Opinion

To harness traits for ecology, let's abandon 'functionality'

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Traits are measurable features of organisms. Functional traits aspire to more. They quantify an organism's ecology and, ultimately, predict ecosystem functions based on local communities. Such predictions are useful, but only if 'functional' really means 'ecologically relevant'. Unfortunately, many 'functional' traits seem to be characterized primarily by availability and implied importance – not by their ecological information content. Better traits are needed, but a prevailing trend is to 'functionalize' existing traits. The key may be to invert the process, that is, to identify functions of interest first and then identify traits as quantifiable proxies. We propose two distinct, yet complementary, perspectives on traits and provide a 'taxonomy of traits', a conceptual compass to navigate the diverse applications of traits in ecology.

Tantalizing but complicated – the conundrum of traits in ecology

In ecology, **traits** (see Glossary) hold great promise for unprecedented insights into complex ecosystems [1–4]. They provide a new perspective on diversity, one that does not ask: who are you? But rather: what do you do? These traits are often termed **functional traits** and their use has been proclaimed as the dawn of a new era of 'predictive ecology' – a scientific discipline that allows the forecasting of future ecological conditions based on the community of organisms present [5,6]. Such a formal framework, an ecological crystal ball, that can quantify and predict ecological processes, is both exceptionally promising and desperately needed [7–9]. 'Functional traits' originated in plant community ecology [1], a discipline characterized by continuing conceptual and data-driven advances in trait ecology [10–14]. Given its attractiveness, the concept has been widely adopted [3,15–28].

Yet, beyond its enthusiastic application, there is a growing body of concern. Titles of publications alone reflect the heated debates and carefully considered caveats (e.g., [29–33]). Ecologists often acknowledge conceptual barriers within trait ecology, noting that the utility of trait assessments hinges on the ecological relevance of the underlying traits [4,6,18,34–37]. Yet it remains difficult to shed the ambiguity around which traits are 'functional', that is, useful for predicting ecological dynamics [38–42] (Box 1). Thus, despite its promises, trait ecology appears to be at a watershed with two potentially risky paths ahead: one focusing on rapidly advancing analytical applications regardless of trait utility, the other mired in the minutiae of theoretical, semantic discussions ('But is this trait really functional?') [33,42–44]. Our goal is to summarize previous developments to identify a middle ground. One that is conceptually rigorous, yet universal enough to remain accessible to ecologists from a variety of disciplines. The key questions are: (i) what do we want to achieve with traits? and (ii) how do we check whether the traits we choose can deliver on those aims?

Moving beyond binary choices: the type of trait, not its functionality is key

Traits are complex. This simple word is used to describe a vast assortment of measurements on organisms. Not everything that may be considered a trait in ecology can be neatly compared,

Highlights

Given the surging impacts of climate change, ecology needs new robust tools that help us to quantify how ecosystems function.

'Functional traits' hold great promise for this goal. They assess communities not via taxonomy, but by their impacts on ecology – ultimately promising ecological insights simply by measuring which organisms are present.

Despite these promises, trait applications in ecology continue to be stalled by a recurring question: which 'functional' traits are ecologically meaningful?

The term 'functional trait' itself is a problem. Its implied utility and versatility are misleading.

We propose to sidestep the preoccupation with 'functionality', and instead focus on traits and their potential uses. We provide a Taxonomy of Traits, a tool designed to help identify whether traits are fit-for-purpose, that is, whether their purported 'functionality' is useful.

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Box 1. Functional traits – Pandora's box or Rosetta stone?

A growing consensus exists: we need better traits to advance trait ecology [4,37,41,42,44]. So, how are we currently evaluating if traits are useful? We seem to rely on a binary choice: functional traits (good!) versus other, nonfunctional traits (bad!). Herein lies a problem. The superficial objectivity of a binary choice conceals the reality that indeed all traits can be functional given the right context [33]; some are just more ecologically informative than others. In the hunt for the Holy Grail of truly functional traits, our target is set in stone, but our scoring system is rubbery.

According to the prevalent definitions, to be 'functional', a trait needs to influence an organism's fitness or performance [6,29]. But, if a trait does not influence fitness or performance, it will not manifest itself in the organism's life history or ecology. How can we ever prove that a trait has no links to performance? Given the perceived value of functional traits for ecology, researchers have ample incentives to justify their traits to be performance related [55]. But if all traits can be 'functional', this 'functional' label adds very little new information [30,33].

This ecological ambiguity of traits often seems acceptable, in exchange for access to comprehensive data. Trait data are useful if they are available at global scales, and with maximal taxonomic coverage. This pragmatism and the access to global trait data is, undoubtedly, a blessing when faced with rapid ecological change [61–67] – or pressure to publish large-scale, high-impact studies. However, to what extent does data availability trump ecological information content? We need to consider if we are making pragmatic use of resources, or sacrificing quality for quantity [68,69].

The intuitive simplicity of the binary choice on 'functional traits' implies scientific objectivity. Instead, we may be dealing with a parasitic word. 'Functional' suggests rigor and gravitas. In fact, it may have become a vague linguistic ornament causing confusion [3,29,42,43]. The 'functionality' of a trait may rely on the researcher's skill in convincing others of its significance, rather than on quantitative evidence of the trait's relevance to ecology. If we wish to address this issue, one way forward could be to tighten the definitions of what constitutes functionality. The other option is to abolish the binary choice, set aside the search for functionality, and focus on the other half of the term: 'trait'.

because no shared scales exist. For example, fur color, seasonal growth, or phosphate excretion are all traits, but comparisons among them are difficult. To increase clarity, it is important to not sacrifice resolution by lumping everything together under one umbrella term (Box 1) [30,43]. After all, the value of a trait for ecological analyses, lies not in a binary choice (is it 'functional' or not?), it lies in the extent of quantifiable ecological information that it contains.

Here, we compile previously published distinctions among different types of traits and set them into a framework – a **Taxonomy of Traits** (Figure 1). These established trait distinctions help classify a given trait after it has been measured, by capturing 'what is measured' and 'what is affected'. We add an additional layer by asking first: what do we want to achieve with traits? This question of intent highlights the co-existence of two different perspectives that have different goals. To suit either one, traits need to capture specific types of data; not all traits will fit all applications. The objective is not about terminology [42]. Instead, our aim is to provide a mental model and a structured approach to engage with, and navigate, the distinctions, hierarchies, and complex linkages within traits, ultimately to maximize their suitability for specific goals.

A Taxonomy of Traits

What do we want to achieve with traits?

If we want to understand whether a given trait is useful, we first need to ask: what do we want to use traits for? We believe this question warrants more attention, than it has received. Explicit clarity might help uncover some of the underlying reasons for frustrations over how traits are (or are not) used. Only if a clear purpose is defined, can we assess whether a trait is fit-for-purpose.

We identify a fundamental, conceptual distinction of two separate, yet complementary, philosophies within trait research. Both perspectives have little overlap, apart from the terminology used: 'functional traits'. We term these perspectives: **Community Cluster Traits** and **Ecosystem Function Traits** (Figure 2A,B).

Glossary

Community Cluster Trait: a perspective where traits translate taxonomic biodiversity into trait diversity; they identify patterns within communities by creating identity via trait similarities and distinctions. These traits can have secondary links to ecology, but their main analytical capability is restricted to assigning identities and clustering (i.e., they are essentially taxonomic traits). Secondary insights into what these clusters mean remain based on speculation, not data.

Ecosystem function: an ecological process defined by the movement or storage of energy or material [55].

Ecosystem Function Trait: a perspective where traits are easier-to-measure proxies to predict higher-order ecological processes which are ultimately of interest, that is, traits which have a direct, known, causal link to specific ecosystem functions, which in turn have specific effects on future ecosystem states.

Effect trait: traits that measure how an organism modulates its environment; effect traits have an outward focus (e.g., 'number of prey items consumed per day').

Functional trait: traits that are perceived to have ecological relevance through generalized links to ecology. Despite these assumptions about ecological information, the prevailing definitions focus on evolutionary measures of organisms, fitness or performance, not ecology [33]: '[Functional traits] impact fitness indirectly via their effects on growth, reproduction, and survival, the three components of individual performance.' [29]; or 'Any trait directly influencing organismal performance' [6].

Hierarchy of proxies: a concept within the Ecosystem Function Trait framework; Highest order levels are ultimately of interest but are highly complex; rather than being measured directly they can be predicted by lower level, simpler, easier-to-measure proxies. For example, (future ecosystem states > ecosystem functions > traits) or (ecosystem functions > rate traits > state traits). However, predictions are only robust if connections between different hierarchy levels are specific, causal, and quantifiable.

Rate trait: traits that capture dynamic processes, that is, any trait that is a rate, any trait that measures a change in states through time, or any trait that is measured per unit of time (e.g.,
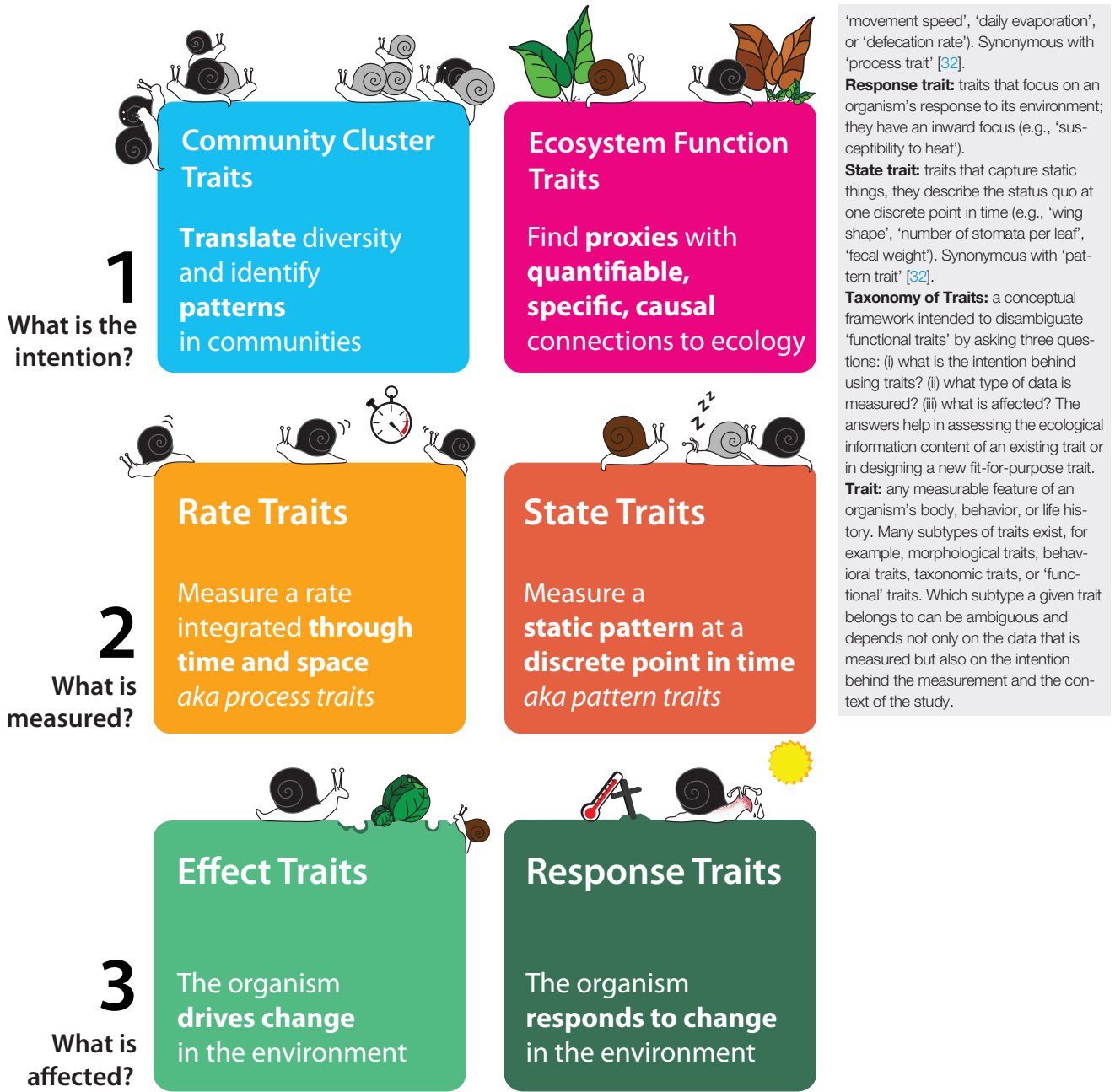
Figure 1. A taxonomy of traits. A framework to characterize traits and navigate their diversity. Previously published distinctions among traits (rate/state and effect/response) can help clarify whether a given trait is fit-for-purpose. However, a first step is to identify this purpose by being clear about our intentions and, thus, requirements for what a trait needs to capture.

'movement speed', 'daily evaporation', or 'defecation rate'). Synonymous with 'process trait' [32].

Response trait: traits that focus on an organism's response to its environment; they have an inward focus (e.g., 'susceptibility to heat').

State trait: traits that capture static things, they describe the status quo at one discrete point in time (e.g., 'wing shape', 'number of stomata per leaf', 'fecal weight'). Synonymous with 'pattern trait' [32].

Taxonomy of Traits: a conceptual framework intended to disambiguate 'functional traits' by asking three questions: (i) what is the intention behind using traits? (ii) what type of data is measured? (iii) what is affected? The answers help in assessing the ecological information content of an existing trait or in designing a new fit-for-purpose trait.

Trait: any measurable feature of an organism's body, behavior, or life history. Many subtypes of traits exist, for example, morphological traits, behavioral traits, taxonomic traits, or 'functional' traits. Which subtype a given trait belongs to can be ambiguous and depends not only on the data that is measured but also on the intention behind the measurement and the context of the study.

These approaches represent different research goals: Community Cluster Traits primarily consider diversity in communities, the presence/absence of traits and, thus, a potential pool of available functions. Ecosystem Function Traits, by contrast, aim to quantify the realized intensity of specific functions. Neither perspective is 'correct', nor are they always mutually exclusive. We
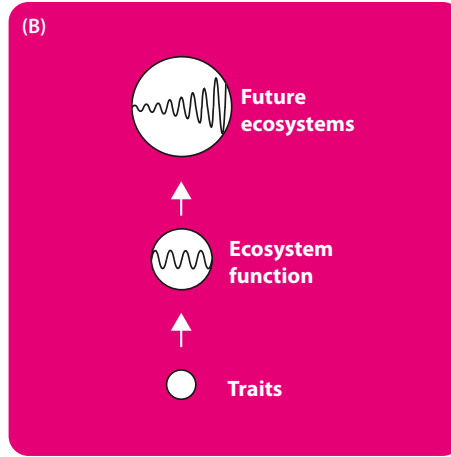
Community Cluster Traits

(A)
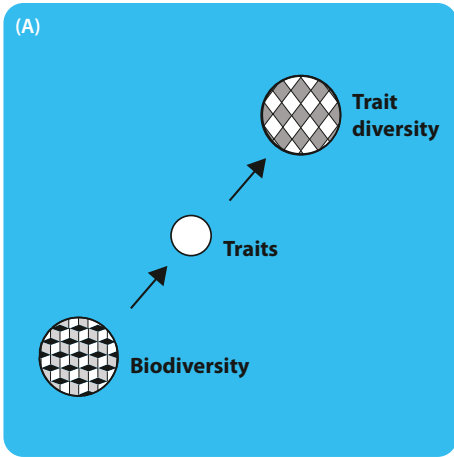
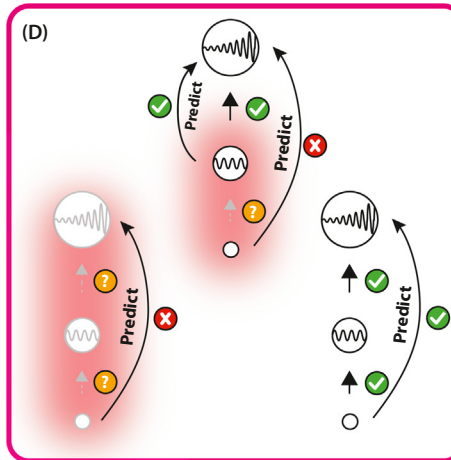are **translators**
of diversity patterns

but

(C)
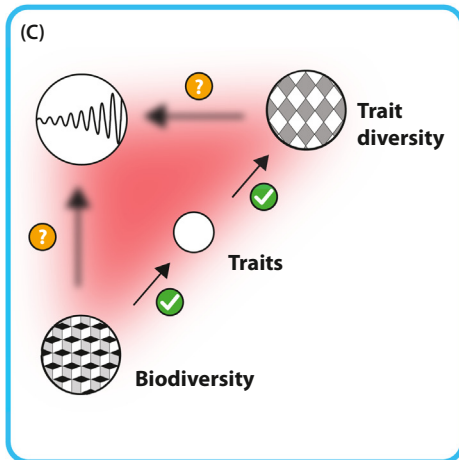
The **ecological meaning** of
clusters remains unknown

Ecosystem Function Traits

(B)

are **proxies to predict**
higher-order ecology

but

(D)

The links in the hierarchy of proxies
must be **quantifiable** and **causal**

Quantifiable, causal connection	Unknown, unproven or assumed connection	Unreliable prediction

Trends in Ecology & Evolution

Figure 2. A new, complementary view of traits in ecology. (A) Community Cluster Traits are translators of diversity (from bio- to trait-), but they are unable to translate either diversity into ecological impacts (C). They are useful to identify patterns in communities but their ability to provide data on what these patterns mean is limited. (B) Ecosystem Function Traits are proxies for higher-order ecological processes, they disregard diversity *per se*, but focus on causal linkages between traits and specific higher-order processes such as ecosystem functions and future ecological trajectories. (D) Causal connections between the different levels of the 'hierarchy of proxies' are required.

propose these complementary perspectives to encourage more balance within trait research. To date, we have primarily invested in the former: in a focus on diversity, not on functions.

Community Cluster Traits

Many current 'functional traits' appear to be aligned with the Community Cluster Trait perspective. Essentially, they focus on diversity and are thus closely related to taxonomy, systematics, or biodiversity research. They act as a promising remedy to a lingering conundrum in ecology (how does biodiversity shape ecosystems?) by translating taxonomic biodiversity into quantifiable trait diversity [8,25,38,44–50] (Figure 2A). Thus, in this philosophy, traits promise a mathematical window onto the potential ecological effects of biodiversity that go beyond quantifying taxonomic diversity itself.

Community Cluster Traits lend an ecological perspective to taxonomic data and allow the detection of patterns that may otherwise go unnoticed (e.g., rarity of trait combinations, redundancy of traits across taxonomic clades, etc.). For example, sorting an imaginary community of beetles by four easily measurable traits – 'carapace color', 'nocturnality', 'diet', and 'mandible size' – may reveal that green, nocturnal, coprophagous beetles with large mandibles are rare, while small-mandibled, brown beetles are common. If phylogenetic relationships are considered, we may conclude that the combination of brown, nocturnal coprophagy arose independently in separate clades, suggesting a relationship between trait combinations and ecological niches. This pattern recognition via traits is quick and resource efficient, compared with studying ecological details of every beetle species. Community Cluster Traits can find patterns quickly and may help identify impending diversity loss or ecological change faster than detailed ecological evaluations. They offer speed and reach.

However, what Community Cluster Traits rarely provide is the translation of diversity into measurable ecological effects (e.g., how exactly is the ecosystem affected if the green nocturnal, large-mandibled dung beetles disappear?). This may not be a shortfall; it may simply not be the intention of the analyses. However, as a result, the actual mechanistic links between diversity and **ecosystem functions** remain hazy (Figure 2C). While Community Cluster Traits reveal patterns in assemblages, they offer few concrete clues of what these patterns mean. A complimentary perspective is needed.

Ecosystem Function Traits

The Ecosystem Function Trait perspective does not focus on diversity. Understanding communities, or organisms, is not the primary focus. Instead, specific ecological functions and their impact on the ecosystem are central. In this perspective, traits are not translators of biodiversity. They are easier-to-measure proxies to predict the higher-order ecological processes which are ultimately of interest (e.g., 'If trait X changes by 10%, how and to what extent does function Y change?').

In this philosophy, predicting future ecosystem conditions is one of the highest goals. Because this goal is hard to accomplish directly, the focus is on stepwise simplification with increasingly easier-to-quantify proxies. This **hierarchy of proxies** (Figure 2B) simplifies predictions about ecosystems (= ultimate goal), firstly through ecosystem functions (= drivers of ecosystems), and secondly through traits (= drivers of functions). These simplifications, however, are only useful if we can ensure that there is a specific, known, causal connection between the proxy we use and the higher levels we want to predict. If proxies are only linked to higher levels through unknown, unproven, or assumed connections, we cannot make reliable predictions (Figure 2D).

To be able to assess the linkages within the hierarchy of proxies, Ecosystem Function Traits must always be considered in relation to a specific ecosystem function. If a trait is considered that has a nonspecific relationship to ecology, it cannot be an Ecosystem Function Trait. This is because no

specific connection exists that can be tested (Figure 2D). The key to identifying useful Ecosystem Function Traits is to: (i) select the ecosystem function of interest, (ii) select traits that have a postulated causal connection to that specific function, and (iii) empirically test this connection and quantify its strength.

Given comprehensive data, a dung beetle's mandible size may be an Ecosystem Function Trait. For example, if the hypothetical ecosystem function of interest is 'pasture productivity', we may want to quantify that large-mandibled dung beetles introduce 0.5 g of nutrients per cubic centimeter of soil per day. If we further had quantified the relationship between soil nutrient content and pasture productivity, we could calculate the contribution of mandible size (trait) to productivity (function) and ultimately to the pasture's resilience to increased grazing pressure (future ecosystem state).

The benefit of the Ecosystem Function Trait approach is the focus on specific processes that have quantifiable ecological outcomes, rather than relying on generic correlations based on the presence/absence of taxa. Nonetheless, this perspective is data intensive, and the quality and quantity of causal links may vary with the given context of measurement. By focusing on a specific context and causal links first, one can establish quantifiable connections that then can underpin robust, up-scaled, community-wide assessments.

### How do we determine if our traits fit our intentions?

The distinction between Community Cluster Traits and Ecosystem Function Traits is foundational within our Taxonomy of Traits (Figures 1 and 2). It defines the intentions and purpose of a given study. But how do we assess whether a given trait is fit-for-purpose, that is, if it can provide the required data? When assessing what a trait can capture, the following two questions are a good framework: what is measured, and what is affected? These questions are reflected in previously published trait distinctions:

What is measured? Rate traits and state traits

Rate traits versus **state traits** are synonymous with the previously described process and pattern traits [32] (Figure 1). Rate traits describe processes, that is, the unit includes a measure of time. Theoretical examples are: 'bites per minute', 'annual growth', 'reproduction rate', or 'daily soil nutrient input'. If the intention is to find Ecosystem Function Traits (i.e., proxies for ecosystem functions), rate traits are higher on the 'hierarchy of proxies' and the first choice (Figure 2B), since both, ecosystem functions and rate traits, describe dynamic processes, not static states. By contrast, state traits are easier to gather since one-time measurements suffice, for example, 'jaw structure', 'leaf area', 'eggs per clutch', or 'mandible size'. However, in the context of Ecosystem Function Traits, state traits are two steps removed, and only valuable as an easy-measure proxy, if they have a causal, quantifiable link to higher levels in the hierarchy of proxies (Figure 2D), that is, to rate traits.

What is affected? Effect traits and response traits

Effect traits and **response traits** relate to the context of the study and question of interest [1,51] (Figure 1). In the context of Ecosystem Function Traits, effect traits are the first choice since they measure the 'outgoing' influence of an organism on the environment (i.e., on ecosystem functions). However, depending on the type of question asked, response traits are also valuable. Response traits can measure how environments affect organisms. Thus, they act as a filter that is applied to effect traits of the same organism [6]. For example, a hypothetical green dung beetle's soil nutrient input (an effect trait) may be modulated by its resistance to desiccation and water loss (a response trait of the same beetle) [20]. Thus, considering both, effect and response traits, can help capture the interactions between traits, environments and their ecological effects [46,52].
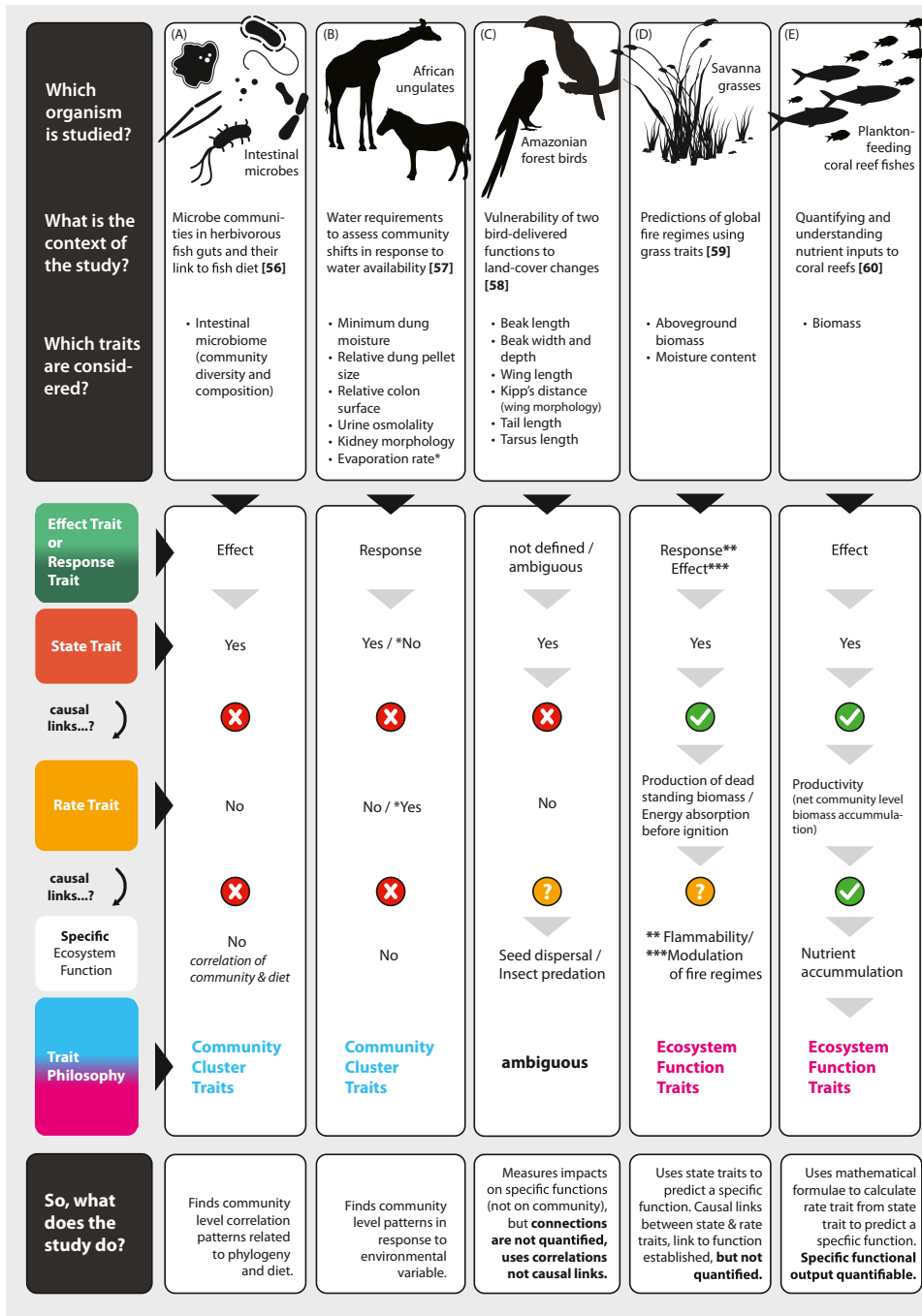
Figure 3. Examples of traits assessed against the Taxonomy of Traits. Selected studies that use traits for different purposes across a variety of taxa: (A) Intestinal microbe communities in herbivorous fishes [56], (B) multiple species of African ungulates [57], (C) Amazonian forest birds [58], (D) savanna grasses across different continents [59], and coral reef fishes that feed on plankton [60]. The colored squares in the left column represent the different trait classes in the Taxonomy of Traits (Figure 1). The curved black arrows in the left column represent their required linkages according to the hierarchy of proxies (Figure 2). When assessing existing traits, as done here, the direction is from top to bottom, that is, assessing the context of the study and the trait types to conclude the underlying 'trait philosophy'. If designing new traits, the direction would be the inverse (from bottom to top),

(Figure legend continued at the bottom of the next page.)

The taxonomy of a trait can be complex – but it is more than an exercise in classification

Traits can be intricately nested within one another, interact with one another, and their classification may depend on the study's objectives (see also [1,7,32]). One rate trait (e.g., 'feeding rate') may contain a multitude of state traits that help describe it (e.g., 'gape size', 'stomach extendibility', 'gut length'). 'Body size' could be an effect trait in a study assessing how trampling by elephants affects grass growth. But even in the exact same dataset, body size could also be a response trait, if studying how drought conditions affect herd composition. If the classification of a given trait is this context dependent, why should we bother? Aren't traits supposed to simplify complex ecosystems?

Yes, traits can help to simplify the complexity of ecology – but they have limits [31]. In plants, long-term, experimental evidence suggests traits are, at best, able to explain one third of variation in ecosystem properties [14]. Stochastic environmental drivers, rather than community traits, may dominate ecological trajectories. Traits *per se* might simply not be suitable for generalizable global predictions about ecosystems. Nonetheless, traits are powerful, they can quantify any states and processes we might desire. Perhaps it is time to stop endorsing sweeping, general promises of traits and talk specifics.

Whether the goal is to assess if existing traits match a study's intentions ('trait triage') or to design new traits ('trait initiation'), the key lies in matching questions and traits. The Taxonomy of Traits helps each user be clearer in what they want to achieve (Ecosystem Function Traits versus Community Cluster Traits), and which trait may be best suited to achieving that particular aim (state traits vs. rate traits and effect traits vs. response traits). Figure 3 provides example assessments of existing traits. By classifying used traits, it is possible to identify which trait philosophy the data can operate in (top to bottom in Figure 3). If the goal was to design new traits for a specific question, the direction would be the inverse (bottom to top).

We hope this framework enables users to put traits into an ecological context and assess whether a given trait is a vague umbrella with nebulous links to ecology, or a specific proxy for a specific question [7]. No one perspective on traits will be comprehensive in capturing ecology. Instead, what is required to advance trait ecology is the acknowledgment that traits are too complex, and this complexity too useful, to be captured by one homogenized term: 'functional trait'.

Concluding remarks

'Functional' perspectives offer new insights as we are developing a more nuanced understanding of ecosystem services and resilience [53,54]. Yet, the future of functional ecology holds exceptionally complex challenges (see Outstanding questions). Traits are no panacea for understanding ecology, but they can be a useful tool to quantify functions if judiciously applied.

When working with functional traits, the most important word may not be 'functional' but 'traits'. The key is in understanding the different classes of traits and their potential for predicting ecological dynamics. The challenge is to ensure traits are selected to fulfill the specific needs of a given study. Much of the complication in current trait-based studies may stem from using Community Cluster Traits to infer functions – we may be struggling with a mismatched tool.

starting with identifying the intention. If the Ecosystem Function Trait approach is chosen, then specific ecosystem functions need to be identified to match causally and quantifiably related rate traits, and ultimately, causally and quantifiably related state traits. Whether effect or response traits are used depends further on the context and goal of the study. Red circle: no causal link; yellow circle: causation or strong correlation, but not quantified; green circle: causal, quantifiable link. Animal illustrations sourced from phylopic.org. Asterisks (*, **, ***) identify the specific connections between traits and trait types (in panel B) or trait types and functions (in panel D).

Outstanding questions

To help balance the utility of traits in ecology, we argue more Ecosystem Function Traits are needed. How can we best rise to the challenging task of elevating this new world of custom-built traits to the vast data richness of currently available 'functional traits'? If we want to get closer to the goal of a predictive ecology, we must attempt to address, in earnest, the known issues with current traits. Rather than retrofitting 'functionality' to pre-existing, often taxonomic measurements, we need to invest in collecting new traits.

If we pick functions first and then select matching traits, the discussion about which traits to study shifts from 'is this trait functional?' to 'which functions are important?' But how do we identify and prioritize 'ecosystem functions of interest'? What constitutes 'importance' for ecosystem functions – benefits for humanity, or ecosystems, or both simultaneously?

Where do we go looking for new Ecosystem Function Traits? As a start, it may help to identify community trait patterns across ecological gradients, or before and after localized disturbances via Community Cluster Traits and subsequently examine whether correlations between trait and environmental patterns have a causal basis. Such trait assessments along gradients are already a common approach, yet rarely do studies go beyond identifying these correlations. Assigning causation to these linkages and quantifying the 'scaling factor' ('A change in trait X, alters the delivery of function Y by Z%') may be a particularly fruitful avenue of research.

How do we best coordinate the development of comprehensive Ecosystem Function Trait databases, that is, how to best facilitate trait assessments and the design of new traits? Accessible, online databases will be required. A significant shift will be to reconsider how we assess 'completeness' of trait datasets, that is, which variable will be the first column. So far it is 'species', a new approach would put 'functions' first.

Declaration of interests

No interests are declared.

References

1. Lavorel, S. and Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.* 16, 545–556
2. McGill, B.J. *et al.* (2006) Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* 21, 178–185
3. Gallagher, R.V. *et al.* (2020) Open Science principles for accelerating trait-based science across the Tree of Life. *Nat. Ecol. Evol.* 4, 294–303
4. Green, S.J. *et al.* (2022) Trait-based approaches to global change ecology: moving from description to prediction. *Proc. R. Soc. B* 289, 20220071
5. Kattge, J. *et al.* (2011) TRY - a global database of plant traits. *Glob. Chang. Biol.* 17, 2905–2935
6. Mouillot, D. *et al.* (2013) A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.* 28, 167–177
7. Funk, J.L. *et al.* (2017) Revisiting the Holy Grail: using plant functional traits to understand ecological processes. *Biol. Rev.* 92, 1156–1173
8. Gladstone-Gallagher, R.V. *et al.* (2019) Linking traits across ecological scales determines functional resilience. *Trends Ecol. Evol.* 34, 1080–1091
9. Elsen, P.R. *et al.* (2021) Accelerated shifts in terrestrial life zones under rapid climate change. *Glob. Chang. Biol.* 28, 918–935
10. Cadotte, M.W. (2017) Functional traits explain ecosystem function through opposing mechanisms. *Ecol. Lett.* 20, 989–996
11. Reich, P.B. (2014) The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. *J. Ecol.* 102, 275–301
12. Díaz, S. *et al.* (2007) Incorporating plant functional diversity effects in ecosystem service assessments. *Proc. Natl. Acad. Sci.* 104, 20684–20689
13. Bongers, F.J. *et al.* (2021) Functional diversity effects on productivity increase with age in a forest biodiversity experiment. *Nat. Ecol. Evol.* 5, 1594–1603
14. van der Plas, F. *et al.* (2020) Plant traits alone are poor predictors of ecosystem properties and long-term ecosystem functioning. *Nat. Ecol. Evol.* 4, 1602–1611
15. de Bello, F. *et al.* (2010) Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodivers. Conserv.* 19, 2873–2893
16. Wong, M.K.L. *et al.* (2019) Trait-based ecology of terrestrial arthropods. *Biol. Rev.* 94, 999–1022
17. Pigot, A.L. *et al.* (2016) Quantifying species contributions to ecosystem processes: a global assessment of functional trait and phylogenetic metrics across avian seed-dispersal networks. *Proc. R. Soc. B Biol. Sci.* 283, 20161597
18. Freschet, G.T. *et al.* (2021) Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs. *New Phytol.* 232, 1123–1158
19. Brandl, S.J. *et al.* (2022) Can metabolic traits explain animal community assembly and functioning? *Biol. Rev.* Published online August 25, 2022. https://doi.org/10.1111/brv.12892
20. Nervo, B. *et al.* (2021) Dung beetle resistance to desiccation varies within and among populations. *Physiol. Entomol.* 46, 230–243
21. Madin, J.S. *et al.* (2016) A trait-based approach to advance coral reef science. *Trends Ecol. Evol.* 31, 419–428
22. Villéger, S. *et al.* (2017) Functional ecology of fish: current approaches and future challenges. *Aquat. Sci.* 79, 783–801
23. McWilliam, M. *et al.* (2020) Deficits in functional trait diversity following recovery on coral reefs. *Proc. R. Soc. B Biol. Sci.* 287, 20192628
24. Bauer, B. *et al.* (2021) Functional trait dimensions of trophic metacommunities. *Ecography (Cop.).* 44, 1486–1500
25. Higham, T.E. *et al.* (2021) Linking ecomechanical models and functional traits to understand phenotypic diversity. *Trends Ecol. Evol.* 36, 860–873
26. Yang, Y. (2021) Emerging patterns of microbial functional traits. *Trends Microbiol.* 29, 874–882
27. Chaudhary, V.B. *et al.* (2022) What are mycorrhizal traits? *Trends Ecol. Evol.* 37, 573–581
28. Richardson, L.E. *et al.* (2018) Mass coral bleaching causes biotic homogenization of reef fish assemblages. *Glob. Chang. Biol.* 24, 3117–3129
29. Violle, C. *et al.* (2007) Let the concept of trait be functional! *Oikos* 116, 882–892
30. Mlambo, M.C. (2014) Not all traits are 'functional': insights from taxonomy and biodiversity-ecosystem functioning research. *Biodivers. Conserv.* 23, 781–790
31. Yang, J. *et al.* (2018) Why functional traits do not predict tree demographic rates. *Trends Ecol. Evol.* 33, 326–336
32. Volaire, F. *et al.* (2020) What do you mean "functional" in ecology? Patterns versus processes. *Ecol. Evol.* 10, 11875–11885
33. Sobral, M. (2021) All traits are functional: an evolutionary viewpoint. *Trends Plant Sci.* 26, 674–676
34. Denis, V. *et al.* (2019) Biogeography of functional trait diversity in the Taiwanese reef fish fauna. *Ecol. Evol.* 9, 522–532
35. Feilich, K.L. and López-Fernández, H. (2019) When does form reflect function? Acknowledging and supporting ecomorphological assumptions. *Integr. Comp. Biol.* 59, 358–370
36. Mbaru, E.K. *et al.* (2020) Functional traits illuminate the selective impacts of different fishing gears on coral reefs. *J. Appl. Ecol.* 57, 241–252
37. Kearney, M.R. *et al.* (2021) Where do functional traits come from? The role of theory and models. *Funct. Ecol.* 35, 1385–1396
38. Petchey, O.L. and Gaston, K.J. (2006) Functional diversity: back to basics and looking forward. *Ecol. Lett.* 9, 741–758
39. Lefcheck, J.S. *et al.* (2015) Choosing and using multiple traits in functional diversity research. *Environ. Conserv.* 42, 104–107
40. Ladds, M.A. *et al.* (2018) Creating functional groups of marine fish from categorical traits. *PeerJ* 2018, e5795
41. Malaterre, C. *et al.* (2019) Functional diversity: an epistemic roadmap. *Bioscience* 69, 800–811
42. Dawson, S.K. *et al.* (2021) The traits of " trait ecologists ": an analysis of the use of trait and functional trait terminology. *Ecol. Evol.* 11, 16434–16445
43. Kissling, W.D. *et al.* (2018) Towards global data products of Essential Biodiversity Variables on species traits. *Nat. Ecol. Evol.* 2, 1531–1540
44. Mammola, S. *et al.* (2021) Concepts and applications in functional diversity. *Funct. Ecol.* 35, 1869–1885
45. Diaz, S. and Cabido, M. (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.* 16, 646–655
46. de Bello, F. *et al.* (2021) Functional trait effects on ecosystem stability: assembling the jigsaw puzzle. *Trends Ecol. Evol.* 36, 822–836
47. Kohli, B.A. and Jarzyna, M.A. (2021) Pitfalls of ignoring trait resolution when drawing conclusions about ecological processes. *Glob. Ecol. Biogeogr.* 30, 1139–1152
48. Hagan, J.G. *et al.* (2021) We should not necessarily expect positive relationships between biodiversity and ecosystem functioning in observational field data. *Ecol. Lett.* 24, 2537–2548
49. Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* 86, 902–910

50. Tilman, D. *et al.* (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379, 718–720

51. Hadj-Hammou, J. *et al.* (2021) Response and effect traits of coral reef fish. *Front. Mar. Sci.* 8, 640619

52. D'agata, S. *et al.* (2016) Unexpected high vulnerability of functions in wilderness areas: evidence from coral reef fishes. *Proc. R. Soc. B Biol. Sci.* 283, 20160128

53. Woodhead, A.J. *et al.* (2019) Coral reef ecosystem services in the Anthropocene. *Funct. Ecol.* 33, 1023–1034

54. Williams, G.J. *et al.* (2019) Coral reef ecology in the Anthropocene. *Funct. Ecol.* 33, 1014–1022

55. Bellwood, D.R. *et al.* (2019) The meaning of the term 'function' in ecology: a coral reef perspective. *Funct. Ecol.* 33, 948–961

56. Scott, J.J. *et al.* (2020) Intestinal microbes: an axis of functional diversity among large marine consumers. *Proc. R. Soc. B Biol. Sci.* 287, 20192367

57. Kihwele, E.S. *et al.* (2020) Quantifying water requirements of African ungulates through a combination of functional traits. *Ecol. Monogr.* 90, e01404

58. Bregman, T.P. *et al.* (2016) Using avian functional traits to assess the impact of land-cover change on ecosystem processes linked to resilience in tropical forests. *Proc. R. Soc. B Biol. Sci.* 283, 20161289

59. Simpson, K.J. *et al.* (2022) Savanna fire regimes depend on grass trait diversity. *Trends Ecol. Evol.* 37, 749–758

60. Morais, R.A. *et al.* (2021) Spatial subsidies drive sweet spots of tropical marine biomass production. *PLoS Biol.* 19, e3001435

61. Stuart-Smith, R.D. *et al.* (2013) Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature* 501, 539–542

62. Kunstler, G. *et al.* (2015) Plant functional traits have globally consistent effects on competition. *Nature* 529, 204–207

63. Farley, S.S. *et al.* (2018) Situating ecology as a big-data science: current advances, challenges, and solutions. *Bioscience* 68, 563–576

64. Lapierre, J.-F. *et al.* (2020) Is limnology becoming increasingly abiotic, riverine, and global? *Limnol. Oceanogr. Lett.* 5, 204–211

65. Xia, J. *et al.* (2020) Research challenges and opportunities for using big data in global change biology. *Glob. Chang. Biol.* 26, 6040–6061

66. McLean, M. *et al.* (2021) Trait similarity in reef fish faunas across the world's oceans. *Proc. Natl. Acad. Sci. U. S. A.* 118, e2012318118

67. Auber, A. *et al.* (2022) A functional vulnerability framework for biodiversity conservation. *Nat. Commun. 2022 131* 13, 4774

68. Clarke, R. (2016) Big data, big risks. *Inf. Syst. J.* 26, 77–90

69. Bayraktarov, E. *et al.* (2019) Do big unstructured biodiversity data mean more knowledge? *Front. Ecol. Evol.* 6, 239