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Streit, Robert P., and Bellwood, David R. (2023) *To harness traits for ecology, let's abandon 'functionality'*. Trends in Ecology and Evolution, . (In Press)

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To harness traits for ecology, let's abandon 'functionality' Robert P Streit^{1,2,3}, David R Bellwood^{1,3}

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- 14 Keywords
- 15 ecosystem function, functional trait, global change, resilience, trait ecology
- 16

17 Highlights

18 Given the surging impacts of climate change, ecology needs new robust tools that 19 • help us to quantify how ecosystems function. 20 21 'Functional traits' hold great promise for this goal. They assess communities not via 22 • taxonomy, but by their impacts on ecology – ultimately promising ecological insights 23 24 simply by measuring which organisms are present. 25 Despite these promises, trait applications in ecology continue to be stalled by a 26 • recurring question: Which 'functional' traits are ecologically meaningful? 27 28 The term 'functional trait' itself is a problem. Its implied utility and versatility are 29 • 30 misleading. 31 We propose to sidestep the preoccupation with 'functionality', and instead focus on 32 • traits and their potential uses. We provide a Taxonomy of Traits, a tool designed to 33 help identify whether traits are fit-for-purpose, i.e., whether their purported 34 'functionality' is useful. 35

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37 Abstract

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39 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 40 41 communities. Such predictions are useful, but only if 'functional' really means 'ecologically relevant'. Unfortunately, many 'functional' traits seem to be characterised primarily by 42 availability and implied importance - not by their ecological information content. Better traits 43 are needed, but a prevailing trend is to 'functionalise' existing traits. The key may be to invert 44 the process, i.e., to identify functions of interest *first* and *then* identify traits as quantifiable 45 proxies. We propose two distinct, yet complementary, perspectives on traits and provide a 46 'taxonomy of traits', a conceptual compass to navigate the diverse applications of traits in 47 48 ecology.

49 Tantalising but complicated - the conundrum of traits in ecology

In ecology, traits (see Glossary) hold great promise for unprecedented insights into 50 complex ecosystems [1–4]. They provide a new perspective on diversity, one that does not 51 ask: who are you? But rather: what do you do? These traits are often termed functional traits 52 and their use has been proclaimed as the dawn of a new era of 'predictive ecology' -a53 scientific discipline that allows the forecasting of future ecological conditions based on the 54 community of organisms present [5,6]. Such a formal framework, an ecological crystal ball, 55 56 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 57 discipline characterised by continuing conceptual and data-driven advances in trait ecology 58 [10–14]. Given its attractiveness, the concept has been widely adopted [3,15–28]. 59

Yet, beyond its enthusiastic application, there is a growing body of concern. Titles of 60 publications alone reflect the heated debates and carefully considered caveats (e.g. [4,29-61 33]). Ecologists often acknowledge conceptual barriers within trait ecology, noting that the 62 utility of trait assessments hinges on the ecological relevance of the underlying traits 63 [4,6,18,34–37]. Yet it remains difficult to shed the ambiguity around which traits are 64 'functional', i.e., useful for predicting ecological dynamics [38-42] (see Text Box). Thus, 65 despite its promises, trait ecology appears to be at a watershed with two potentially risky 66 paths ahead: one focussing on rapidly advancing analytical applications regardless of trait 67 utility, the other mired in the minutiae of theoretical, semantic discussions ('But is this trait 68 69 really functional?') [33,42–44]. Our goal is to summarise previous developments to identify a middle ground. One that is conceptually rigorous, yet universal enough to remain accessible 70 to ecologists from a variety of disciplines. The key questions are: A) What do we want to 71 72 achieve with traits? and B) How do we check whether the traits we choose can deliver on those aims? 73

74 Moving beyond binary choices: The type of trait, not its

75 functionality is key

Traits are complex. This simple word is used to describe a vast assortment of 76 measurements on organisms. Not everything that may be considered a trait in ecology can be 77 neatly compared, because no shared scales exist. For example, *fur colour, seasonal growth*, 78 or phosphate excretion are all traits, but comparisons among them are difficult. To increase 79 clarity, it is important to not sacrifice resolution by lumping everything together under one 80 umbrella term (see Text Box) [30,43]. After all, the value of a trait for ecological analyses, 81 82 lies not in a binary choice (is it 'functional' or not?), it lies in the extent of quantifiable 83 ecological information that it contains.

Here we compile previously published distinctions amongst different types of traits 84 and set them into a framework – a Taxonomy of Traits (Fig. 1). These established trait 85 distinctions help classify a given trait after it has been measured, by capturing what is 86 measured and what is affected. We add an additional layer by asking first: what do we want 87 to achieve with traits? This question of intent highlights the co-existence of two different 88 perspectives that have different goals. To suit either one, traits need to capture specific types 89 90 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 91 navigate, the distinctions, hierarchies, and complex linkages within traits; ultimately to 92 maximise their suitability for specific goals. 93

95 A Taxonomy of Traits

96 What do we want to achieve with traits?

97 If we want to understand whether a given trait is useful, we first need to ask: What do 98 we want to use traits for? We believe this question warrants more attention, than it has 99 received. Explicit clarity might help uncover some of the underlying reasons for frustrations 100 over how traits are (or are not) used. Only if a clear purpose is defined, can we assess whether 101 a trait is fit-for-purpose.

102 We identify a fundamental, conceptual distinction of two separate, yet

103 complementary, philosophies within trait research. Both perspectives have little overlap,

apart from the terminology used: 'functional traits'. We term these perspectives: Community

105 **Cluster Traits** and **Ecosystem Function Traits** (Fig. 2a, b).

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 realised intensity of specific functions. Neither perspective is 'correct', nor are they always mutually exclusive. We 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.

113

114 Community Cluster Traits

115 Many current 'functional traits' appear to be aligned with the Community Cluster Trait 116 perspective. Essentially, they focus on diversity and are thus closely related to taxonomy, 117 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] (Fig. 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 122 123 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 124 community of beetles by four easily measurable traits - 'carapace colour', 'nocturnality', 125 'diet', and 'mandible size' - may reveal that green, nocturnal, coprophagous beetles with 126 large mandibles are rare, while small-mandibled, brown beetles are common. If phylogenetic 127 relationships are considered, we may conclude that the combination of brown, nocturnal 128 coprophagy arose independently in separate clades, suggesting a relationship between trait 129 combinations and ecological niches. This pattern recognition via traits is quick and resource-130 efficient, compared to studying ecological details of every beetle species. Community Cluster 131 Traits can find patterns quickly and may help identify impending diversity loss or ecological 132 change faster than detailed ecological evaluations. They offer speed and reach. 133

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 (Fig. 2c). While Community Cluster
Traits reveal patterns in assemblages, they offer few concrete clues of what these patterns
mean. A complimentary perspective is needed.

142 *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. 149 Because this goal is hard to accomplish directly, the focus is on stepwise simplification with 150 increasingly easier-to-quantify proxies. This hierarchy of proxies (Fig. 2b) simplifies 151 predictions about ecosystems (= ultimate goal), firstly through ecosystem functions (= 152 drivers of ecosystems), and secondly through traits (=drivers of functions). These 153 simplifications, however, are only useful if we can ensure that there is a specific, known, 154 causal connection between the proxy we use and the higher levels we want to predict. If 155 proxies are only linked to higher levels through unknown, unproven, or assumed connections, 156 we cannot make reliable predictions (Fig. 2d). 157

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 non-specific relationship to ecology, it cannot be an Ecosystem Function Trait. This is because no specific connection exists that can be tested (Fig. 2d). The key to identifying useful Ecosystem Function Traits is to: **1**) select the ecosystem function of interest, **2**) select traits that have a postulated causal connection to that specific function, and **3**) 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 grams of nutrients per cubic centimetre 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 dataintensive, and the quality and quantity of causal links may vary with the given context of measurement. By focussing on a specific context and causal links *first*, one can establish quantifiable connections that *then* can underpin robust, up-scaled, community-wide assessments.

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180 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 (Figs. 1, 2). It defines the intentions and purpose of a given study. But how do we assess whether a given trait is fit-for-purpose, i.e., 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:

188 What is measured? Rate traits and State traits

189

Rate traits versus state traits are synonymous with the previously described process 190 191 and pattern traits [32] (Fig. 1). Rate traits describe processes, i.e. the unit includes a measure of time. Theoretical examples are: 'bites per minute', 'annual growth', 'reproduction rate', or 192 'daily soil nutrient input'. If the intention is to find Ecosystem Function Traits (i.e., proxies 193 for ecosystem functions), rate traits are higher on the 'hierarchy of proxies' and the first 194 choice (Figs. 2b), since both, ecosystem functions, and rate traits, describe dynamic 195 processes, not static states. By contrast, state traits are easier to gather since one-time 196 measurements suffice, for example 'jaw structure', 'leaf area', 'eggs per clutch', or 'mandible 197 size'. However, in the context of Ecosystem Function Traits, state traits are two steps 198 removed, and only valuable as an easy-measure proxy, *if* they have a causal, quantifiable link 199 to higher levels in the hierarchy of proxies (Fig. 2d), i.e. to rate traits. 200

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201

202 What is affected? Effect traits and Response traits

Effect traits and response traits relate to the context of the study and question of 203 interest [1,51] (Fig. 1). In the context of Ecosystem Function Traits, effect traits are the first 204 205 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 206 are also valuable. Response traits can measure how environments affect organisms. Thus, 207 they act as a filter that is applied to effect traits of the same organism [6]. For example, a 208 hypothetical green dung beetle's soil nutrient input (an effect trait), may be modulated by its 209 210 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, 211 environments and their ecological effects [46,52]. 212

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 215 216 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', 217 'stomach extendibility', 'gut length'). 'Body size' could be an *effect trait* in a study assessing 218 how trampling by elephants affects grass growth. But even in the exact same dataset, body 219 size could also be a *response trait*, if studying how drought conditions affect herd 220 221 composition. If the classification of a given trait is this context-dependent, why should we bother? Aren't traits supposed to *simplify* complex ecosystems? 222

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 generalisable 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* versus *Rate Traits* and *Effect Traits* versus *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 Fig. 3). If the goal was to design new traits for a specific question, the directionwould 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 homogenised term: 'functional trait'.

245

246 Concluding Remarks

²⁴⁷ 'Functional' perspectives offer new insights as we are developing a more nuanced
²⁴⁸ understanding of ecosystem services and resilience [53,54]. Yet, the future of functional
²⁴⁹ ecology holds exceptionally complex challenges (see **Outstanding Questions**). Traits are no
²⁵⁰ panacea for understanding ecology, but they can be a useful tool to quantify functions if
²⁵¹ 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.

Outstanding Questions:

261	•	To help balance the utility of traits in ecology, we argue more Ecosystem Function
262		Traits are needed. How can we best rise to the challenging task of elevating this new
263		world of custom-built traits, to the vast data-richness of currently available 'functional
264		traits'? If we want to get closer to the goal of a predictive ecology, we must attempt to
265		address, in earnest, the known issues with current traits. Rather than retrofitting
266		'functionality' to pre-existing, often taxonomic measurements, we need to invest in
267		collecting new traits.
268		
269	•	If we pick functions first and then select matching traits, the discussion about which
270		traits to study shifts from 'is this trait functional?' to 'which functions are important?'.
271		But how do we identify and prioritize 'ecosystem functions of interest'? What
272		constitutes 'importance' for ecosystem functions – benefits for humanity, or
273		ecosystems, or both simultaneously?
274		
275	•	Where do we go looking for new Ecosystem Function Traits? As a start, it may help
276		to identify community trait patterns across ecological gradients, or before and after
277		localized disturbances via Community Cluster Traits and subsequently examine
278	~	whether correlations between trait and environmental patterns have a causal basis.
279		Such trait assessments along gradients are already a common approach, yet rarely do
280		studies go beyond identifying these correlations. Assigning causation to these
281		linkages and quantifying the 'scaling factor' ("A change in trait X, alters the delivery
282		of function Y by Z%.") may be a particularly fruitful avenue of research.
283		

How do we best coordinate the development of comprehensive Ecosystem Function
 Trait databases, i.e., 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, i.e., which variable will be
 the first column. So far it is 'species', a new approach would put 'functions' first.

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290	Glossary
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292	•	Community Cluster Trait: a perspective where traits translate taxonomic bio <u>diversity</u>
293		into trait diversity; they identify patterns within communities by creating identity via trait
294		similarities and distinctions. These traits can have secondary links to ecology, but their
295		main analytical capability is restricted to assigning identities and clustering (i.e. they are
296		essentially taxonomic traits). Secondary insights into what these clusters mean remain
297		based on speculation, not data.
298	•	Ecosystem Function: an ecological process defined by the movement or storage of
299		energy or material [55].
300	•	Ecosystem Function Trait: a perspective where traits are easier-to-measure proxies to
301		predict higher-order ecological processes which are ultimately of interest, i.e. traits which
302		have a direct, known, causal link to specific ecosystem functions, which in turn have
303		specific effects on future ecosystem states.
304	•	Effect Trait: traits that measure how an organism modulates its environment; effect traits
305		have an outward focus (e.g., 'number of prey items consumed per day').
306	•	Functional Trait: traits that are perceived to have ecological relevance through
307		generalized links to ecology. Despite these assumptions about ecological information, the
308		prevailing definitions focus on evolutionary measures of organisms, fitness or
309		performance, not ecology [33]: "[Functional traits] impact fitness indirectly via their
310		effects on growth, reproduction and survival, the three components of individual
311		performance." [29]; or "Any trait directly influencing organismal performance" [6].
312	•	Hierarchy of Proxies: a concept within the Ecosystem Function Trait framework;
313		Highest order levels are ultimately of interest but are highly complex; rather than being
314		measured directly they can be predicted by lower-level, simpler, easier-to-measure

315	proxies.	For examp	le (fut	ure ecos	system	states 2	> ecos	ystem	functions	>	traits)	or
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316 (*ecosystem functions > rate traits > state traits*). However, predictions are only robust if

317 connections between different hierarchy levels are specific, causal, and quantifiable.

- Rate Trait: traits that capture dynamic processes, i.e., 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., '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').
- 326 Synonymous with 'pattern trait' [32].
- Taxonomy of Traits: a conceptual framework intended to disambiguate 'functional traits' by asking three questions: 1) What is the intention behind using traits? 2) What
 type of data is measured? 3) 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, behaviour, or life history. Many
 subtypes of traits exist, e.g. morphological traits, behavioural 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.

338 Acknowledgements

- 339
- 340 We thank the members of the Research Hub for Coral Reef Ecosystem Functions, especially
- 341 CR Hemingson, AC Siqueira, and SB Tebbett for helpful discussions. Insightful comments
- by Dr Andrea Stephens, Dr Gareth Williams and three anonymous reviewers greatly
- 343 improved this paper. Funding was provided to DRB by the Australian Research Council (LF

copy-reviewed

344 190100062).

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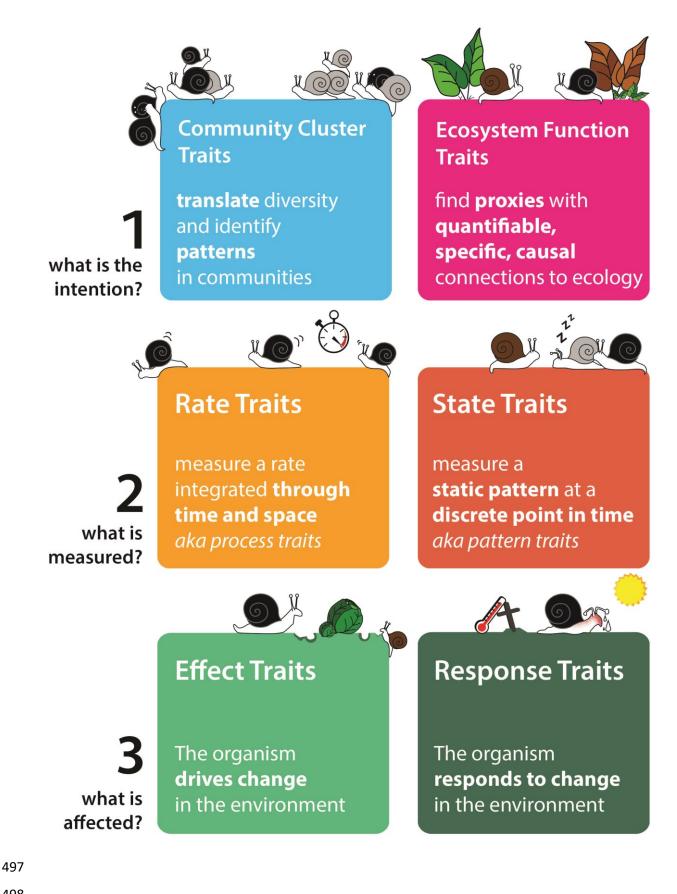
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Figures 489

469	rigui cs
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491	Figure 1. A taxonomy of traits. A framework to characterize traits and navigate their
492	diversity. Previously published distinctions among traits (rate / state and effect /
493	response) can help clarify whether a given trait is fit-for-purpose. However, a first
494	step is to identify this purpose by being clear about our intentions and, thus,
495	requirements for what a trait needs to capture.
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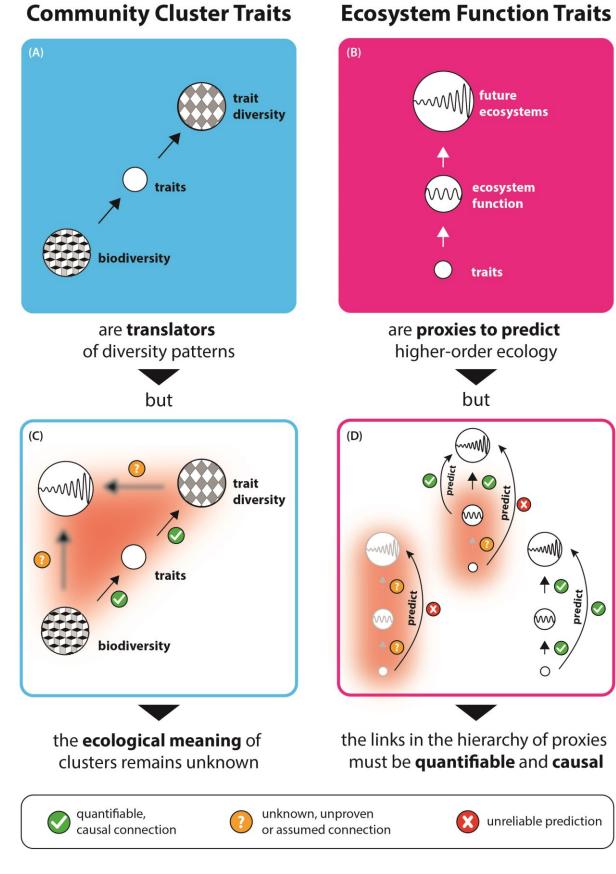
499 Figure 2. A new, complementary view of traits in ecology. (a) Community Cluster Traits

are translators of diversity (from bio- to trait-), but they are unable to translate 500

either diversity into ecological impacts (c). They are useful to identify patterns in 501

communities but their ability to provide data on what these patterns mean, is limited. 502

- (b) Ecosystem Function Traits are proxies for higher-order ecological processes, 503
- they disregard diversity per se, but focus on causal linkages between traits and 504
- specific higher-order processes such as ecosystem functions and future ecological 505
- trajectories. (d) Causal connections between the different levels of the 'hierarchy of 506
- Jor copy revues 507 proxies' are required.

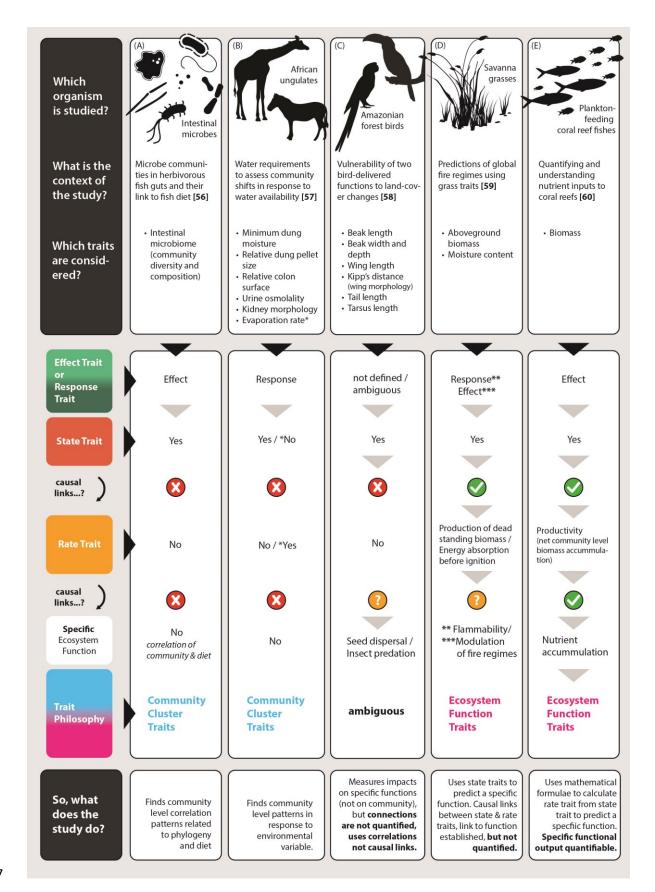


511 Figure 3. Examples of traits assessed against the Taxonomy of Traits.

The coloured squares in the left column represent the different trait classes in the 512 Taxonomy of Traits (Fig. 1). The curved black arrows in the left column represent 513 their required linkages according to the Hierarchy of Proxies (Fig. 2). When assessing 514 existing traits ('trait triage'), as done with these examples, the direction is from top to 515 bottom, i.e., assessing the context of the study and the types of traits to conclude the 516 underlying 'trait philosophy'. If designing new traits ('trait initiation'), the direction 517 would be the inverse (from bottom to top), starting with identifying the intention. If 518 519 the Ecosystem Function Trait approach is chosen, then specific Ecosystem Functions need to be identified to match causally and quantifiably related Rate Traits, and 520 ultimately, causally and quantifiably related *State Traits*. Whether *Effect* or *Response* 521 Traits are used depends further on the context and goal of the study. Red circle: no 522 causal link; Yellow circle: causation or strong correlation, but not quantified; Green 523 circle: causal, quantifiable link. Animal illustrations sourced from phylopic.org. 524 Studies: (A) [56], (B) [57], (C) [58], (D) [59], (E) [60]. 525

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529 Text Box

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531 Functional traits - Pandora's Box or Rosetta Stone?

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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, non-functional 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 performancerelated [55]. But if all traits can be 'functional', this 'functional' label adds very little new information [30,33].

547 This ecological ambiguity of traits often seems acceptable, in exchange for access to 548 comprehensive data. Trait data are useful if they are available at global scales, and with 549 maximal taxonomic coverage. This pragmatism and the access to global trait data is -550 undoubtedly - a blessing when faced with rapid ecological change [61–67] – or pressure to 551 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 ofresources, or sacrificing quality for quantity [68,69].

The intuitive simplicity of the binary choice on 'functional traits' implies scientific 554 objectivity. Instead, we may be dealing with a parasitic word. 'Functional' suggests rigour 555 and gravitas. In fact, it may have become a vague linguistic ornament causing confusion 556 [3,29,42,43]. The 'functionality' of a trait may rely on the researcher's skill in convincing 557 others of its significance, rather than on quantitative evidence of the trait's relevance to 558 ecology. If we wish to address this issue, one way forward could be to tighten the definitions 559 , and is to the other half of the the other half of the other half of the other half of the other half of the the other half of the other of what constitutes functionality. The other option is to abolish the binary choice, set aside 560 the search for functionality, and focus on the other half of the term: 'trait'. 561