how these relationships are to play any significant role in ecological management (Steffen et al. 2015, Garnier et al. 2016). Although a few studies have successfully linked trait combinations to processes, scaling up to relevant management scales (Orwin et al. 2010, Lavorel et al. 2011, both in grasslands), many challenges remain to extend this approach to a range of different ecosystems, notably because of a lack of sufficient local trait data (Garnier et al. 2016). Furthermore, because of the complexity of ecosystems and the nonlinear dynamics of ecological variables, it is likely that the optimization of one function could be detrimental for other functions in any given ecosystem. A multifunctional perspective appears therefore necessary (Wuethrich 2007), which adds a layer of complexity in the prediction of the outcome of any specific intervention. The greatest care should therefore be taken if one wants to ground current management action on a functional account of biodiversity.

It is also important to note that functional approaches to ecological management and conservation contrast with the more traditional approaches, such as those that focus on natural heritage or that attribute a non-instrumental value to species, naturalness or wilderness (Wuerthner et al. 2014). In particular, by putting the emphasis on functional traits independently of the species, the functional approach to

conservation may open the door to a type of management in which anything goes, as long as some ecosystem services are provided, thereby increasing the risk of overlooking species (Simberloff et al. 2015). Moreover, under a changing climate, conservationists and ecosystem managers may require new services that are more adaptive, in order to prevent ecosystem degradation (Lavorel et al. 2019), therefore requiring further analyses of underlying processes and controlling traits. Much, therefore, hinges on the choice of *normative* objectives to pursue, be they framed in terms of sustainable agriculture, ecological restoration and engineering, or biodiversity and nature conservation. Goals that concern ecosystem functioning and services (e.g., biomass production, resilience, carbon fixation) are well served by functional approaches, whereas other objectives (e.g., historical continuity, naturalness, conservation of the entities themselves rather than what they do) may require a different focus and axiology (Perring et al. 2015). Such ethical considerations reinforce the need to adopt not only an adaptive but also a pluralistic and collaborative management framework, in which various stakeholders and different social and economic goals are integrated and reevaluated along the way (Maris and Béchet 2010). Finally, another relevant aspect to consider is the scale at which functional diversity should be investigated. To effectively guide ecological management, studies should range from a local piecemeal approach to a broader geofunctional perspective that aim at capturing the complexity of social–ecological networks and their interactions with the rest of nature (Hobbs et al. 2011, Desjardins et al. 2019).

Beyond an epistemic roadmap

As the functional diversity framework is increasingly adopted in many branches of ecology, clarifying the meaning of concepts such as functional trait or functional diversity becomes critical, at least to ensure mutual understanding and to facilitate comparisons and integration among findings. But as the epistemic roadmap presented above shows, such conceptual clarification is but one of the many epistemic challenges that functional approaches in ecology must face. The functional diversity framework is nevertheless showing signs of maturity as its influence over explanations, theoretical models or ecosystem management options grows. Perhaps one of the strongest hopes about the framework is that it may enable integration across studies that typically focus—for the sake of dealing with complexity—on specific trophic levels, but that could and must be combined to elucidate larger-scale ecological phenomena. Because functional diversity tackles ecosystems through more mechanistic lenses than does taxonomic diversity, it holds the promise of a deeper understanding of ecosystem processes and of improved predictability of ecosystem functioning. The degree to which this promise will be fulfilled is still, of course, undetermined. To date, focusing on functional traits has successfully provided heuristics to identify candidate variables for ecosystem modeling. But, in the end, the epistemic fruitfulness of functional diversity will hinge on its capacities to explain

and predict across several domains. In this respect, it is still an open question to what extent functional diversity will account for community assembly patterns or predict ecosystem processes, or whether more detailed insights about the very mechanisms that link functional traits together and to local abiotic conditions will also be required. After all, having the list of components of a mechanism is always a good start, but knowing how these components interact often remains necessary to understand the actual operation of that mechanism, and most notably so in the case of ecosystems. Uncovering the mechanistic links among functional components—and not just the diversity of these functional components—may henceforth prove necessary when investigating ecosystems and some of their more challenging dynamical properties. It is also important to note that even though functional diversity may be key to achieving the epistemic goals of a better understanding of ecosystem functioning and possibly of ecosystem services, it may or may not be appropriate for achieving conservation objectives, depending on the normative goals attached. Also, the extent to which conservation legislation will be shaped by functional diversity or by species diversity, possibly depending on their epistemic successes, will most certainly influence which normative goals are pursued. Knowledge and values, although often intertwined in practice as is shown by our epistemic roadmap, remain two distinct facets of how we may go about understanding nature.

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Authorship statement

Christophe Malaterre, Antoine C. Dussault and Ely Mermans conceived of paper based on a workshop organized in collaboration with Frédéric Bouchard. Sections structured by Christophe Malaterre, Antoine C. Dussault, Alison Munson, Beatrix E. Beisner, Ely Mermans, Steven W. Kembel, Geneviève Lajoie, Eric Desjardins and additional writing by Gillian Barker, Frédéric Bouchard, I. Tanya Handa, Jay Odenbaugh, Timothée Poisot, Virginie Maris, B. Jesse Shapiro, Curtis A. Suttle. Manuscript revised by all authors.

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