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Concepts and Questions

Harnessing trait–environment interactions to predict ecosystem functions

Manuel Blouin^{1*}, Florence Dubs², and Jean-François Ponge³

¹*Agroécologie, Institut Agro Dijon, INRAE, Université Bourgogne, Université Bourgogne Franche-Comté, Dijon, France* *(manuel.blouin@agrosupdijon.fr); ²*UPEC, CNRS, IRD, INRA, UMR 7618, Institute of Ecology and Environmental Sciences-Paris, iEES Paris, Sorbonne Université, Université de Paris, Paris, France*; ³*Museum National d’Histoire Naturelle, CNRS UMR 7179, Brunoy, France*

Running heads:

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Predicting ecosystem functions

In a changing world, predicting ecosystem functions is essential to ensuring human well-being and survival. However, commonly used trait-based predictive approaches frequently lack predictive power. Statistical and conceptual attempts to better incorporate environmental factors into trait-based predictions have done so by integrating indirect, trait-mediated effects therein. Here, we define ecosystem functions as changes in the state, position, or nature of energy or matter within an ecosystem, and then illustrate how environmental factors can directly affect ecosystem functions. Given that the effects of organismal traits and environmental factors are not necessarily additive, we also propose that interactions between organismal traits and environmental factors (hereafter, trait–environment interactions) have explanatory power. We propose a conceptual framework in which organismal traits, environmental factors, and trait–environment interactions, together with the environment’s effects on traits (plasticity) and traits’ effects on the environment (ecosystem engineering), can explain ecosystem functions. We conclude by discussing the importance of considering trait–environment interactions and identifying future avenues of exploration.

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In a nutshell:

- To provide robust recommendations to managers, scientists must be able to better predict ecosystem functions
- Although trait-based prediction approaches increasingly account for environmental factors, their impact is always treated as trait mediated
- Organismal traits, environmental factors, trait–environment interactions, phenotypic plasticity, and ecosystem engineering can be integrated into a conceptual framework to predict ecosystem functions
- This new framework helps clarify previously paradoxical situations in which traits were poor predictors of ecosystem functioning (for instance, because variation in an ecosystem function was better explained by a trait–environment interaction)

The environmental and agricultural sciences face the major task of predicting ecosystem functions and related ecosystem services, which are essential for human well-being and survival (MA 2005). This task has become increasingly urgent given that climate change is currently destabilizing communities and ecosystems, leading to new challenges in agricultural and environmental management (Howden *et al.* 2007). Because many species provide ecosystem services (Kremen 2005), these challenges are exacerbated by the global biodiversity crisis. Up to now, many community ecologists have focused on using the biotic components of ecosystems—either species, species functional groups, or species traits—to predict ecosystem properties (Loreau *et al.* 2001). This approach has generated valuable insights into the relationship between species richness and ecosystem stability (Tilman and Downing 1994) or productivity (Hector *et al.* 1999). Extensive research efforts were dedicated to predicting ecosystem functions from traits, for example in the case of plants (Lavorel and Garnier 2002); more recently, scientists have advocated that greater effort be made to identify relevant traits, describe intraspecific trait variation, and scale up from traits to ecosystem processes (Funk *et al.* 2017). However, despite numerous studies, often with ambitious experimental or sampling designs, having relied on the trait-based approach, it has generated ambiguous results. Even the most comprehensive study to date—in which 41 traits of plants growing in 78 grassland plots were monitored over a 10-year period, with the objective of explaining 42 different ecosystem properties—concluded that traits accounted for only 12.7% of variation in ecosystem properties, with a maximum of 18% being reached when the trait number was unlimited (van der Plas *et al.* 2020). This low level of predictive power was attributed to the fact that abiotic and biotic environmental factors had been ignored. Similarly, the findings of the Jena Experiment, a 15-year grassland study in central Germany, revealed that plant traits were plastic and depended on the identity of other species in the community, making them poor individual predictors of ecosystem functions (Weisser *et al.* 2017).

Here, we analyze how the trait-based approach has treated environmental factors, and show that the latter can have direct effects on ecosystem functions—independent of organismal traits: a fact that has been overlooked in trait-based approaches. These direct environmental effects strongly suggest the existence of interactions between organismal traits and environmental factors (hereafter, trait–environment interactions), which could have strong explanatory power in certain situations. From this, we developed a new conceptual framework that links organismal traits, the environment, and ecosystem functions and illustrate how the framework can clarify ultimate and proximate causes in efforts to explain ecosystem functions. We also discuss the epistemological foundations of the relationships between organisms and ecosystem properties.

The history of predicting ecosystem functions

Past attempts at predicting ecosystem functions have been based on three central concepts: (i) an ecosystem function is a dependent variable to be explained, (ii) organismal traits represent a set of independent variables, and (iii) the environment inhabited by the trait-bearing organisms can be treated as a separate set of independent variables. While different frameworks exist, they arise—to varying degrees—explicitly from these three concepts.

Since its conceptual beginnings (Tansley 1935), consideration of the ecosystem has always included the abiotic environment. As the field of ecosystem ecology matured, ecosystem functions were primarily explained through the lens of the abiotic environment, with a particular focus on solar energy flux; this flux determines the maximum levels of primary production, which are subsequently modulated by water and nutrient availability (Odum and Odum 1981). Many ecological phenomena can indeed be explained by the principles of thermodynamics (Jørgensen and Fath 2004). In this approach, a crucial role is attributed to environmental factors (the external conditions capable of system modification), while organismal traits are largely ignored (Figure 1a).

In the trait-based approach, ecologists try to explain changes in ecosystem functions in various situations using organismal traits, which are treated as surrogates for organism performance (Violle *et al.* 2007). In the specific field of plant traits, the logic is that, because primary production is the result of an assemblage of functional traits, it should be possible to predict primary production across various environmental circumstances by examining species responses to varying environmental factors, where these responses result from “response traits”. Many studies have thus made use of environmental gradients, with the objective of identifying trait association syndromes in different environmental contexts (eg Diaz and Cabido 1997). Given the strong correlation between the net assimilation rate of leaves and traits such as specific leaf area (SLA), plant communities are occasionally represented by big-leaf models (Figure 1b) despite such scaling approaches having little empirical support (McGill 2019) (see Discussion). In this approach, environmental factors are generally considered as filters that act on the response traits of individual species, constraining a species arrival and persistence within communities (Figure 1b; Keddy 1992; Violle *et al.* 2007).

However, a key weakness of the trait-based approach is that organismal traits are plastic and vary in response to environmental factors. McGill *et al.* (2006) stressed the importance of considering organismal traits in tandem with environmental gradients and interaction settings to better predict community assembly patterns. Consequently, different statistical methods have been developed to examine how functional traits vary in response to environmental gradients (Miller *et al.* 2019). These methods include (i) the community-weighted mean, or the mean of the trait values for species at a given site weighted by species abundance (Lavorel *et al.* 2008; Ricotta and Moretti 2011); (ii) correlations between organismal traits and environmental variables weighted by species abundances within sites, which are tested via permutations (Peres-Neto *et al.* 2017); and (iii) statistical multilevel models that attempt to describe “the full structure of the data” (Brown *et al.* 2014).

An alternative to these statistical methods is a conceptual approach that explains the context dependence of ecosystem functions based on flexibility in the expression of functional traits (Schmitz *et al.* 2015). By explicitly accounting for the trophic context of a focal species, Schmitz *et al.* (2015) demonstrated that it is important to consider trait flexibility (due to allele variation or phenotypic plasticity) in response to the presence of a given resource or predator. For example, wrinkleleaf goldenrod (*Solidago rugosa*) is a dominant competitor in its plant community in the absence of grasshopper herbivores and spider predators. In their presence, *S. rugosa* serves as a refuge for grasshoppers, which feed on *S. rugosa*, thereby offsetting its dominance (Schmitz 2003). Ultimately, it is crucial to grasp the cascading effects of predation to understand herbivore behavior, plant community structure, and primary production (Schmitz

2008). Schmitz *et al.* (2015) illustrated the relevance of the “resource–focal species–predator” module at other trophic levels, providing a more complete picture of interactions across trophic levels, from soil detritus to carnivores. However, although it is applicable to all trophic levels, defines ecosystem functions independently of species traits, and is based on matter and energy fluxes, this approach strictly considers the influence of predators and resources and does not account for the influence of abiotic factors. In addition, it is not useful in characterizing ecosystem functions that are better described as state-changes (see below).

Although the above-described statistical and conceptual studies constitute progress because they consider the effect of the environment on organismal traits, the central tenet that environmental effects on ecosystem functions are always mediated by organismal traits still holds (Figure 1b). As a result, research to date has largely failed to provide a working framework for unifying ecosystem ecology (Figure 1a) and trait ecology (Figure 1b).

Redefining the relationships between traits, the environment, and ecosystem functions

In ecology, the term “function” can have different meanings (Jax 2005). Whereas the above (traditional) frameworks can *clarify how traits relate to organismal fitness* (Violle *et al.* 2007), they do not help in *understanding if traits can be good predictors of ecosystem functions*. To this end, Bellwood *et al.* (2019) proposed that an ecosystem function be defined as the “movement or storage of energy or material” in the ecosystem. These fluxes are expressed as quantities of matter or energy per unit of time, which are unlikely to be captured by a single measurement of a trait value. We suggest retaining the idea that function is synonymous with process (Jax 2005) and expanding Bellwood *et al.*’s (2019) definition by extending it beyond trophic relationships to any kind of change over time, including those of a non-trophic nature. Indeed, organisms change their environments not only through consumption but also by transforming living or nonliving materials from one physical state to another via various mechanisms (Jones *et al.* 1994).

To fold trophic and non-trophic relationships into the same concept, we propose the following definition:

An ecosystem function is a change in the state, position, or nature of energy or matter in an ecosystem.

This definition covers the range of organismal activities within ecosystems, such as initiating changes in physical state (eg from liquid to gas during water transpiration), changes in spatial position (eg the dispersal or construction of biogenic structures from environmental materials, such as a beaver dam or an earthworm burrow), and changes in the nature of bodies (eg biogeochemical reactions or trophic relationships). Inspired by the distinction between autogenic and allogenic engineers proposed by Jones *et al.* (1994), we suggest distinguishing between *autogenic functions*, for which a certain degree of overlap exists between traits and functions (eg plant biomass, height, and SLA as proxies of primary production; Figure 1b), and *allogenic functions*, where an organism (often an animal or a microbe) carries out transformations that do not modify its own organismal structure (Figure 1c).

This definition makes it possible for all taxa (plants, animals, microbes) to exist within the same conceptual framework: traits and functions are a priori distinct (Figure 1c) but can be treated as identical in the case of autogenic functions (Figure 1b), at least in instances where traits reflect a change over time. In addition, establishing a distinction between traits (causes)

and functions (consequences) opens the door to consideration of other determinants (or causes) of ecosystem functions, such as environmental factors or components. Indeed, changes in the state, position, or nature of matter and energy can arise even without organisms. For example, atmospheric nitrogen (N_2) can be fixed as ammonium (NH_4^+) (a change in the state of matter) by various abiotic processes, such as lightning, catalysis by titanium dioxide (TiO_2), and, in hydrothermal systems, catalysis by iron–nickel alloys (Stüeken *et al.* 2016). Likewise, wind can transport particles of matter over short to long distances (a change in spatial position). In such cases, there is no need to evoke organismal traits to explain ecosystem functions (Figure 1a). If the scientific objective is to predict ecosystem functions with a maximum degree of generality, then it is necessary to develop a conceptual framework that can explain or predict ecosystem functions even in the absence of organisms.

Moreover, changes in ecosystem functions can arise in the presence of organisms without necessitating variation in organismal traits. For example, in deforested pasturelands, the tropical earthworm *Pontoscolex corethrurus* compacts soil, which inhibits plant growth and reduces primary production (Chauvel *et al.* 1999; Hallaire *et al.* 2000). However, in its natural forested habitat, this earthworm species ingests and breaks down charcoal, releasing a product that is incorporated into the mineral soil. The earthworm's activity likely contributed to the historical formation of fertile Amazonian “dark earth” soils, which boost levels of primary production (Ponge *et al.* 2006b). The same species thus has opposing impacts on primary production in two environmental contexts, in which soil properties differ even though the biological trait of importance—the earthworm's digestive apparatus—is the same.

These observations emphasize that ecologists may need to rethink how the environment should be treated in a predictive framework of ecosystem functions. We propose the following definition:

The environment is a complex of physical, chemical, and biological factors capable of influencing ecosystem function either directly, by affecting the state, position, or nature of energy or matter, or indirectly, by affecting organismal traits.

In addition to addressing the issue of the environment's effects on organismal traits highlighted by the examples above, this definition recognizes that an environmental factor, whether biotic or abiotic, can influence an ecosystem function without mediation by organismal traits. For example, soil pH (an environmental factor) can modify nitrate uptake by plants (a flux of matter), either via changes in root morphology (an indirect environmental effect mediated by an organismal trait) or via nitrification dynamics (a direct environmental effect on a flux).

Adding a trait–environment interaction to the framework

Once organismal traits and environmental factors have been defined as independent determinants of ecosystem functions, we can further refine our conceptual framework. Changes in an ecosystem function can result from variation in traits alone (Figure 1, b and c), variation in environmental factors alone (Figure 1a), or the combined effects of variation in traits and environmental factors. However, in many cases, these combined effects are not additive, and a significant trait–environment interaction effect is observed (Figure 1d).

As an example, lateral root proliferation in nutrient-rich patches (trait variation) has been interpreted as a clear illustration of plants adapting to heterogeneous environments, in that they are maximizing fitness presumably by increasing nutrient uptake (ecosystem function).

Yet, a paradox has emerged when nutrient fluxes have been measured: for plants grown in individual pots, root proliferation was not associated with higher levels of nutrient uptake or primary production (Robinson 1996). This apparent paradox was resolved when two plants were grown together in a single pot (variation in environmental factors). In this situation, a positive correlation was observed between lateral root emission and nutrient uptake/primary production (Hodge *et al.* 1999). This finding underscores that environmental variation, such as the presence or absence of neighboring plants (as well as the presence or absence of mycorrhizae or microorganisms mineralizing organic matter), can change the nature of the relationship between organismal traits (eg lateral root proliferation) and ecosystem functions (eg nutrient uptake) (Hodge 2004). In other words, the effects of trait variation and environmental variation are not necessarily additive.

When searching the literature for cases in which traits and the environment varied independently to estimate the respective effects of traits, environment, and trait–environment interaction, we found an intriguing case involving springtails, soil mesofauna belonging to the taxonomic class Collembola. Springtail species have been categorized as “fast” versus “slow” dispersers based on their morphological traits. More specifically, species with long legs and antennae, a well-developed jumping apparatus (furcula), and a complete visual apparatus are thought to be capable of more rapid dispersal (“fast” dispersers), whereas species with less well-developed locomotor and vision systems are thought to engage in slower dispersal (“slow” dispersers) (Ponge *et al.* 2006a). In an experimental study of springtail colonization (ie an ecosystem function corresponding to a change in spatial position), soil blocks were collected from two different environments (a meadow and a nearby forest), and their resident fauna were removed via drying and heating; the blocks were then returned to their respective environments; the researchers found no link between springtail traits and the rate of soil block colonization (Auclerc *et al.* 2009). We reanalyzed this dataset, focusing on the data collected from the fauna-free blocks 1 week after they had been returned to their environment of origin; the goal was to avoid counting the colonizers’ offspring as colonizers. As in the original study, we found no significant relationship between springtail traits and the rate of soil block colonization (1.09% of variance explained; Table 1; Figure 2a), nor was there an effect of environment type (meadow or forest, 0.07% of variance; Figure 2b). However, when we examined the trait–environment interaction (path 3 in Figure 1d), we found that it explained a significant amount (30%) of variation in the colonization rate (Figure 2c). This was not due to species environmental preferences (path 4) given that “fast” and “slow” dispersing species were independently distributed across environments (meadow, forest, or both; $X^2 = 6$, $P = 0.20$). In the meadow, 77% of the colonizers were fast dispersers, where their morphological traits likely facilitated displacement; by contrast, in the forest, only 38% of the colonizers were fast dispersers, perhaps because these same traits impeded movement through the leaf litter on the forest floor. To achieve even more explanatory power would require more precisely identifying the specific environmental factors that interact with species traits (eg the size of the organic matter particles composing the leaf litter). Taken together, these results illustrate how considering trait–environment interactions can improve predictions about ecosystem functions (from 1% to 31% of explained variance).

Structural model linking organismal traits, the environment, and ecosystem functions

By including environmental and trait–environment interaction variables, this conceptual framework helps bridge the gap between the deterministic visions held by ecosystem ecology and trait ecology and should allow for more reliable predictions of ecosystem functioning (Figure 1d). Notably, the framework considers that ecosystem functions can be modified (i) directly by environmental factors, as assumed in ecosystem ecology (path 2); (ii) directly by organismal traits, as assumed in trait ecology (path 1); or (iii) directly through the interaction between environmental factors and organismal traits, as assumed in the emergentist perspective (path 3; see Discussion). In addition, ecosystem functions can be modified indirectly (path 4 + 1 or 5 + 2), when environmental factors and organismal traits influence one another. For example, the environment can filter species traits (path 4) on evolutionary timescales via natural selection (Darwin 1859) or on ecological timescales via phenotypic plasticity (Bradshaw 1965). Reciprocally, organisms, through their traits, can influence the environment (path 5) on evolutionary timescales via niche construction (Odling-Smee *et al.* 1996) or on ecological timescales via ecosystem engineering (Jones *et al.* 1994).

Organismal traits may be interpreted as the ultimate cause of variation in ecosystem functions (path 1) when they may only be a proximate cause, notably when variations in both organismal traits and ecosystem functions are in fact due to variation in environmental factors (path 4 + 1). For instance, a study was conducted along a regional climatic gradient in central western Argentina ($n = 63$ sites), which spanned more than 400 km between the subhumid high plateaus of the Córdoba Mountains and the semiarid to arid western plains; the researchers concluded that recurrent patterns in trait associations along the climatic gradient (eg in photosynthetic pathway, SLA, leaf weight ratio, deciduousness, leaf succulence) accounted for the observed variation in primary production (path 1; Diaz and Cabido 1997). However, the causal relationship between climatic conditions (annual rainfall differed by 800 mm and temperature by 11°C between the two extremes of the gradient) and primary production is well documented in ecosystem ecology and ecophysiology (path 2), and the trait correlation observed in the study likely arises from the joint action of climatic factors influencing primary production (path 2) and natural selection filtering plant traits (path 4 + 1).

Conversely, environmental factors may be interpreted as the ultimate cause of variation in ecosystem functions (path 2) when they may only be a proximate cause, as they are responses to changes in species traits (path 5 + 2). Such has been seen in plant–soil feedback experiments, where plant species can change their biotic or abiotic environments by modifying pathogen abundance or nutrient availability, for example. Also known as engineering effects, these environmental changes have reverberating impacts on ecosystem functions, which are often positive (Jones *et al.* 1997) but are occasionally negative, as in the case of plant–soil feedback (Kulmatiski *et al.* 2008).

Discussion

When explaining ecosystem functions, there are several advantages to considering environmental factors: such factors can account for variation in ecosystem functions when no organisms are present, or when organismal traits do not vary; augment the predictive power of traits when trait effects are influenced by the environment; and help to clear up confusion between ultimate and proximate causes. All of these improvements arise from a more precise general definition of ecosystem functions.

The attempt to explain ecosystem functions using traits alone reflects an epistemological position known as reductionism. Simply put, reductionists believe that, if it has not been demonstrated that it is impossible to explain the properties at the $n + 1$ level of organization (eg the population, community, or ecosystem) by the properties at the n level of organization (eg the organism, population, and community/abiotic factors, respectively), then it is accepted that the $n + 1$ level is reducible to the n level. According to the 19th-century British philosopher John Stuart Mill (Mill 1882), if the effects of two different agents (“causes”), when acting independently from one another, are known, then the effects of those same agents, when acting jointly under the same conditions as before, can be predicted a priori. This result is what is often called “additivity” in ecology, whereby organism-level properties can be summed to explain changes at the population level, population-level properties can be summed to explain changes at the community level, and the properties of community or abiotic factors can be summed to explain changes at the ecosystem level. Thus, organism-level properties should ultimately be able to explain changes at the ecosystem level.

In contrast, emergentists consider that, if it has not been demonstrated that it is possible to explain all the properties at the $n + 1$ level of organization by the properties at the n level of organization, then one can consider the properties at the $n + 1$ level as emergent. A simple example is the passage from atoms to molecules: as separate elements, hydrogen (H) and oxygen (O) have specific properties that do not allow the properties of water (H₂O) to be predicted (eg specific heat, viscosity). In ecology, this result is often referred to as an interaction. The concept of an “ecosystem” as an entity composed of a community and its biotope (Tansley 1935) is rooted in this emergentist viewpoint. Because interactions exist between organisms, populations, communities, and abiotic factors, it can be expected a priori that ecosystem properties are not the summed effects of organismal traits. It is essential to understand intraspecific, interspecific, and biotic–abiotic interactions to perceive how organismal traits come together to shape ecosystem functions, in the same way that knowledge of dominance and epistasis are essential to understanding how genetic factors come together to shape a phenotype.

From this vantage point, it seems likely that the predictive power of many previously published trait datasets would improve if a trait–environment interaction was considered, as illustrated by the above example of the springtails. We invite trait ecologists to revisit their datasets and explore whether the focal traits demonstrate a relationship with environmental factors, with the aim of more effectively predicting ecosystem functions. Direct effects (paths 1–3) are unlikely to provide the only means of understanding variation in ecosystem functions. Indeed, indirect causal relationships are also possible, as when there is selection on or plasticity in traits as a product of environmental factors (path 4 + 1) or engineering effects (path 5 + 2). In this regard, structural equation modeling could be particularly well suited to the process of evaluating the likelihood of different causal chains. For example, in the Jena Experiment (Weisser *et al.* 2017), path analyses revealed that the effects of diversity on ecosystem processes often stemmed from the effects of plant diversity on species interactions (path 3). The weighty task of predicting ecosystem properties must be shouldered by a broad range of environmental scientists, including ecophysiologicals, ethologists, community ecologists, soil scientists, and climatologists. Such collaborations can help identify the causal patterns at play and allow us to more effectively predict ecosystem functions. Moreover, this work can

highlight which traits are relevant in a specific environmental context, guiding managers who try to manipulate ecosystem functions and associated ecosystem services.

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Data Availability Statement

The springtail colonization data are available on Zenodo (<https://doi.org/10.5281/zenodo.11032648>). No novel code was used in this work.

References

- Auclerc A, Ponge JF, Barot S, and Dubs F. 2009. Experimental assessment of habitat preference and dispersal ability of soil springtails. *Soil Biol Biochem* **41**: 1596–604.
- Bellwood DR, Streit RP, Brandl SJ, and Tebbett SB. 2019. The meaning of the term “function” in ecology: a coral reef perspective. *Funct Ecol* **33**: 948–61.
- Bradshaw AD. 1965. Evolutionary significance of phenotypic plasticity in plants. *Adv Genet* **13**: 115–55.
- Brown AM, Warton DI, Andrew NR, *et al.* 2014. The fourth-corner solution—using predictive models to understand how species traits interact with the environment. *Methods Ecol Evol* **5**: 344–52.
- Chauvel A, Grimaldi M, Barros E, *et al.* 1999. Effects of earthworms on plant growth in the tropics. *Nature* **389**: 32–33.
- Darwin C. 1859. *On the origin of species*. London, UK: John Murray.
- Diaz S and Cabido M. 1997. Plant functional types and ecosystem function in relation to global change. *J Veg Sci* **8**: 463–74.
- Funk JL, Larson JE, Ames GM, *et al.* 2017. Revisiting the Holy Grail: using plant functional traits to understand ecological processes. *Biol Rev* **92**: 1156–73.
- Hallaire V, Curmi P, Duboisset A, *et al.* 2000. Soil structure changes induced by the tropical earthworm *Pontoscolex corethrurus* and organic inputs in a Peruvian ultisol. *Eur J Soil Biol* **36**: 35–44.
- Hector A, Schmid B, Beierkuhnlein C, *et al.* 1999. Plant diversity and productivity experiments in European grasslands. *Science* **286**: 1123–27.
- Hodge A. 2004. The plastic plant: root response to heterogeneous supplies of nutrients. *New Phytol* **162**: 9–24.
- Hodge A, Robinson D, Griffiths BS, and Fitter AH. 1999. Why plants bother: root proliferation results in increased nitrogen capture from an organic patch when two grasses compete. *Plant Cell Environ* **22**: 811–20.
- Howden SM, Soussana J-F, Tubiello FN, *et al.* 2007. Adapting agriculture to climate change. *P Natl Acad Sci USA* **104**: 19691–96.
- Jax K. 2005. Function and “functioning” in ecology: what does it mean? *Oikos* **111**: 641–48.
- Jones CG, Lawton JH, and Shachak M. 1994. Organisms as ecosystem engineers. *Oikos* **69**: 373–86.

- Jones CG, Lawton JH, and Shachak M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* **78**: 1946–57.
- Jørgensen SE and Fath BD. 2004. Application of thermodynamic principles in ecology. *Ecol Complex* **1**: 267–80.
- Keddy PA. 1992. Assembly and response rules: two goals for predictive community ecology. *J Veg Sci* **3**: 157–64.
- Kremen C. 2005. Managing ecosystem services: what do we need to know about their ecology? *Ecol Lett* **8**: 468–79.
- Kulmatiski A, Beard KH, Stevens JR, and Cobbold SM. 2008. Plant–soil feedbacks: a meta-analytical review. *Ecol Lett* **11**: 980–92.
- Lavorel S and Garnier E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct Ecol* **16**: 545–56.
- Lavorel S, Grigulis K, McIntyre S, *et al.* 2008. Assessing functional diversity in the field—methodology matters! *Funct Ecol* **22**: 134–47.
- Loreau M, Naeem S, Inchausti P, *et al.* 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**: 804–08.
- MA (Millennium Ecosystem Assessment). 2005. Ecosystems and human well-being: synthesis. Washington, DC: Island Press.
- McGill BJ. 2019. The what, how and why of doing macroecology. *Global Ecol Biogeogr* **28**: 6–17.
- McGill BJ, Enquist BJ, Weiher E, and Westoby M. 2006. Rebuilding community ecology from functional traits. *Trends Ecol Evol* **21**: 178–85.
- Mill JS. 1882. Of the composition of causes. In: A system of logic, ratiocinative and inductive (8th edn). New York, NY: Harper & Brothers.
- Miller JED, Damschen EI, and Ives AR. 2019. Functional traits and community composition: a comparison among community-weighted means, weighted correlations, and multilevel models. *Methods Ecol Evol* **10**: 415–25.
- Odling-Smee FJ, Laland KN, and Feldman MW. 1996. Niche construction. *Am Nat* **147**: 641–48.
- Odum HT and Odum EP. 1981. Energy basis for man and nature. New York, NY: McGraw-Hill.
- Peres-Neto PR, Dray S, and ter Braak CJF. 2017. Linking trait variation to the environment: critical issues with community-weighted mean correlation resolved by the fourth-corner approach. *Ecography* **40**: 806–16.
- Ponge J-F, Dubs F, Gillet S, *et al.* 2006a. Decreased biodiversity in soil springtail communities: the importance of dispersal and landuse history in heterogeneous landscapes. *Soil Biol Biochem* **38**: 1158–61.
- Ponge J-F, Topoliantz S, Ballof S, *et al.* 2006b. Ingestion of charcoal by the Amazonian earthworm *Pontoscolex corethrurus*: a potential for tropical soil fertility. *Soil Biol Biochem* **38**: 2008–09.
- Ricotta C and Moretti M. 2011. CWM and Rao's quadratic diversity: a unified framework for functional ecology. *Oecologia* **167**: 181–88.
- Robinson D. 1996. Resource capture by localized root proliferation: why do plants bother? *Ann Bot-London* **77**: 179–86.

- Schmitz OJ. 2003. Top predator control of plant biodiversity and productivity in an old-field ecosystem. *Ecol Lett* **6**: 156–63.
- Schmitz OJ. 2008. Effects of predator hunting mode on grassland ecosystem function. *Science* **319**: 952–54.
- Schmitz OJ, Buchkowski RW, Burghardt KT, and Donihue CM. 2015. Functional traits and trait-mediated interactions: connecting community-level interactions with ecosystem functioning. In: Pawar S, Woodward G, and Dell AI (Eds). Trait-based ecology—from structure to function. Cambridge, MA: Academic Press.
- Stüeken EE, Kipp MA, Koehler MC, and Buick R. 2016. The evolution of Earth's biogeochemical nitrogen cycle. *Earth-Sci Rev* **160**: 220–39.
- Tansley AG. 1935. The use and abuse of vegetational terms and concepts. *Ecology* **16**: 284–307.
- Tilman D and Downing JA. 1994. Biodiversity and stability in grasslands. *Nature* **367**: 363–65.
- van der Plas F, Schröder-Georgi T, Weigelt A, *et al.* 2020. Plant traits alone are poor predictors of ecosystem properties and long-term ecosystem functioning. *Nat Ecol Evol* **4**: 1602–11.
- Violle C, Navas M-L, Vile D, *et al.* 2007. Let the concept of trait be functional! *Oikos* **116**: 882–92.
- Weisser WW, Roscher C, Meyer ST, *et al.* 2017. Biodiversity effects on ecosystem functioning in a 15-year grassland experiment: patterns, mechanisms, and open questions. *Basic Appl Ecol* **23**: 1–73.

Figures

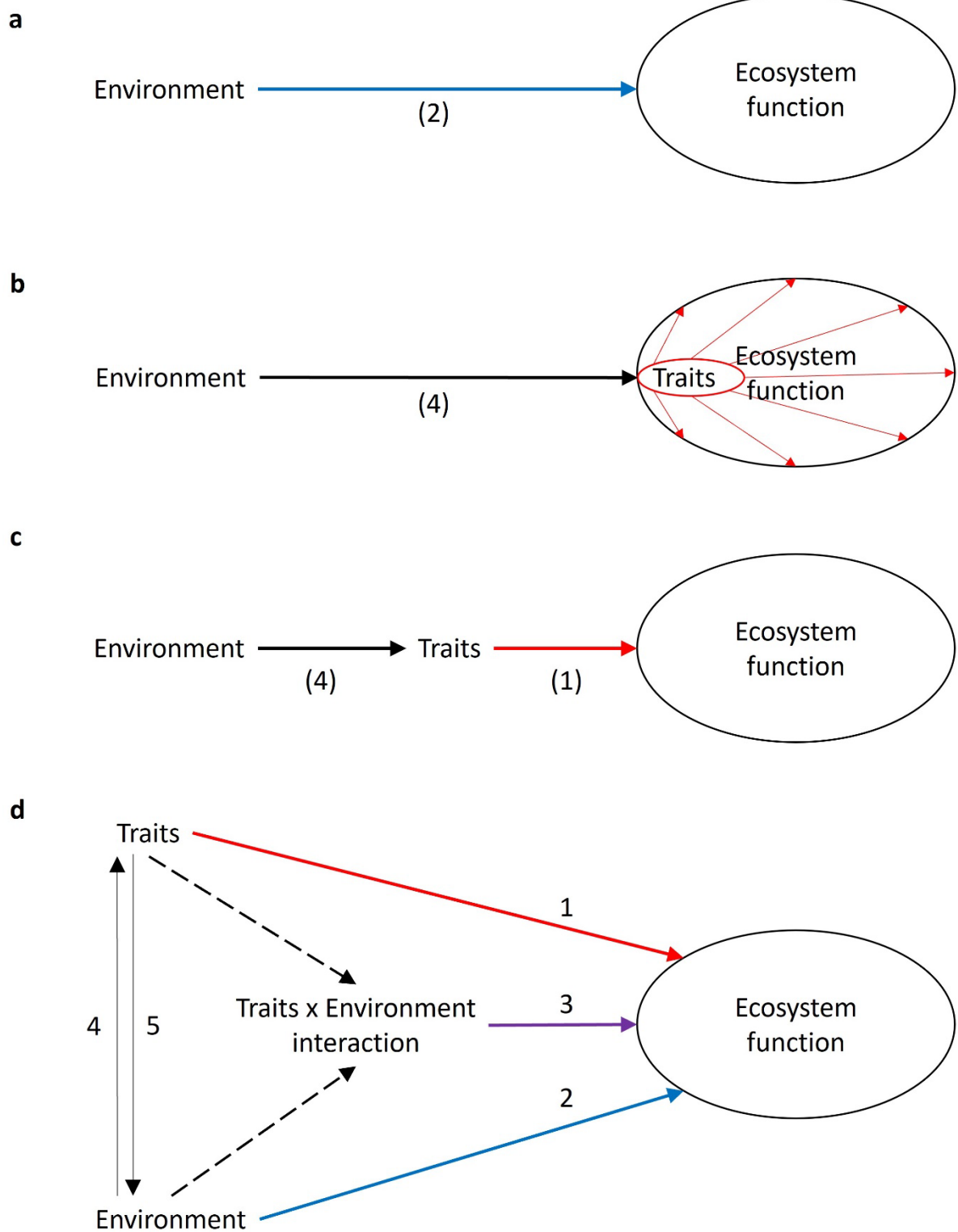


Figure 1. Different ways to explain ecosystem functions: (a) exclusively using abiotic environmental factors; (b) by viewing species and trait assemblages as the product of environmental filters, operating from the assumption that organismal traits can be scaled up to

ecosystem functions (autogenic functions); (c) same as (b), except that a distinction is made between traits and functions (allogenic functions); and (d) by considering the respective effects of traits (path 1), environmental factors (path 2), trait–environment interactions (path 3), phenotypic plasticity (path 4 + 1), and ecosystem engineering (path 5 + 2). Misinterpretations can arise when proximate causes are mistaken for ultimate causes (eg path 1 instead of path 4 + 1, path 2 instead of path 5 + 2). A solid arrow represents an effect or causal link; a dashed arrow represents a contribution to an interaction.

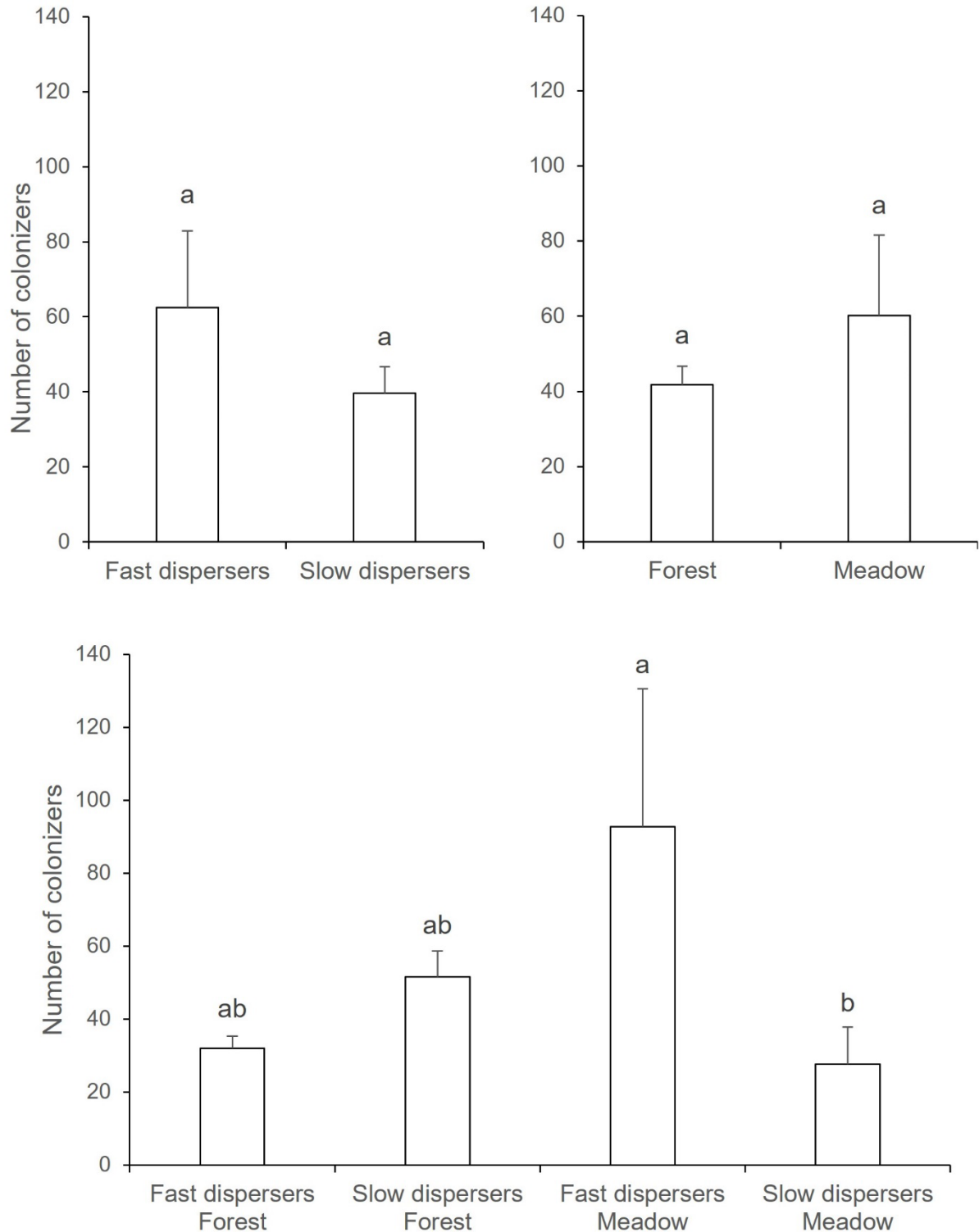


Figure 2. Number of springtails that colonized soil blocks from which resident fauna had been removed. (a) Number of “slow” versus “fast” dispersers, where dispersal category was determined by springtail morphological traits. (b) Number of colonizers in the soil blocks in the two environments to which the blocks were returned (meadow versus forest). (c) Number of colonizers according to springtail dispersal category (ie organismal traits) and soil block environment. Bars represent mean \pm standard error, with (a and b) $n = 10$ per group or (c) $n =$

5 per group. Significant differences ($P < 0.05$) are indicated by different letters (Dunn's test following a Scheirer–Ray–Hare test for nonparametric data).

Table 1. Results of the nonparametric Scheirer–Ray–Hare test analyzing the effects of organismal traits, environmental factors, and the trait–environment interaction on the number of colonizers in soil blocks from which resident fauna had been removed ($n = 20$).

	Degrees of freedom	Sum of squares	% Sum of squares	<i>H</i> statistic	<i>P</i> value
traits	1	7.2	1.09	0.2065	0.6495
environment	1	0.45	0.07	0.0129	0.9096
trait × environment	1	198.45	29.96	5.6914	0.0171
residuals	16	456.4	68.90	–	–

Notes: *P* value in bold font indicates significance between 0.01 and 0.05.