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REVIEW

Raunkiæran shortfalls: Challenges and perspectives in trait-based ecology

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Abstract

Trait-based ecology, a prominent research field identifying traits linked to the distribution and interactions of organisms and their impact on ecosystem functioning, has flourished in the last three decades. Yet, the field still grapples with critical challenges, broadly framed as Raunkiæran shortfalls. Recognizing and interconnecting these limitations is vital for designing and prioritizing research objectives and mainstreaming trait-based approaches across a variety of organisms, trophic levels, and biomes. This strategic review scrutinizes eight major limitations within trait-based ecology, spanning scales from organisms to the entire biosphere. Challenges range from defining and measuring traits (SF 1), exploring intraspecific variability within and across individuals and populations (SF 2), understanding the complex relationships between trait variation and fitness (SF 3), and discerning trait variations with underlying evolutionary patterns (SF 4). This review extends to community assembly (SF 5), ecosystem functioning and multitrophic relationships (SFs 6 and 7), and global repositories and scaling (SF 8). At the core of trait-based ecology lies the ambition of scaling up processes from individuals to ecosystems by exploring the ecological strategies of organisms and connecting them to ecosystem functions across multiple trophic levels. Achieving this goal necessitates addressing key limitations embedded in the foundations of trait-based ecology. After identifying key SFs, we propose pathways for advancing trait-based ecology, fortifying its robustness, and unlocking its

This study coincides with Sandra Lavorel's CNRS Gold Medal rewarding 30 years of research on trait-based ecology.

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full potential to significantly contribute to ecological understanding and biodiversity conservation. This review underscores the significance of systematically evaluating the performance of organisms in standardized conditions, encompassing their responses to environmental variation and effects on ecosystems. This approach aims to bridge the gap between easily measurable traits, species ecological strategies, their demography, and their combined impacts on ecosystems.

KEYWORDS
biodiversity, ecosystem functioning, functional groups, functional traits, growth form, intraspecific trait variability, life history, phylogeny, traits databases

INTRODUCTION

The expanding field of trait-based ecology endeavors to elucidate the roles of organismal traits in shaping species distribution, their interactions, and their consequent impacts on ecosystem functioning (de Bello et al., 2021; Garnier et al., 2016; Kattge et al., 2011). Diverging from approaches based on taxonomic identity or position in the Tree of Life, trait-based ecology focuses on the intrinsic characteristics of organisms (Duckworth et al., 2000; Grime, 2001) and their strategies for inhabiting different environments (Laughlin, 2023). This approach holds promise for establishing mechanistic links between organismal performance and functions at broader organizational levels such as populations, communities, and ecosystems (Fontana et al., 2021; Lavorel et al., 1997; McGill et al., 2006; Shipley et al., 2016). Trait-based ecology endeavors to identify how critical traits, irrespective of taxa, underlie organismal performance under given environmental conditions. This approach facilitates the extension of findings to wide-ranging taxa, enabling comparisons across sites with diverse species pools and enhancing predictions for organisms for which there is limited ecological knowledge.

Despite its roots in ecological research spanning many decades, trait-based ecology experienced a renaissance 25–30 years ago, coinciding with seminal publications and the emergence of international science and policy initiatives on the global change crisis (Lavorel et al., 1997; Smith et al., 1997). The conceptual foundation of trait-based approaches, linking the “form” of organisms to the prediction of their “functions,” dates back centuries, often with a focus on the plant kingdom. Theophrastus, a pupil of Aristotle in the third century BC, proposed a basic plant classification based on physical characteristics. Over time, visionaries like von Humboldt (1806), Darwin (1859), Warming (1895), Schimper et al. (1903), and Raunkiær (1934) connected the characteristics of organisms to their geographic distribution and biotic and abiotic interactions. Building on this legacy, more contemporary ecologists have proposed classification schemes based on traits or responses to abiotic conditions (Grime, 1974; Noble & Slatyer, 1980; Westoby, 1998). Trait-based ecology has expanded significantly in recent decades (Cadotte et al., 2011; Shipley et al., 2016), particularly across a variety of organisms and trophic levels. This has delivered major advances in identifying crucial differences in traits between organisms, improving concepts (Lavorel et al., 1997; Violle et al., 2007), and developing field-specific thesauri (Garnier et al., 2017; Pey et al., 2014) and multiple analytical tools linking traits to the environment and ecosystem functioning (de Bello et al., 2021) while addressing a wide array of theoretical and applied evolutionary and ecological questions.

Broadly, trait-based studies focus on two overarching ecological questions: which traits determine organism and community variation along environmental and disturbance gradients (i.e., “response traits”) and which traits drive trophic interactions, ecosystem processes, and ecosystem services (i.e., “effect traits”). These trait categories overlap and rather reflect the question being asked. The traits concept and its application encompass both the differentiation among organisms of adaptive traits, emphasizing trade-offs, coordination among traits, life history strategies, and underlying evolutionary constraints, alongside the potential effects of these organisms on ecosystem functioning (Díaz et al., 2004; Garnier et al., 2016; Laughlin, 2023; Lavorel & Garnier, 2002; Wright et al., 2004). A key objective of the trait concept is to provide the basic tools to connect response and effect traits to meet the ambition of scaling up from the performance and effects of individuals or species to ecosystem functions.

Despite major advances, trait-based ecology grapples with several enduring challenges (Hortal et al., 2015, including the “Raunkiæran shortfalls” [SFs]—named after

Raunkiær's long-standing plant life-form classification—representing major aspects of the "dearth of knowledge on species traits and their functionality"; Gonçalves-Souza et al., 2023). The limitations identified by Hortal et al. (2015) include the complex connection between traits and fitness; the frequent use of simple-to-measure traits as proxies of the actual functions of interest because they are often more laborious to quantify; a lack of trait standards and information for most organisms and regions; and the need to better incorporate intraspecific trait variation, trait covariation, and trait interactions in trait-based ecology. Shipley et al. (2016) added to these concerns and emphasized the importance of understanding links between traits and environmental gradients. Recent in-depth analyses (Gonçalves-Souza et al., 2023; Maitner, Gallagher, et al., 2023) of specific Raunkiær's SFs confirmed biases toward easily measured traits and under-sampling in areas with high biodiversity.

These insights underscore the lack of information but also inherent limitations in trait-based approaches, necessitating a critical examination to prioritize future research objectives. In this review, we identify major limitations that constrain the progress of trait-based ecological research across a variety of organism types and trophic levels, aiming to guide the development of the next generation of trait-based ecological studies. The relevance of different SFs (Table 1 and below) is context-dependent and covers a range of scales (Figure 1): from organs and organisms (definition and measurement of traits at (sub)individual levels, SF 1) to populations (intraspecific variability [ITV], the relationship between traits and fitness and trait evolution, SFs 2–4), communities (assembly, SF 5), ecosystems (response-effect traits framework and multitrophic relationships, SFs 6 and 7), and biomes (global scaling, SF 8).

SF 1—DEFINITIONS AND STANDARDIZATION

Despite sustained efforts during the last decades, different concepts, methods, and procedures are still used to define and collect trait data, within and across disciplines, in a standardized way. We contend that further progress would include clarifying and overcoming the issues summarized below.

Trait definitions

The definitions of traits and functional traits proposed by Violle et al. (2007) are broadly used and generally well accepted (but see e.g., Dawson et al., 2021; de Bello et al., 2021; Sobral, 2021). The work proposed the following definition of "traits": "any morphological, physiological, phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization." "Functional traits" are then often defined as heritable morpho-physio-phenological traits (including social and behavioral traits for animals) that impact fitness via their effects on growth, reproduction, and survival (Garnier et al., 2016; Laughlin, 2023). Violle et al. (2007) stated that a relevant interpretation of the trait values expressed by the organism requires that the environment in which traits are measured should be carefully described (see SFs 2 and 8). But environmental preferences (e.g., Ellenberg indicator values, habitat occupation), which combine information on traits and environment based on multiple individuals, cannot be considered "traits" (see discussion in Garnier et al., 2017 on "environmental associations"). Environmental preferences, which reflect species' niches, inform about patterns at the population or meta-population level (e.g., defining conditions in which most of the individuals within a species thrive better).

Violle et al. (2007) also reported the critical difference between "response" and "effect" traits concepts, depending on the question for which traits are considered (Lavorel & Garnier, 2002). The "Response traits" concept is used to understand trait-environment-fitness relationship. This can be either understood more broadly as traits varying in response to environmental conditions (Violle et al., 2007) or, more narrowly, by focusing on which traits cause organisms to cope with given environments. Recently, such subtle but substantial differences in perspective have caused some uncertainties in the way response traits can be identified (Lepš & de Bello, 2023). The "Effect traits" concept is most often used to understand the organism's impact on other trophic levels and ecosystem functioning (Lavorel et al., 2013).

These definitions might still cause some uncertainty among researchers from different disciplines and require further conceptual development. The organizational and physiological specificities of different organisms, for instance, add nuances to those concepts and the trait-based framework. For instance, in social insects, animals living in colonies, clonal plants, and micro-organisms, the identification of "individuals" on which to measure traits is extremely difficult or not necessarily relevant. The ability of individuals to engage in collective behavior, such as sociality or types of colonies, with clear importance for the success of an organism (e.g., Pausas & Parr, 2018), should be formally considered in the definition of traits and their assessments.

TABLE 1 Main shortfalls (SFs) in trait-based ecology and their components.

Main type of SFs	SF subsection	Specific SFs
1. Definitions and standardization	Trait definitions	Unsolved issues in some aspects of trait definitions
	Protocols for trait measurements	Limitations in the development of the protocols for trait measurements
2. Intraspecific trait variability (ITV)	Disentangling the different sources of ITV	Uncertainty on the relative effects of different sources of intraspecific trait variability
	Modeling ITV	Underdeveloped integration of intraspecific trait variability into modeling
3. Relation with fitness	Proximal versus distal links to fitness	Unclear link between different traits and fitness
	Environmental context	Shortage of evidence on how the environment modifies trait–fitness relationships
	Alternative strategies	Limited tests of the effect of alternative design and integrated phenotypes on fitness
4. Phylogenetic relations to traits	Phylogenetic uncertainty	Imprecise phylogenetic data to quantify trait evolution
	Matching traits with phylogenetic trees	Unclear matching of intraspecific trait variability with phylogenetic trees
	Tests and assumptions on trait conservatism	Simplistic models and tests of trait evolution
5. Community assembly	Tools and indices	Confusion in the tools and indices to detect assembly patterns
	Distinguishing versus predicting different assembly mechanisms	Difficulties in distinguishing the effect of multiple abiotic and biotic conditions on trait diversity
6. Response-effect traits frameworks	Coupling response and effect traits	Complex response-effect trait linkages
	Elusive trait effects	Incomplete understanding of when and how different components of community trait structure are predictive of ecosystem functions
7. Multitrophic interactions	Lack of common traits across taxonomic groups	Lack of definition of common traits that allow integration of different taxa across trophic groups
	Theoretical and analytical frameworks	Underdevelopment of a theoretical and analytical framework that enables traits to be incorporated in different types of interactions
8. Global repositories and scaling	Global trait datasets: data formatting, gaps, and gap-filling	Incomplete and unstandardized data coverage, formatting, and reliability of global traits databases
	Lack of robust methods and currency for global extrapolations	Lack of robust methods and currencies to scale up trait data distribution and abundances

A crucial aspect for the identification of functional traits is their link to individual organisms' fitness via the so-called "performance traits" (Violle et al., 2007). Put simply, the problem of linking traits to fitness (see SF 2) is made more manageable by dividing the task into a two-step approach: (1) measuring the relationship between common traits and individual performance and (2) assessing the impact of performance on fitness (Arnold, 1983). Nevertheless, the definition of performance traits, central to this scheme, still poses some challenges. One widely accepted definition focuses on differences in growth, mortality, and reproduction among individuals (Violle et al., 2007). Simultaneously, other aspects, such as "sprint performance" in lizards, which contributes to survival by evading predators, or swallowing big prey, have been cited as examples of performance traits (Arnold, 1983; Violle et al., 2007). The potential complementarity among these concepts

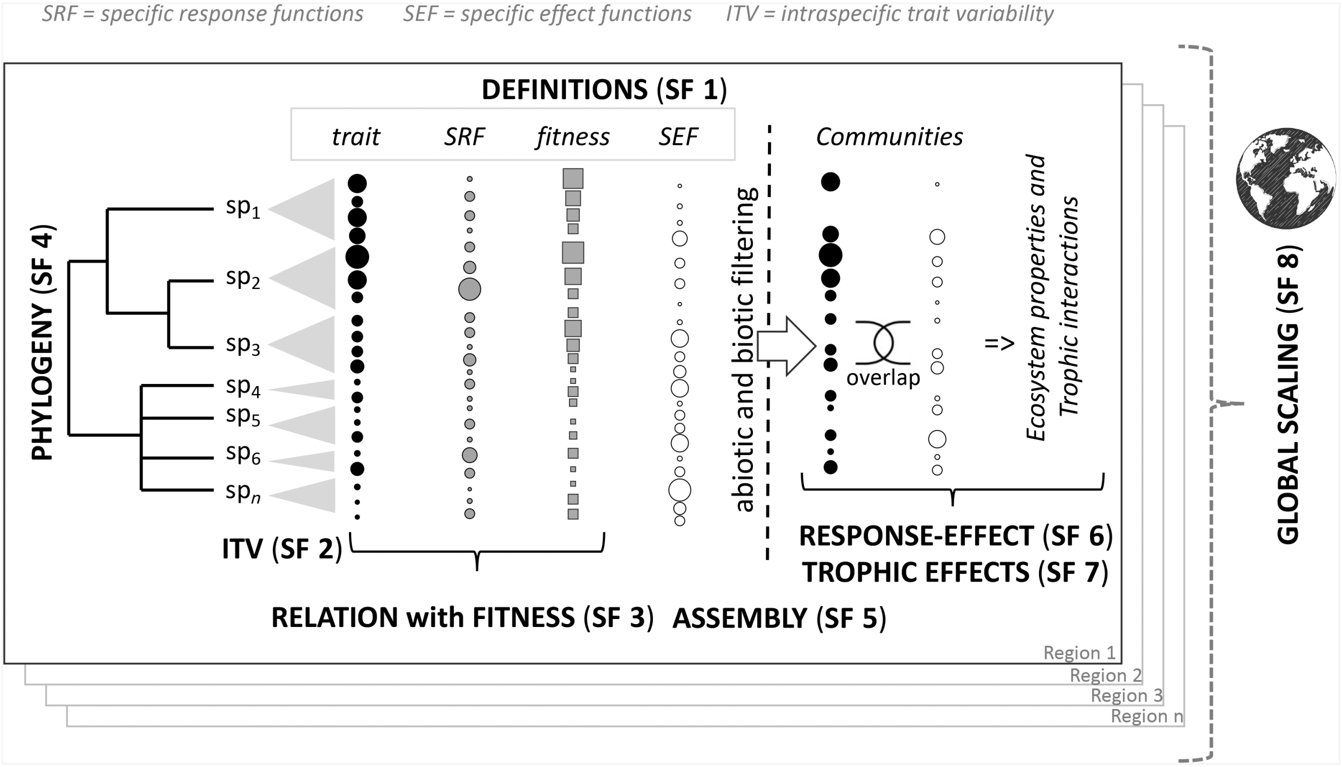

FIGURE 1 Scheme representing and connecting the eight SFs (shortfalls) considered in this review. See also Table 1. We distinguish traits *sensu stricto* from specific response functions (SRFs) and specific effect functions (SEFs) as, respectively, the potential responsiveness of species to given environmental conditions and the potential effect on given ecosystem functions. For graphical purposes, we represent different species (from 1 to *n*) belonging to different branches of a (unresolved) phylogenetic tree. We represent trait variability across individuals within a species as black circles with varying sizes depending on their values. A similar approach is used to represent SRF, fitness, and SEF values (respectively gray circles, gray squares, and white circles). Abiotic and biotic filtering is represented as a dotted line by which certain organisms either become part of, or not, of a local community, based on their trait values. The overlap between trait and SEF values (represented by the mathematical overlap symbol) controls community effects on ecosystems and other trophic levels. The study of these connections across multiple regions (represented as overlapping images of the scheme for "Region" 1 to *n*) is the basis of the global scaling related to SF 8. The drawing of the world was taken from Freepik.com.

offers a valuable yet largely unexplored array of possibilities in trait-based ecology.

As part of the two-step approach described above, Díaz et al. (2013) introduced the concept of "specific response functions" (SRFs) to quantify organism performance. Ideally, SRFs should reflect organisms' tolerances to various abiotic stresses (e.g., frost, drought, pollution, low nutrient availability), biotic pressures (e.g., competitors, pathogens, herbivores, predators, parasites), or specific disturbance regimes (e.g., fire, wind, waves; Austin & Austin, 1980; Craine et al., 2012; Lavorel et al., 2013; Marcante et al., 2012; Moretti et al., 2017; Pausas & Parr, 2018; Tilman, 1980). As Arnold (1983) suggested, defining these "performances" can be achieved in the lab or under controlled conditions. This involves assessing responses in ecophysiological parameters or "integrative traits," such as survival and growth across individuals of a population, grown in experimental conditions where only one environmental factor varies. This SRF approach helps determine organisms' potential responses to the environment (i.e., responsiveness) which can inform about the ecological limits of species (e.g., lowest temperature at which some species can be found in the field) and the overall "strategy" of organisms in adapting to the environment (Laughlin, 2023). Typically, SRFs result from a combination of traits that impact species performance. Therefore, relating these SRFs to functional traits *sensu stricto* constitutes a step toward the identification of the underlying mechanisms controlling species ecological limits (see also SF 3) as an intermediate link to fitness components.

Díaz et al. (2013) further advanced this framework by proposing the assessment of a species' potential impact on the ecosystem through what they termed "specific effect functions" (SEFs). Similar to SRFs, SEFs help disentangle the link between common traits and ecosystem functions. SEFs represent the potential of organisms, populations, or species to influence a given ecosystem function. Once SEFs are estimated, a two-step approach would involve: (1) measuring the relationship between common traits and SEFs and (2) assessing the impact of SEFs on ecosystem functions. Examples of SEFs include plant palatability, decomposability, flammability, the volume of water transpired per unit leaf area per unit time in a tree leaf, and the amount of heavy metal absorbed per unit length of hyphae in mycorrhizas. Ideally, SEFs are assessed in controlled conditions, where the effects of organisms are compared under standard environments (e.g., for litter mass loss, using monospecific mesh bags to decompose litter species at given humidity and temperature conditions; see Cornelissen, 1996).

In recent years, the term "functional" in the expression "functional trait" has faced criticism. It has been argued that all trait expressions result from evolutionary processes acting on the organism's integrated phenotype. Consequently, any given trait may have been—or may become—"functional" depending on the environmental context, either directly or indirectly through phenotypic correlations within the organism (Sobral, 2021). For instance, some traits may have lost their original function, such as spines in regions where megaherbivores are extinct (Dantas & Pausas, 2022). The term "functional" may also be used to describe effects that extend beyond the organism's fitness (Caron et al., 2022), such as effect traits and the extended phenotype (discussed below in SFs 6 and 7). This broad usage can create ambiguity regarding which traits are genuinely functional and in what context. From a pragmatic standpoint, however, and given its widespread use, retaining the term "functional traits" remains advisable—as we do in this review—while recognizing that in many cases, the term may be somewhat redundant.

Finally, an important aspect of trait definitions recently stressed by Laughlin (2023) emphasizes the potential differences between traits as defined so far, and "life history traits" with the latter reflecting emergent properties of populations related to demography that cannot be measured necessarily on single individuals. Several definitions of life history traits can be found in the literature, but an overall consensus is emerging that they would ideally refer to demographic parameters like population growth while traits, *sensu stricto*, would be related to individuals. Laughlin (2023) provides several examples referring to Salguero-Gómez et al. (2015), with some life history traits varying at the population level such as generation time (i.e., number of years necessary for the individuals of a population to be fully replaced by new ones). In some other cases, as for, for example, life span, or age at maturity, life history traits can be ideally assessed at the individual level. The existing confusion in terminology is probably the consequence of different research traditions—for example, between trait ecologists and evolutionary biologists, luckily closing in recent years (Garnier et al., 2016; Kelly et al., 2021; Laughlin, 2023). Recently, progress has been made toward creating a bridge between measurable traits at the individual level and the overall strategy of organisms on the one hand and population performance in different environments on the other hand (Kelly et al., 2021).

Protocols for trait measurements

There is a growing interest in handbooks for trait measurements, which provide standardized protocols for collecting, measuring, and summarizing trait information in different groups of organisms (e.g., Perez-Harguindeguy et al., 2013 for plants, Moretti et al., 2017 for terrestrial invertebrates). The emphasis of these protocols is sometimes based on different contexts (e.g., Wigley et al., 2020 for plant traits in open ecosystems), body parts (e.g., Freschet et al., 2021 for root traits), or specific groups of organisms (e.g., deCastro-Arrazola et al., 2023 for dung beetles). Such approaches enable the creation of remarkably extensive datasets (SF 8), facilitating the synthesis of trait distributions at a global scale (as demonstrated by Díaz et al., 2016; Wright et al., 2004).

Yet, there are several limitations in the development and applications of these trait handbooks. Among these, the lack of handbooks for the less charismatic but ecologically important taxa, such as nematodes and fungi, or groups of traits that are less represented within taxa, is a major issue. Also, when authors develop a common currency of traits for a broad group of taxa (e.g., terrestrial invertebrates, Moretti et al., 2017 or vascular plants, Cornelissen et al., 2003), this is done at the expense of selecting more "functional" traits that are limited within specific groups of species (e.g., specific traits only relevant within pollinators or hemi-parasitic plants, respectively). Comprehensive approaches to combine traits across different taxa are clearly required, but they are still in their infancy (Luza et al., 2023).

Then, since not all species and individuals can be sampled in a community or region, traits are more frequently measured for the most abundant species (Pakeman & Quested, 2007) and on specific individuals selected, that is, fully developed, healthy-looking individuals (Moretti et al., 2017; Perez-Harguindeguy et al., 2013). These measurements describe the best organism capacities under given environmental conditions, which are often considered to be a good marker of species' performances. However, these "standards" might not be good representatives of the state of the individuals, populations, or communities in particular conditions (e.g., by collecting only sun-exposed leaves in a dense forest, while most of the leaves are under shade conditions). Specifically, this approach might be deficient for subordinate and transient species (Grime, 1998), functionally rare ones (Violle et al., 2017), and individuals at different life stages (ontogeny) which can play a significant role in ecosystem functions.

In this context, a key limitation of trait standardized protocols is a general lack of focus on ecologically relevant ITV, which is generally not properly covered in the description of standardized protocols (see SF 2). This is particularly true when it comes to including individuals of different ontogenetic stages and/or developing in suboptimal environments (e.g., foliage in shade, undersized fish in overfished waters). Furthermore, measuring a trait at a single point in time (i.e., on fully developed individuals, see above) carries the risk of not capturing phenotypic variation during phenology, ontogeny, and senescence, and its effect on the organism's fitness (Barton, 2023). Ecologists tend to concentrate trait sampling within given field campaigns, with the consequence that not all species can be measured at their "optimum" of the different life stages. Yet, the potential consequences of these choices on the outcomes of ecological studies have not been thoroughly explored.

SF 2—INTRASPECIFIC TRAIT VARIABILITY

ITV has been increasingly accounted for in trait-based functional ecology (Messier et al., 2010; Violle et al., 2012). A growing body of literature has acknowledged its importance (de Bello et al., 2021; Des Roches et al., 2018; Sanderson et al., 2023; Shipley et al., 2016; Westerband et al., 2021; Whitman & Agrawal, 2009) and when it is essential to consider it, that is, small-scale studies or broad-scale studies with only one species (Albert et al., 2011). Below, we identify some critical SFs related to ITV that still limit its understanding and modeling.

Disentangling the different sources of ITV

ITV could stem from different co-occurring mechanisms and their interplay: genetic variation, plasticity, phenological stage, and ontogenetic development. How these effects vary and interact remains largely unresolved.

Trait differences due to genetic dissimilarity should increase with increasing spatial distance, because of limited dispersal or due to selection and local adaptation processes across different regions and habitats. At the same time, trait expression within genotypes in response to the environment is also modulated by phenotypic plasticity (Price et al., 2003) and could be of highly variable duration, from short-transient modifications operating within the lifetime of individuals (within-generation plasticity) to inherited across generations (transgenerational plasticity; Herman et al., 2014; Puy, de Bello, et al., 2021; Turcotte & Levine, 2016). Recent studies suggest that plasticity is often supported by epigenetic mechanisms (Puy, de Bello, et al., 2021; Sobral et al., 2021; Zhang et al., 2013). Evidence is increasing on how non-genetically originated ITV can affect community and ecosystem properties such as species coexistence (Puy, de Bello, et al., 2021; van Moorsel et al., 2019) and underpin effects of diversity on ecosystem functioning (Latzel et al., 2013, 2023; Puy, Carmona, et al., 2021; van Moorsel et al., 2018). Studies crossing genetic and epigenetic analyses with ITV data will be increasingly necessary in the future.

It should also be noted that sub-individual variation (e.g., trait variations across leaves in a canopy) can sometimes be greater than among individual or among population variation in many traits of many species (Herrera, 2017). Sub-individual variation is mainly due to organ-level phenotypic plasticity (due to multiple reruns of the same genotype under different micro-environmental conditions). It also has a genetic and an epigenetic basis (Alonso et al., 2018; Herrera et al., 2021) and it can be heritable (Kulbaba et al., 2017; March-Salas et al., 2021). It can also enhance whole-organism performance via bet-hedging effects: for example, variations in fruit size within trees increased the seeds dispersed by animals (Sobral et al., 2019) and variation in plant nutrients reduced the harm of herbivores (Wetzel et al., 2016) while variation in leaf shape within canopies optimized resource exploitation (Herrera et al., 2015). Such sub-individual variation (e.g., trait distribution within the individual) is rarely assessed (Herrera, 2024), although it might impact function across levels of organization (Sobral, 2023).

Modeling ITV

Important methodological advances increasingly allow the integration of ITV when modeling trait variation and effects, for example, for estimating community functional structure and diversity (Carmona et al., 2016; Lepš et al., 2011; Maitner, Halbritter, et al., 2023; Puglielli et al., 2022; Wong & Carmona, 2021). However, we still lack data for most species on their within-population ITV in databases, which often include only a mean value per species (see SF 8). For the few species associated with a large amount of data, it is often hard to model and interpret their ITV due to uncertainties and variabilities in the methodology used to collect these data (see SF 8). This makes it difficult to disentangle the different sources of ITV variation (Sanderson et al., 2023).

As a consequence, it remains largely unknown whether ITV patterns are similar to the better-known interspecific trait variation (Shipley et al., 2016; Vellend et al., 2014), and more studies are needed to identify the main macroecological drivers of ITV and its components. One approach to address this problem might be measuring trait variation in response to changes in the environment in controlled conditions (e.g., assess reaction norms, Briggs & Walters, 2016) in a way similar to what is suggested for SRFs and SEFs (SF 1). This information can be accompanied by variation in fitness components ("performance traits" in SF 1). Recent work navigates in this direction (Stotz et al., 2021), synthesizing trait information to develop global patterns of ITV.

SF 3—RELATION TO FITNESS

The core of trait-based ecology, including the definition of functional traits (SF 1), relies on the identification of traits that can affect, directly or indirectly, the fitness of organisms (Laughlin, 2023; Violle et al., 2007). However, such a link is still incomplete for several reasons.

Proximal versus distal links to fitness

Collecting data on the actual fitness components, or any function of interest, for many organisms is daunting. Hence, trait-based ecology often relies on proxies, that is, traits that approximate the function of interest and which are easier to assess and measure (Duarte et al., 1995; Garnier et al., 2016; Weiher et al., 1999). However, the accuracy with which the proxy describes the actual function has seldom been tested (but see Garnier et al., 2016; Laughlin, 2023; Wilson et al., 1999). Also, while fitness is an "individual" property, tests are often done comparing populations or species. Proxies may also differ across different groups of organisms or ecosystems.

Traits exist within a complex web of cause–effect relationships, with some traits being more closely related (causally proximal) than others to individual fitness. However, such proximal traits might be more difficult to measure or approximate. As such, among proxies of functions, we can also distinguish "distal" traits, whose effects on the ecological functions are indirect, mediated by other traits, from the "proximal" traits, more closely linked to functions. In the past, these have also been referred to as "soft" and "hard" traits, a terminology criticized by Violle et al. (2007). An example, in plants, would be specific leaf area (SLA) as a possible distal trait and relative growth rate as a more proximal link to fitness and demography. Performance traits (SF 1) are actually more closely approaching fitness components (or "ultimate functions" according to Calow, 1987).

Since trait-based ecology has often focused on broad-scale interspecific trends, it sometimes concentrates on easily measured (often morphological) traits, such as height and seed mass in plants or body size in animals. These traits are likely less directly linked to fitness but probably reflect more integrated functions (Fontana et al., 2021). In this sense, it is often claimed that the easiest traits to measure are also the most distal traits, while the most difficult traits to measure are more proximal. But, this might not be the case because the more a given trait integrates different functions (like SLA reflecting leaf photosynthetic capacity, leaf longevity, and leaf protection, to mention some, or body size reflecting a suite of coordinated underlying traits), the more it can be linked directly to organismal functionality (Dias et al., 2020). Answering this key question is also difficult because, with few exceptions (Belluau & Shipley, 2018; Enquist et al., 2015; McWilliam et al., 2022), we have not quantitatively modeled the links between fitness, multiple proximal traits, and more distal traits. Because of this, we do not know (1) how much predictive ability functional ecologists lose by replacing proximal with distal traits or (2) which distal traits, or combinations of distal traits, are the best proxies for proximal traits and functions (Laughlin, 2014; Rubio et al., 2021).

As introduced in SFs 1 and 3, a crucial step in detecting relationships between traits and fitness is the consideration of performance traits, particularly SRFs. We posit that an often overlooked approach is to establish connections between simple traits (both distal and proximal) to SRFs, that is, changes in growth, mortality, and reproduction along environmental gradients (but see Austin & Austin, 1980; Craine et al., 2012; Ellenberg, 1953 for plants) also called reaction norms (Briggs & Walters, 2016; de Bello et al., 2021; Salguero-Gómez et al., 2018). The utilization of curves to estimate traits and performance traits variation along environmental gradients can enhance the comprehension of the biological dimension of many traits and their association with species functions (Goolsby, 2015).

Environmental context

Most of the hypothesized causal links between traits and fitness are expected to vary along abiotic or disturbance gradients (Ackerly et al., 2000; Worthy & Swenson, 2019). For instance, traits related to drought tolerance, which are important when an individual is growing in dry habitats, will not be strongly related to fitness in wet habitats. While this will inevitably result in trait replacement along gradients (Shipley, 2009), it might cause stronger and weaker trait relationships with demographic parameters in different environmental contexts. This might make it difficult to identify the functions of traits (Kamimura et al., 2023; Worthy & Swenson, 2019). Different trait values and their interactions could therefore be selected in different environments, resulting in different "fitness landscapes" (Laughlin & Messier, 2015). This is of particular importance when assessing the effect of trait interactions and combinations (see next section).

Traditionally, the "functional" role of traits has been assessed by examining the relationship between traits and environments (Shipley et al., 2016). While this approach is essential for linking trait changes to ecosystem effects (SFs 6 and 7), questions remain regarding the most appropriate methods for relating traits to environmental factors (Lepš & de Bello, 2023). Furthermore, environmental gradients are often measured using methods and scales that are not comparable across studies and locations.

Alternative strategies

We expect the causal links between traits and fitness to be many-to-many; that is, many distal traits will affect the same proximal trait and the same proximal trait will affect many performance functions (SRFs) and ultimately fitness (Marks & Lechowicz, 2006). Clearly, approaches synthesizing information from multiple traits, either into simplified multivariate axes (e.g., leaf economics spectrum, global spectrum of plant form and function, Díaz et al., 2016; Freschet et al., 2010; Wright et al., 2004; as well as root Bergmann et al., 2020, flower spectrum E-Vojtkó et al., 2022) or into different trait-fitness landscapes (Laughlin, 2023), offer promise to get closer to fitness in a tractable way. Similarly, growing attention to "integrated" traits, that is, traits that combine the effect of several underlying traits, is gaining momentum (Fontana et al., 2021; Rubio et al., 2021).

In this context, it is possible that different combinations of trait values will result in the same performance (González-M et al., 2021), referred to as "alternative designs" where different trait combinations could reach similar values of fitness components for the same environment (Dias et al., 2020). This idea has received great attention in recent years, based on the classic distinction of different strategies to cope with, for example, water stress (drought tolerance vs. avoidance) with different quasi-equivalent "strategies" underlined by different sets of traits. Equivalent fitness can also be reached by trait trade-offs (Rees & Westoby, 1997) with "opposed" phenotypes giving similar high values for fitness but through different fitness components (i.e., a phenotype being good at survival, another at growth, another at reproduction). In addition, these alternative designs and these different combinations of trait values may change along environmental gradients (*SF 3—Relation to fitness: Environmental context*). For instance, postfire seeding and postfire resprouting are two very different plant strategies for persisting in fire-prone ecosystems (two solutions to the problem), and they coexist in Mediterranean landscapes (Pausas & Keeley, 2014; Vilagrosa et al., 2014). Alternative designs were also observed for seedling growth strategies in tropical rainforest (Worthy et al., 2020) and for tree survival in a subtropical forest (Li et al., 2021). Also, a synthesis of alternative designs in woody species for abiotic stressors is described by Puglielli et al. (2021).

In this context, the question of how to better merge concepts like the "integrated phenotype" and multiple ecologically stable strategies among co-occurring species (Májekova et al., 2014; Rees & Westoby, 1997) or even within the same individual (Castro Sánchez-Bermejo et al., 2023) into modeling remains to be more fully addressed in trait-based ecology (but see Puglielli et al., 2022). Moving toward the use of multidimensional phenotypes instead of individual traits might add realism to trait-based ecology (Adams & Collyer, 2018; Goolsby, 2015). At the same time, it seems necessary to scale up different trait trade-offs into emerging strategies (Laughlin, 2023).

SF 4—COMBINING TRAITS AND PHYLOGENY

Trait-based ecologists are increasingly combining phylogenies with trait information for various purposes, although uncertainty regarding their use persists. First, comparative trait analyses (e.g., phylogenetic independent contrasts) are used to test the extent to which trait–environment relationships reveal coordinated evolution within and across different clades (de Bello et al., 2016; Moles et al., 2005; Westoby et al., 2023). Second, phylogenies can be used to impute missing trait data, assuming a robust phylogenetic signal, that is, closely related species tend to have more similar trait values than more distantly related taxa (Madin et al., 2016; Schrodt et al., 2015), although this is not always the case (see *SF 4—Combining traits and phylogeny: Tests and assumptions on trait conservatism*). Third, phylogenetic diversity has been used as a proxy or complement to functional and taxonomic diversity to understand community assembly and ecosystem functioning relationships (Cadotte et al., 2013; de Bello et al., 2017; Pavoine & Bonsall, 2011). As we discuss here, these applications may be limited by several methodological and conceptual issues in linking traits with phylogeny, as well as a lack of clarity on when such links are actually necessary.

Phylogenetic uncertainty

Phylogenetic trees are constructed with errors (sometimes called the Darwinian SF, Hortal et al., 2015), but this uncertainty is rarely incorporated into trait-based analyses (Debastiani et al., 2021; Rangel et al., 2015). This is especially relevant in studies of regional species pools or research fields where phylogenetic relationships of the organisms are poorly known (Rudbeck et al., 2022) and are typically reconstructed from short DNA sequences, as in microbial ecology (Pérez-Valera et al., 2018). Incorporating phylogenetic uncertainty should be a routine step in trait-based ecology to ensure the robustness of the observed patterns (Huelsenbeck et al., 2000).

Matching traits with phylogenetic trees

Combining traits and phylogenetic trees in trait-based ecology typically involves disregarding ITV (also see SF 2). Phylogenetic trees, which represent relationships between taxa, are usually combined with traits averaged at the species level, assigning a single value per species. Although phylogenetic comparative methods that incorporate ITV are available (Ives et al., 2007; Revell & Reynolds, 2012), most ecological studies still assign fixed trait values to species, overlooking measurement error and ITV when using phylogenies as a proxy for traits or studying trait evolution.

Tests and assumptions on trait conservatism

Trait-based studies often assume that phylogenetic distances serve as a direct proxy for phenotypic distances (Letten & Cornwell, 2015). The rationale behind this assumption is that species sharing a recent common ancestor are likely to have diverged less in their traits compared to species with a more distant ancestor. When this occurs, the trait is considered evolutionarily conserved, allowing researchers to infer a species' trait value based on its position in the phylogeny. However, a particular trait may evolve at different rates across times or among different lineages due to evolutionary convergence or divergence (Gerhold et al., 2015), which can lead to either the erosion or amplification of the phylogenetic signal (Díaz et al., 2013). Accounting for evolutionary rate heterogeneity when calculating phylogenetic distances could improve the alignment between phylogenetic and trait information. Since the phenotype is a multidimensional combination of many traits, phylogenetic distances may be informative for some traits but not for others, such as rapidly evolving traits (Letten & Cornwell, 2015). A classic example of the lack of trait conservatism is observed in the bark traits of closely related tropical species living in different environments (Hoffmann et al., 2003; Hoffmann & Franco, 2003).

Tests used to assess trait conservatism are often based on simple models of trait evolution and measures of the phylogenetic signal of traits. These measures, such as Pagel's λ and Blomberg's K (Münkemüller et al., 2012), aim to summarize in a single value the complexity of trait evolution across different clades in a phylogenetic tree. In this regard, recently developed frameworks and methodologies may offer a more comprehensive approach. For example, non-parametric methods for visualizing phenotypic space can group traits according to their evolutionary histories (Lewitus et al., 2020). Understanding the evolutionary histories of traits could help ecologists select the most relevant traits for explaining species coexistence at the community level.

SF 5—COMMUNITY ASSEMBLY

One of the most controversial questions in ecology is whether it is possible to identify "rules" that govern the assembly of biological communities (Diamond, 1975; HilleRisLambers et al., 2012; Keddy, 1992; Kraft, Godoy, et al., 2015; Vellend, 2016). Understanding how community assembly operates through the traits of organisms is an essential goal of trait-based ecology (McGill et al., 2006). In the current global change context, reaching such knowledge is particularly important for building realistic models to predict future biodiversity changes. The last two decades have seen a proliferation of studies using the distributions of trait values within communities to infer the mechanisms underlying community assembly: changes in dominant trait values (via community weighted means, CWM; Lepš & de Bello, 2023; Pillar & Duarte., 2010) and functional diversity, the extent of trait dissimilarity between species (Cornwell & Ackerly, 2010), have been extensively used to do so. Despite advances in this field, two main issues limit further progress: (1) methodological uncertainty in the tools and indices needed to detect such assembly mechanisms and (2) difficulties in understanding the relative effects of multiple abiotic and biotic drivers on trait diversity patterns and their interpretation. We detail these uncertainties below.

Tools and indices

A common approach to identify assembly mechanisms consists of assessing how (much) the functional trait structure of communities varies along environmental gradients. This is mainly done by different tests (Lepš & de Bello, 2023), for example, by considering CWM of trait values and indices of functional diversity (Pillar et al., 2009) or phylogenetic diversity as a proxy or complement (see SF 4; Pillar & Duarte., 2010). Changes in CWM trait values along gradients are routinely considered to understand assembly in different environmental conditions (de Bello et al., 2013; Garnier et al., 2004; Shipley et al., 2006), although criticisms have been raised on the interpretation of the patterns detected (Lepš & de Bello, 2023; Zelený, 2018). Altogether, different indices of the functional trait structure of populations, communities, and biomes can be assessed by characterizing the trait probability distribution (Carmona et al., 2016), holding the potential to connect analyses at different scales.

Common community assembly tests frequently assess deviations from random expectations of indices of, for example, functional diversity, using null-models (Cornwell et al., 2006; de Bello, Price, et al., 2012; Mayfield & Levine, 2010). A wealth of research has addressed the choice of indices of functional diversity (Mason et al., 2013) and null-models (Götzenberger et al., 2016; Hardy, 2008; Münkemüller et al., 2012); researchers often face a labyrinth of options when computing functional diversity and selecting the best null-model for the ecological mechanism being assessed. No standardized approach and guidelines have been developed yet. There is only consensus that the selection of the species pool used in the design of the randomization, and the corresponding spatial resolution at which tests are defined, strongly affects test results (de Bello, Price, et al., 2012; Gotelli & Graves, 1996; Götzenberger et al., 2012).

Distinguishing versus predicting different assembly mechanisms

There is generally a broad consensus on the different types of mechanisms expected to drive community assembly (Kraft, Adler, et al., 2015; Vellend, 2016). Besides stochasticity, two broad families of environmental filtering effects can be expected: habitat, or environmental, filtering (i.e., abiotic effects) and species interactions (i.e., biotic effects). Ample evidence confirms the effects of abiotic environmental filtering in limiting the range of variation in trait values within communities (de Bello et al., 2021; Kraft, Adler, et al., 2015). At the same time, ecologists have long recognized that coexisting species are far from being similar to each other. Several syntheses confirm that many studies have demonstrated that species are more different from each other than expected under random expectations, supporting the idea that biotic interactions play a role in community assembly (Götzenberger et al., 2012). Such mechanisms are usually interpreted as an effect of competition causing different species to coexist to avoid competing for similar resources, mechanisms like Janzen–Connell effects, or competition for enemy-free space (de Bello et al., 2021).

Although guidelines are increasingly proposed to advance the field (Götzenberger et al., 2016; Münkemüller et al., 2020), uncertainties remain as to (1) how should the relative effects of abiotic versus biotic assembly processes be disentangled; (2) how do these effects vary in different conditions; and (3) how should trait patterns be used to achieve these goals. Altogether, this limits our ability to predict changes in community structure under global change scenarios. Several studies have proposed ways to analyze and interpret different functional, or phylogenetic, patterns (e.g., Cornwell et al., 2006; de Bello, Janeček, et al., 2012; Mayfield & Levine, 2010; Pillar & Duarte., 2010) but interpretations are often complicated because different mechanisms may cause the same expected pattern on the same traits or different patterns across different traits. Such uncertainty in conclusions remains, particularly if not based on specifically designed experiments (Kraft, Adler, et al., 2015). While some hypotheses have been generated on which selective pressure should cause greater trait dissimilarity ("divergence," sometimes called "overdispersion") or similarity ("convergence" or "clustering") in community assembly in different environments and different traits (e.g., Bernard-Verdier et al., 2012; Freschet et al., 2011; Grime, 2006), mixed evidence and different hypotheses tested for different taxa have led to a lack of consensus in the literature.

Prediction of community assembly would be facilitated by using traits more tightly reflecting adaptation to the prevailing environmental conditions and disturbance regimes on the one hand and traits reflecting species biotic interactions (such as competition or facilitation) on the other hand. In the real world, however, species traits often reflect the interplay of both abiotic and biotic conditions on the phenotype, making an unequivocal selection of traits difficult, if not impossible. For example, habitat filtering is expected to cause species to share similar phenotypes as expressed by trait values, hence decreasing functional diversity compared to random expectations (i.e., trait clustering). However, asymmetric competition, for example, due to differences in plant height between species in productive conditions, could cause the exclusion of weaker competitors, also causing trait clustering (de Bello, Janeček, et al., 2012; Mayfield & Levine, 2010). Therefore, a careful selection of traits and the pool of species used in the randomizations is essential. For example, to test the effect of competition, one could focus on traits related to asymmetric competition (e.g., plant height) and randomize across species expected for the habitat being considered (i.e., selecting a species pool that excludes species from other habitats; de Bello, Janeček, et al., 2012). Nonetheless, even with a careful selection of traits and species pool, the overlapping effects of abiotic and biotic factors cannot be completely excluded. Solving this issue should ultimately allow us to make predictions as to whether convergence and divergence in trait values can be modeled and predicted satisfactorily in different types of environments (e.g., disturbed vs. non-disturbed, productive vs. unproductive), a challenge that is far from resolved.

SF 6—LINKING TRAITS TO ECOSYSTEM FUNCTIONS

Trait-based approaches promised to link species and community responses to environmental change to ecosystem functioning (Cornelissen et al., 2014; Cornelissen & Makoto, 2014; Díaz et al., 2013; Lavorel & Garnier, 2002; Suding et al., 2008). However, this predictive power has not always been realized, nor are trait-environment models always the most parsimonious explanation of responses of ecosystem functioning (Orwin et al., 2021; van der Plas et al., 2020). This is possibly caused by two limitations in trait-based approaches. First, distinguishing and coupling response (addressed in SFs 2, 3, and 5) and effect traits (this SF) is essential to translate changes in community assembly to changes in ecosystem functioning. Yet, despite intensive recent work, this coupling remains sometimes elusive (Chacón-Labella et al., 2023). Second, in some cases, the direct effects of traits on ecosystem functioning and services might be weak due to (1) lack of proper frameworks accommodating different trait components of communities or considering some idiosyncratic species effects and (2) the possible overriding effects of abiotic and management conditions (Díaz et al., 2007).

Coupling response and effect traits

Coupling trait responses to effects on ecosystem functions requires, as the first step, a clear definition of potential traits at play. Determining response traits associated with a particular environmental change that results in shifts in species composition can be challenging (see SFs 3 and 5). Similar problems can apply to the detection of effect traits that impact a particular ecosystem process, a problem that is aggravated by the paucity of studies on effect traits. In some cases, response traits can also be effect traits, predicting processes such as primary productivity, where at least one component of fitness (growth) is directly linked to processes or body size related to decomposition and resource consumption. In others, response and effect traits might be decoupled or indirectly coupled. For example, the response of root and leaf traits to fertilization can indirectly affect pollination through their whole-plant association with differences in floral traits, for instance, in legumes. Similarly, traits related to fire tolerance might be unrelated to traits determining flammability. In this regard, the novel focus on metabolic traits can provide an integrated and more direct insight into the link between response and effect traits (Walker et al., 2022).

Measuring species effects on ecosystem properties in standardized conditions (see SEFs in *SF 1—Definitions and standardization: Trait definitions* and Figure 1), like allelopathy on seed development, leaf and root decomposability, or invertebrate consumption rate on leaf litter, and the underlying processes can also be useful (Heemsbergen et al., 2004; Ibanez, Lavorel, et al., 2013). Taking direct measures of ecosystem properties, for instance through spectral imagery (see also SF 8), offers exciting prospects for linking environmental change to shifts in trait composition and its consequences for ecosystem functions (Cavender-Bares et al., 2022).

Once specific response and effect traits can be identified, their interconnection might be complex. Strong tests of trait effects on ecosystem functions require approaches that effectively and explicitly elucidate the links between phenotypes, differential fitness (SF 3), community assembly (SF 5), and ecosystem functioning (Chacón-Labella et al., 2023). In this context, an important limitation of the response-to-effect trait framework is that response and effect traits might be based on different "currencies" spanning different scales (such as population, communities, and ecosystem properties). While species responses can be observed in terms of temporal changes in per capita rates and ontogenetic variation in relevant traits, the effect of species will likely greatly depend on the abundance or biomass of organisms and how this translates into the functional structure of communities. For instance, flammability traits of dominant species determine the fire regime of the community (Pausas et al., 2017). Although this "Mass-Ratio Hypothesis" (Díaz et al., 2007; Grime, 1998) has been shown to be valid across a large range of ecosystem processes (Garnier et al., 2016), whether, how, and when the functional composition of communities also affects ecosystem properties is unresolved. More broadly, functional composition is generally assumed to be related to the trait probability distribution, but often simply characterized by the mean and variance, even though other approaches exist (Carmona et al., 2016; Enquist et al., 2015). Apart from that, although the effects of traits are often cumulative throughout the year and across years, they are usually only linked with targeted species surveys (once per year), which can be particularly problematic for seasonal ecosystems

(Fischer et al., 2023). Hence, how to connect the different facets of trait distributions across species, and over time, to ecosystem functions is an open and challenging task.

Elusive trait effects

While evidence is increasing for linkages between response and effect traits (Lavorel et al., 2017; Miedema Brown & Anand, 2022), we still lack a comprehensive quantitative and mechanistic understanding of the relative roles of the traits of different organisms as compared to direct abiotic drivers. For example, while variations in plant traits along climate and management intensity gradients exert significant effects on soil functions such as nutrient retention and cycling, these often remain weaker than the direct effects of soil physical and chemical properties (Weil et al., 2021). Likewise, variation in nutrient cycling rates with altitude was largely affected by indirect concurrent changes in climate and soil parameters (Martinez-Almoyna et al., 2019). As a consequence, in some conditions, using soil physical and chemical properties or fertilizer inputs provides stronger predictions of ecosystem functions than plant traits alone (Díaz et al., 2007; van der Plas et al., 2020).

In some cases, relevant effect traits might extend well beyond those usually considered in resource economics and include a wide diversity of other functions, such as the production of beneficial or toxic chemicals, herbivores, diseases, or association with mycorrhiza or nitrogen fixer symbionts (Orwin et al., 2022; see also trophic interactions SF 7). These effects will be determined by very specific traits, owned by few phylogenetic groups. Therefore, modeling these effects might be inconclusive since these traits are sometimes linked to only a few taxa, or a few keystone species, and they are thus seldom considered in the characterization of community trait distribution. These effects might be best examined by adding single species or specific phylogenetic groups to the model (Díaz et al., 2007).

Another important aspect is that different dimensions of the trait distribution (e.g., functional diversity, CWMs, or the entire trait probability distribution) could predict different ecosystem functions, but only careful experiments can tease their effects apart, due to the non-independence of the metrics considered (Dias et al., 2013). This is particularly important in the context of temporal variation in trait-based controls of ecosystem functions (i.e., stability), which remains a critical, largely unexplored, frontier (de Bello et al., 2021). Trait-based legacies of species and communities, especially on soils, have rarely been considered but may account for seemingly poor evidence for response-effect trait relationships (Boeddinghaus et al., 2019; de Bello et al., 2021; Orwin et al., 2022).

SF 7—MULTITROPHIC INTERACTIONS

Trophic interactions play an important role in both the fitness of individual organisms and in key ecosystem processes. Knowing the traits involved in trophic interactions, and their relative importance, ideally allows one to understand the possible mechanisms driving interactions and cascades on ecosystem functions. The study of traits involved in multitrophic interactions has progressed significantly over the past decade (e.g., Dehling et al., 2022; Gravel et al., 2016; Lavorel et al., 2013; Marjakangas et al., 2022), but existing evidence is mostly limited to interactions between two trophic groups (Moretti et al., 2013; Schleuning et al., 2015; but see Schmitz, 2008). This limitation reflects two basic knowledge gaps. First, the difficulty to define common traits that can be measured across different taxonomic groups involved in a given trophic interaction (Dehling & Stouffer, 2018; Pausas, 2019; but see Moretti & Legg, 2009). Second, the lack of unified theoretical and analytical trait frameworks that incorporate traits across types of interactions (bi- and tripartite networks, mutualistic and antagonistic interactions, and entire food webs). These limitations are discussed below, with their implications on influencing individual fitness (SF 3) and ecosystem effects (SF 6).

Lack of common traits across taxonomic groups

Identifying common traits that control trophic interactions across different taxonomic groups within a trophic level can be extremely challenging (Dehling & Stouffer, 2018). This is mainly due to differing body plans and behaviors of interacting species (Landim et al., 2024). For instance, polyphagous insectivorous birds often feed on many different groups of invertebrate prey. Each of these groups of invertebrates might have developed different mechanisms to avoid predation (i.e., escape, camouflage, protective structures). Each of these avoidance mechanisms is based on different traits (e.g., color, cuticle thickness, poison) that are specific to different prey groups (see also SF 3 on alternative strategies). Therefore, it is often not possible to merge all prey species in the same trait-based analysis, as a common trait currency mediating trophic interactions is missing. The body size of prey has often been used as a proxy, but camouflage and protective structures are generally not reflected by body size.

Most ecological processes derived from trophic interactions involve a wide range of taxonomic groups with different body plans. For instance, pollination is performed by taxonomic groups as distinct as birds, mammals, and insects. An alternative is to build a trait space of the resources (e.g., floral traits or fruit traits) used by different consumers to depict their process-related niche (Dehling & Stouffer, 2018). This concept was traditionally encapsulated by the idea of guilds (Blondel, 2003). This allows to understand species' roles in interaction networks and the possible consequences of changing community composition for ecological processes (e.g., pollination or seed dispersal, Landim et al., 2024). Another approach to overcome the lack of common trophic interaction traits across taxonomical groups involves directly measuring species effects on processes in controlled conditions, as mentioned for SEFs (see SF 1 and Figure 1) like pollination, decomposition, litter fragmentation, N-consumption (Heemsbergen et al., 2004; see also SF 6). Leaf-litter feeders such as earthworms, millipedes, isopods, insect larvae, termites and snails play an important role in litter decomposition. However, their mouth parts differ substantially, challenging the use of morphological effect traits. Alternatively, measuring litter consumption rate in standard conditions allows for integrating the combined action of these various organisms as an "emergent" functional trait.

Theoretical and analytical frameworks

For many multitrophic interactions, we lack knowledge and understanding of different types of interactions (bi- and tripartite networks, mutualistic and antagonistic interactions, and entire food webs) and "who interacts with whom" (and who not) to establish tests for the traits involved and understand the underlying mechanisms. While interactions can be estimated through observations, for example, in pollination studies (Forrest, 2015; Grange et al., 2021), or metabarcoding linked to diet (Ibanez, Manneville, et al., 2013), lack of direct interactions (through avoidance and defense traits) is more difficult to identify and to disentangle from the many missing stochastic interactions, especially when involving behavioral traits (Brousseau et al., 2018). Controlled feeding experiments conducted in the laboratory can initially identify and quantify these traits and how they are influenced by evolutionary history (Ibanez, Lavorel, et al., 2013); such approaches can be potentially transferred to natural communities in the field (e.g., Neff et al., 2021). Additionally, most of the known traits driving trophic interactions are related to biomechanical and temporal trait matching (i.e., traits that allow a match between consumers and resources, making the interaction possible; Schleuning et al., 2015), while the potential role of stoichiometry (N:C:P ratios), nutritional composition (vitamins, proteins, amino acids, fatty acids, sterols), and metabolic rates in explaining multitrophic interactions and how these influence fitness is potentially promising but remains poorly understood (Kantsa et al., 2018; Ruedenauer et al., 2023).

Finally, although promising attempts to couple interaction networks with traits and phylogeny have been proposed (Bastazini et al., 2017; Lavorel et al., 2013; Marjakangas et al., 2022; O'Connor et al., 2020; Schleuning et al., 2015), at present the direct use of traits in bi-/tri-partite networks is still poorly explored and specific analytical frameworks using traits are poorly developed. This strongly limits the possibility to assess trait-based mechanisms underlying multitrophic networks and food webs (but see Laigle et al., 2018; Litchman et al., 2021), as well as how trophic interactions affect consumer species fitness and/or resource assemblages, and their effects on ecosystems.

SF 8—GLOBAL DATA REPOSITORIES AND SCALING

Over the last two decades, studies that use traits to assess and generalize biological patterns at a global scale have proliferated. These narratives play an important role in macroecology (Martins et al., 2023), both in their own right and by providing the context for more detailed, finer grained studies. Here, we highlight examples of SFs in global-scale trait ecology, mostly focusing on: (1) incomplete coverage, formatting, and reliability of global traits datasets; and (2) a lack of robust methods and currency when "scaling" up local trait measurements, for example, to generate global trait maps.

Global trait datasets: data formatting, gaps, and gap-filling

The number of trait databases across different taxonomic groups has been rapidly growing. There are now "global" trait databases for most organismal groups, for example, for plants (Kattge et al., 2020; Maitner et al., 2018), lichens (Rambold et al., 2014), animals (Herberstein et al., 2022), amniotes (Myhrvold et al., 2015), birds (Tobias et al., 2022), lizards (Meiri, 2018), mammals (Jones et al., 2009; Soria et al., 2021), fish (Lecocq et al., 2019), ants (Parr et al., 2017), Collembola (Joimel et al., 2021; Potapov et al., 2023), freshwater invertebrates (Kunz et al., 2022), corals (Madin et al., 2016), fungi (Põlme et al., 2020; Zanne et al., 2020), benthic organisms (de Juan et al., 2022), and bacteria (Cébron et al., 2021; Madin et al., 2020).

Building these databases is a complex task as the data are collated from numerous distinct studies designed with different aims and protocols and providing data at different scales (Feng et al., 2022). To make datasets truly FAIR (findable, accessible, interoperable, and reusable: Wilkinson et al., 2016), they must satisfy established standards at all stages of data preparation and curation (e.g., Falster et al., 2021). Established terminological resources such as standardized vocabularies that can be used for storing and sharing ecological trait data (e.g., the recently proposed Ecological Trait-Data Standard, ETS; Schneider et al., 2019), dictionaries and thesauri (e.g., Pey et al., 2014 for soil invertebrates; Garnier et al., 2017; Wenk et al., 2024 for plants) have been designed in this context. Ideally, traits should be conceptualized as a quality (e.g., mass) of an entity (e.g., seed or body). Metadata associated with trait data should include information on geographical location, environmental conditions (field or lab), and methodology of sampling and measurements (Michener et al., 1997). Such additional data, which are of prime importance to interpret the trait values, are often insufficient or missing.

Another important limitation in assembling datasets across studies is that of conflicting or doubtful taxonomic concepts (Grenié et al., 2023). For example, the same taxon might be identified by synonyms in different datasets, making the matching of data based on species names difficult. Tools such as the Catalogue of Life (Bánki et al., 2024) can be used for name standardization. To facilitate matching by species across datasets, metadata should thus ascertain the species concept and the reference used for a given set of data (Schellenberger Costa et al., 2023). The lack of clear taxonomy for many species or groups (known as the Linnean SF, Hortal et al., 2015) and consequent reliance on operational taxonomic units (OTUs) or morphospecies is also hugely problematic for comparing across datasets in trait-based ecology (Madin et al., 2020).

Even where taxa are clearly identified, the trait values available in the databases may have been obtained under very different conditions, resulting in highly variable values (Hortal et al., 2015). This can cause problems when intraspecific trait variation is large in response to an environmental gradient (Auger & Shipley, 2013) or when communities from different regions and species pools are compared (Mudrák et al., 2019). This reinforces the need for thorough standardized descriptions of the environment, in addition to trait values.

Global data organization and storage are also sometimes problematic. The level at which data are stored, that is, aggregated (e.g., species means) or individual measurements, is extremely variable. Ideally, several types of measurements should be available and easy to obtain (Feng et al., 2022), although this is not often the case (but see Falster et al., 2021). The recorded data should be at the finest resolution possible, that is, one record per trait measurement, which can even include the within-individual or within-organ level. However, this is often not possible with legacy datasets or when data have been extracted from tables and figures. The decision as to which level is relevant for analyses should be left to the end users, allowing them to assemble appropriate data for their specific research questions (Gallagher et al., 2020; Kattge et al., 2020), and placing the responsibility of recording, storing, and publishing the finest trait value resolution possible on the data creator. As the number of original datasets made available with research publications increases, it is critical that data are provided in formal, standardized ways to allow us to build reliable aggregated, wide-ranging trait databases (Aubin et al., 2020; Keller et al., 2023). The ultimate step that should motivate users to provide better quality and more accessible data is undoubtedly the writing of data papers (Costello et al., 2013 in the context of biodiversity) which, in addition, constitutes a tangible reward for the initial data collectors (as implemented, e.g., in Falster et al., 2021).

Most trait databases inevitably suffer from the “sparse matrix” issue (Hortal et al., 2015). That is, while there is comprehensive coverage across species for some traits, for most traits the species coverage is sparse. Data gaps in trait databases are, unfortunately, rarely random (Cornwell et al., 2019), and filling these gaps presents a number of issues. For example, body size is measured universally, whereas physiological and cellular traits requiring specialized instruments to measure tend to have poor coverage. Few phenotypic trait data exist for bacteria, archaea, and fungi that cannot be cultured in the lab, whereas genomic traits for unculturable strains are rapidly amassing via single-cell genomics and metagenomics. For plants, aboveground trait data far outweigh belowground trait data in species coverage (Carmona et al., 2021). Similarly, trait data for ant colonies are much sparser than data on worker morphological traits (Parr et al., 2017). There may be imbalances in data availability in relation to ecology (e.g., rarity), difficulty of access (e.g., deep-sea corals, subterranean creatures), or geography. For example, in the TRY plant trait database (Kattge et al., 2020), there are relatively fewer data from Canada, northern Africa, the Middle East, or Russia; and in GlobalAnts (Parr et al., 2017), there are fewer data from Asia.

While reducing data gaps is a priority in trait-based ecology, in many understudied regions and under-sampled organisms when the amount of missing data is not excessive, data imputation can be considered. Data imputation or “gap-filling” can be used to estimate missing trait data, for example, based on phylogeny, environmental information, and other traits available for a given species, for example (Kim et al., 2018; Pennell et al., 2016; Schrodt et al., 2015). However, some caution is warranted. For example: (1) robustly estimating missing trait values is challenging for clades that are poorly represented in a database; (2) if trait values vary widely within a clade, that is, traits are not strongly conserved (see SF 6), then evolutionary history might not be very useful for imputation (e.g., Hoffmann et al., 2003; Hoffmann & Franco, 2003); (3) for traits that vary little among individuals or populations of a species, this gap-filling is presumably robust, but extra caution is warranted for traits that vary widely within species (e.g., in relation to ontogeny, environmental factors, or biotic interactions; see SF 3) (Hortal et al., 2015). Finally, there is potential for circularity in subsequent analyses based on gap-filled data, for example, when quantifying trait–trait or trait–climate relationships, if traits and climate have themselves been used in the gap-filling process.

Lack of robust methods and currency for global extrapolations

Global extrapolations based on traits are—in principle and in practice—limited by the availability of trait information. Even when trait information is available, a key issue is identifying the best approach to scale information between individual organisms and community and habitat levels. For plant traits key to vegetation modeling (e.g., leaf nitrogen and phosphorus concentrations; leaf dry mass per area), considerable efforts have been made to generate global trait maps by "upscaling" observational trait datasets (Dechant et al., 2024). Typically, species-level trait data are first aggregated into a small number of broad plant functional types (e.g., shrubs, evergreen broadleaved trees, C4 grasses) that can be detected and quantified via remote sensing (Moreno-Martínez et al., 2018) or other means. Global patterns in plant traits can then be estimated from the distribution of plant functional types and their specific trait values (Vallicrosa et al., 2022). The simplification into plant functional types, within which traits vary widely (Kattge et al., 2011), will always introduce considerable uncertainty. However, the chief alternative—to use species-level data—will always be problematic as measured relative abundance data are spatially patchy. Other approaches to trait-mapping are possible, for example, using empirical trait–environment relationships only (van Bodegom et al., 2014), or basing predictions on optimality principles (Dong et al., 2023). An important limitation is that it is difficult to validate which approach to producing trait maps is the most precise and robust. In fact, there is no obvious way to robustly assess the relative accuracy of trait maps other than via comparison to trait estimates made via remote sensing, for example, from leaf spectral data (e.g., Cavender-Bares et al., 2022; Durán et al., 2019), the accuracy of which is also largely unknown. What is the potential for scaling up observational data for taxa other than plants? Mound-building termites (Wijas et al., 2022) and corals (Madin et al., 2016) are potential candidates for upscaling, and both groups play important roles in ecosystem resource fluxes, with global consequences, and with potential to be detected via remote sensing. However, similar limitations may also apply to these groups.

CONCLUDING REMARKS

This review identifies and underscores eight SFs in trait-based approaches associated with different research questions and, consequently, different constraints. Our overall aim was to highlight issues arising when using a trait-based approach to ecology, irrespective of the organism considered. Although we treated the different SFs rather independently, they are mostly related to each other, as highlighted in specific sections of this review.

Possibly one of the main distinctions between types of trait-based studies is whether they focus mostly on the relationship between traits and environment (Lepš & de Bello, 2023) or how traits affect ecosystem processes, including trophic cascades. For the first objective, identifying response traits and establishing their relationship with fitness competitive abilities (mostly SFs 3–5) is crucial in understanding "why species are where they are," that is, driving their distribution patterns within ecosystems. Meanwhile, SFs regarding effect traits (mostly SFs 6 and 7) are primarily associated with the question, "how do organisms affect ecosystem functions and services?" Identifying emerging species strategies, including trait trade-offs and evolutionary differentiation between species, has been a pivotal objective in trait-based ecology. Further progress in this endeavor will help address these two objectives by connecting easily measurable traits to the demography and performance of species in different habitats (Laughlin, 2023) and their consequent effects on ecosystems (de Bello et al., 2021; Garnier et al., 2016). In this respect, this review highlights the need to better account for species performance in terms of both response to the environment (e.g., performance traits, reaction norms, and plasticity, broadly referred to as SRFs following Díaz et al., 2013) and their effects on the ecosystem (e.g., consumption rate) measured in standardized conditions (SEFs).

At the core of trait-based ecology is, undoubtedly, the ambition of connecting traits (through their environmental responses and effects) from individual performances to ecosystem processes (Carmona et al., 2016), and this on its own involves several SFs (Chacón-Labella et al., 2023). This requires approaches and activities, including carefully designed experiments, that reveal the links between phenotypes, differential fitness, demography, community assembly, and ecosystem functioning (Chacón-Labella et al., 2023). Such steps, and corresponding research fields, are essential but they all require considering some key limitations imbedded in the foundations of trait-based ecology. Across the different limitations, we highlight possible ways forward. We also point out limitations that remain inherent in the field of trait-based ecology. These need to be acknowledged for not only improving the potential of trait-based ecology but also recognizing that, as in other tools in ecology, they are and will be imperfect to understand the complexity of nature. Although the search for Holy Grails has its own appeal, any "miracle" ecological approach related to trait variations should be used with consideration of the real-world diversity and complexity of ecosystem functioning.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The literature considered for the different sections of this review are available in Götzenberger (2025) in Figshare at https://doi.org/10.6084/m9.figshare.28500689.

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