Rebuilding community ecology from functional traits

Brian J. McGill[1], Brian J. Enquist[2], Evan Weiher[3] and Mark Westoby[4]

[1]Department of Biology, McGill University, Montreal, QC, Canada, H3A 1B1
[2]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA
[3]Department of Biology, University of Wisconsin – Eau Claire, Eau Claire, WI 54702, USA
[4]Department of Biological Sciences, Macquarie University, NSW 2109, Australia

There is considerable debate about whether community ecology will ever produce general principles. We suggest here that this can be achieved but that community ecology has lost its way by focusing on pairwise species interactions independent of the environment. We assert that community ecology should return to an emphasis on four themes that are tied together by a two-step process: how the fundamental niche is governed by functional traits within the context of abiotic environmental gradients; and how the interaction between traits and fundamental niches maps onto the realized niche in the context of a biotic interaction milieu. We suggest this approach can create a more quantitative and predictive science that can more readily address issues of global change.

Whither community ecology?

Community ecology is the study of a set of species co-occurring at a given time and place. MacArthur suggested that the goal of community ecology (as of all science) is to find general rules [1], whereas Lawton [2] suggested that 'community ecology is a mess' with respect to this search. Simberloff [3] countered that general rules cannot be achieved owing to the complex nature of communities. We disagree with Simberloff's view and suggest that there is hope for general rules in community ecology. Much (but not all, e.g. [4–7]) of community ecology from the 1960s onwards has pursued a program based on studying the population dynamics of pairs of species [8–10] and building this up into models of communities. This has had some success in explaining one- or few-species systems, but rarely in providing general principles about many species communities [2,3]. In response to this shortcoming, a variety of fresh approaches to community ecology have emerged recently [11–13]. We suggest that a focus on four research themes can clean up the 'mess', bringing general patterns to community ecology.

Corresponding author: McGill, B.J. (mail@brianmcgill.org).
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Functional traits research program

The four themes that we suggest are traits, environmental gradients, the interaction milieu and performance currencies. These themes are linked by taking a more physiological approach, by using concepts that are

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Glossary

Community matrix: a square (S×S) matrix describing interactions in a community with S species. The community matrix, together with a vector of intrinsic rates of increase (r), specifies the parameters of the generalized (S species) Lotka–Volterra differential equations, which can be solved for equilibrium abundances (N).

Distinct preference niche: a model of a niche in which each closely related species has a performance optimum at a different point along an environmental gradient (Figure 1c, main text). This model is assumed correct in most of community ecology, but might be less common than shared preferences.

Fundamental niche: the subset of n-dimensional environmental space of all possible conditions in which a species can maintain itself in the absence of competition (Figure 1c,d, main text).

Gradient analysis: the measurement of the abundance of different species either in the field along an indirect gradient, such as elevation, or in the laboratory along a direct gradient, such as moisture or pH (Figure 1b, main text).

Habitat modeling: the development of a regression model (usually nonlinear) that predicts the abundance (or presence versus absence) of a species given a set of environmental conditions by estimating model parameters from observations of abundance versus environment in the field.

Performance currency: a measurable quantity with physical units that enables the comparison of performance (the capacity of an organism to maintain biomass over many generations) between species and across environmental gradients. The appropriate currency should be chosen based on the organisms and can vary depending on the question (e.g. fundamental versus realized niche processes), but is usually related to the acquisition and allocation of energy and nutrients.

Physiological response curve (i.e. environmental response curve): a relationship giving fitness (or a component of fitness) as a function of one (occasionally several) environmental variables (Figure 1a, main text).

Population dynamics models: a differential or difference equation model of abundance (N) that models changes in N over time either primarily or exclusively as a function of N at previous time intervals. It has usually been assumed that community ecology is best conceptualized as the development of multispecies population dynamic models.

Realized niche: the subset of n-dimensional environmental space where a species is present. It is usually assumed that the realized niche is a subset of (smaller than) the fundamental niche (Figure 1c,d, main text).

Shared preference niche: an alternative to distinct preferences where a set of species prefer one environment (often warm, moist, nutrient-rich, sheltered conditions). Coexistence is achieved by a tradeoff between the ability to tolerate less desirable conditions and the ability to be competitively dominant (Figure 1d, main text).

Trait: a well-defined, measurable property of organisms, usually measured at the individual level and used comparatively across species. A **functional trait** is one that strongly influences organismal performance.

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measurable in well defined units and by avoiding short-term population dynamics:

Traits

Examples of functional traits (see Glossary) include basal metabolic rate, beak size, seed or egg size, nutrient concentrations and stoichiometries, adult body mass, frost tolerance, potential photosynthetic rate, and leaf mass per area with associated fast–slow leaf economics [14]. To be useful to community ecology, traits should vary more between than within species and preferably be measured on continuous scales. Although being interested in the role of traits in ecology is not new [15], community ecologists have preferred to emphasize a nomenclatural approach by focusing on species identities, which has resulted in a loss of ecological generality [16]. For example [17], the trait-based statement 'compact plants with canopy area $<30\,cm^2$ and small or absent leaves are restricted to marshes with $<18\,\mu g\;g^{-1}$ soil P' is more useful than the nomenclatural statement '*Campanula aparinoides* is found only in infertile habitats.' Statements about traits give generality and predictability, whereas nomenclatural ecology tends towards highly contingent rules and special cases [2,3].

Environmental gradients

Much of recent community ecology ignores the fact that real communities occur on gradients of temperature, moisture and soil chemistry. This is justified if we believe that community properties are determined mainly by interactions among species, but a major goal of community ecology is to explain why communities change in a systematic fashion across space. For example, predicting the ecological impact of global warming requires an understanding of how communities are affected by the environment, which is most easily understood by investigating variation along gradients.

Interaction milieu

Community ecologists must also address biotic interactions (e.g. competition, predation, etc.), but the key question is how. The favored approach since the 1960s focuses on specific pairs of interacting species, their population dynamics and assembly into a community matrix. However, for many communities, interactions are diffuse [1,18,19], and considering each pairwise interaction as a separate process is difficult [20]. Thus, we argue that biotic interactions are best modeled as a milieu or biotic background with which an organism interacts. Frequency distributions of traits that are important for a given type of interaction give an operational definition of this milieu. For example, a histogram of heights of individuals at a site gives a good first approximation to a plant light competition milieu. Competition can often best be conceptualized as a frequency-dependent game-theoretic model in which an invader plays 'against the field' [21] of strategies or milieu. We can then ask whether a new strategy can invade depending on the milieu already present [22], but the dynamical time-course need not be treated in detail. Predators, herbivores, pathogens and mutualists might sometimes be as important as competition in the interaction milieu, but we argue that, as with competition, the diffuse, game-theoretic approach will be most productive.

Performance currency

To explore how trait variation affects performance, we need a common currency that is comparable across species and along gradients. It has often been assumed (e.g. [9,23]) that the population increase rate (e.g. instantaneous rates of increase, r) is the best such currency. But we argue that these measures become progressively less useful as the number of species increases, because they are hard to measure and are inherently phenomenological and removed from physiology and other connections to the environment. We favor performance currencies, such as energy intake and expenditure (optimal foraging), CO_2 intake per leaf dry mass invested (plant physiological ecology) or seed output (reproductive strategies). Such performance currencies are undeniably related to population-dynamical measures (a positive rate of population increase implies that there is an energy budget surplus) and, moreover, population dynamics have the benefit of integrating separate performance currencies (e.g. survival versus growth). Thus, mapping from performance measures to population dynamics is an important long-term goal [7,9,24]. However, until this connection is understood, we favor a greater emphasis on performance currencies derived from the processes of acquiring, allocating and spending energy and mineral nutrients, because these are closely connected to the physical environment and to interactions in the interaction milieu.

Returning to fundamental and realized niches

The framework that ties these four themes together into a coherent theory is the idea of the fundamental versus realized niche [25]. Current efforts to study fundamental niches focus on measuring growth or growth surrogates in relation to environmental variables [i.e. physiological response curves (PRCs); Figure 1a]. Similarly, current approaches to realized niches involve habitat modeling [26] and gradient analysis [27] (Figure 1b), whereas current models of the transformation from fundamental to realized niche center on community matrix models [1,9] and species interactions.

We argue that these independent approaches do not provide a predictive framework for community ecology. Most PRCs are nomenclatural and are rarely measured with respect to traits. Habitat modeling and gradient analysis provide only an observational, correlative view of the realized niche, with no indications of the fundamental niche and interaction milieu mechanisms that precede the realized niche. Community matrix models and studies of species interactions typically are not positioned on real geographical gradients, take the list of potential co-occurring species as given and do not provide information about the environmental responses of the species that are potentially present. For example, these separate approaches cannot explain why species are not necessarily most abundant at their fundamental-niche optimum [28–31]. Similarly, these approaches provide limited predictive ability if the composition of the interaction
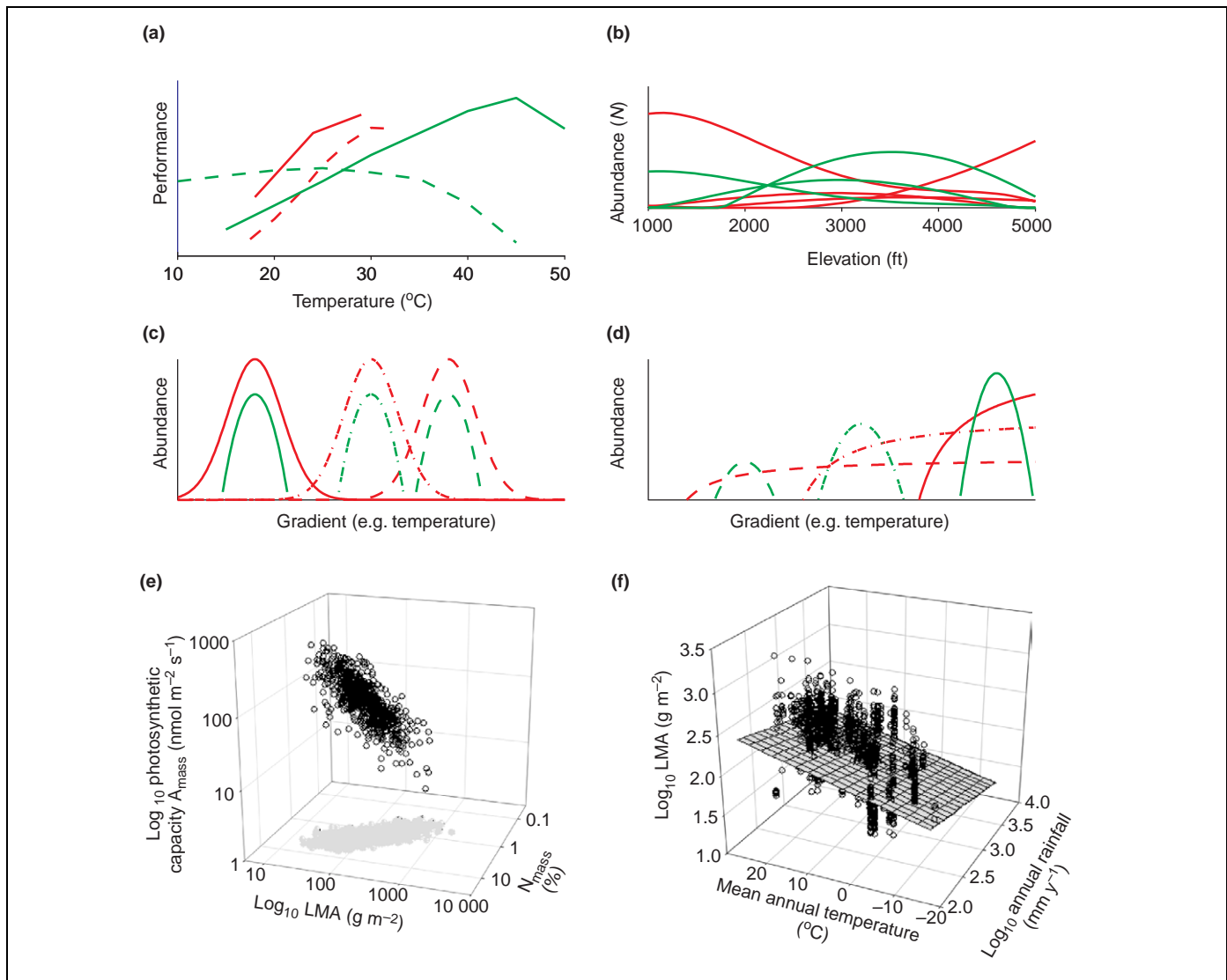
Figure 1. Key concepts in the functional-traits-on-gradients approach. **(a)** A physiological response curve plotting some measure of performance versus some environmental variable, such as temperature or pH. The red lines are intrinsic rate of increase (r) for two species of zooplankton (data from [81]). The green lines are photosynthetic rate for two species of desert plant (data from [82]). **(b)** A gradient analysis plotting the abundance of some species (usually smoothed) versus spatial position, which serves as a surrogate for an environmental variable such as altitude. The red lines are three species of insect and the green lines are three species of trees from a xeric transect in the Appalachians (data from [27]). **(c)** Distinct preference niches: the red lines plot functional fitness, show the fundamental niche and are analogous to the PRC in (a). The green lines correspond to abundance, show the realized niche and are analogous to the gradient analysis in (b). The different line types (solid, dashed and dashed-dotted) represent three species. The realized niche of each species is centered in its fundamental niche. **(d)** The same as for (c) but for a shared preference scenario. All species have the same PRC optimum, but the realized niche is found under this optimum only for the competitive dominant species. More-tolerant species are driven into suboptimal niches. **(e)** A plot of how photosynthetic rate (a performance currency) is related to SLA (specific leaf area) and nitrogen content (reproduced with modification from [14]). **(f)** A plot of how traits vary within and between communities as a function of environmental variables. The mean changes systematically with environment, but the variance is still large (SD are typically 50–60% of the worldwide SD) (reproduced with modification from [14]).

milieu or local environment changes (e.g. as a result of global warming).

This fundamental–realized niche framework begins with performance currencies measured as a function of abiotic environmental gradients and the traits of multiple species (fundamental niche), and then predicts how performance changes as a result of the interaction milieu (realized niche), again as a function of traits. But we have much to learn about even the basics of fundamental and realized niches. Fundamental niches are rarely measured and, as a consequence, we do not know when or if realized niches are narrower than fundamental niches as a result of competition, or if the realized niches can be wider owing to source–sink dynamics [32]. Thus, we need a focused

effort on fundamental and realized niches and the processes that govern them (i.e. our four themes).

Ecologists might also need to expand their view of niches. The classic, pair-wise species-specific model of competition posits a tradeoff in performance along some gradient (e.g. food size), leading each species to prefer a distinct region of niche space along this gradient (Figure 1c); realized niches are narrower than fundamental niches owing to niche overlap, and the realized niches are centered on the region where a species performs optimally. Many communities, however, match an alternative model [33–35], where abundance is governed by a dominance–tolerance tradeoff. Under this scenario, species are characterized by shared preferences

Box 1. Using species traits to investigate ecological communities

Three examples illustrate how a focus on traits, environmental gradients, performance currencies and/or the interaction milieu can lead to an understanding of fundamental and realized niche processes. They also show how the most important traits and environmental factors vary among systems.

Hummingbirds in breeding season

Hummingbirds meet large daily energy expenditures by acquiring nectar. Body size is the trait that is the best single predictor of basal metabolism and also of costs of flying and maintaining body temperature at night. Flower densities and their nectar yields define fundamental niches, and vary along altitudinal gradients. Larger hummingbird species are behaviorally dominant for the purpose of defending territories and the flowers in them, but also require higher nectar-yield flowers to support themselves; therefore, not all available territories can support a large-bodied individual. Nectar can also accumulate in lower yield flowers and be available to smaller bodied species. Thus, species of different body mass can coexist along a tradeoff from behavioral dominance to tolerance for low resources, defined mainly by body mass in relation to the resource supply.

Herbaceous plants in cold-temperate lakeshore communities

All species in the community grow best at sites that have sediment that is rich in mineral nutrients and rarely disturbed. Other sites are less favorable for several reasons, including lower nutrients (sand or cobbles), exposure to strong wave action, or frequent damage by shifting ice. Different species have wider tolerance (i.e. can maintain positive growth) along these different dimensions of unfavorability. This arrangement of fundamental niches has been called 'centrifugal' community organization [62,63]. Competitive dominance is best predicted by the stature of the species as an adult [41], because height confers prior access to light. Taller species tend to be less tolerant of the different kinds of unfavorability owing to allocation of resources to growth rather than to resilience.

Grain beetles in a laboratory

The intrinsic rate of increase (r) is hump shaped for two grain beetle species across a spread of temperatures and humidities. Temperatures and humidities with positive r determine the fundamental niches [64] and abundance is generally positively correlated with r [65]. Because competition is driven by resource consumption, the species having the higher r always competitively excludes the other, even if the other species also has a strongly positive r [66]. The traits involved here are assays of temperature response, but could be traced to more mechanistic traits, such as expression of heat shock proteins and heat loss based on body size.

Box 2. Putting the 'function' in functional traits

We have highlighted four categories of variables (traits, environment, performance currency and abundance) that are usually continuous, have well-defined units, can be measured directly and enable comparison across organisms. These attributes enable one to plot one variable against other variables, and then look for relationships. One might measure performance (P) as a function of environment (E) and/or traits (T), $P = f(E,T)$ or relationships between traits $T_1 = f(T_2, T_3, \ldots)$. Abundance ($N$) can be measured versus traits, $N = f(T)$, the environment, $N = f(E)$ or performance, $N = f(P)$. Other combinations are also possible. The main point is not a particular model, but the emphasis on finding mathematical relationships between continuous, measurable variables.

Arguably, this ability to find functional relationships between continuous, measurable variables is the essence of science (e.g. Newton's law of gravity is a functional relationship between force, mass and distance: $F = cM_1M_2/d^2$). Some ecologists might criticize our emphasis on functional relationships as overly phenomenological; however no mechanism for the law of gravity is yet known, yet its predictive ability enables us to send interplanetary probes to predetermined locations over a billion kilometers away. Moreover, the development of a mechanism first requires a clear description of the phenomenon [11]. Indeed, our focus on measurable units and physiological and behavioral properties of individuals should provide rapid development of mechanisms once phenomena are identified.

This quantitative and functional approach is also associated with a marked shift in statistical outlook. It draws attention to explanatory power, r^2, to effect sizes and to partitioning of variance rather than to hypothesis testing and P values [67]. It suggests new statistical approaches, which can derive functional relationships such as regression trees, path analysis, quantile regression and local regression. In ecology, the problem is not so much that only some effects are genuine (i.e. significance); there are hundreds of genuine forces acting in an ecological system. The problem is to identify the traits and environmental factors that are most responsible for the most striking and important patterns in the field. The use of r^2 or similar measures gives an objective criterion for the prioritization process discussed here. This emphasis on r^2 is badly needed; for example, one recent survey [68] suggested the average r^2 of an ecological experiment was 0.04 (i.e. only 4% of the variance was explained by the study factors).

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or inclusive niches [31,33,35–38] (Figure 1d), where most species perform best in benign, productive sites (i.e. undisturbed sites with a higher concentration of resources). However, the ability to dominate productive sites or to sequester high-quality resources trades off with the ability to persist on low-quality resources or to tolerate harsh conditions. For example, a species can allocate resources to either frost tolerance or growth rate [39] and, similarly, a desert rodent can have either predator escape mechanisms (tolerance) or competitive dominance [40] (Box 1). In some cases, there might be a mixture of the two; animals might have shared preferences for habitat and distinct preferences for food or the appropriate model might change with scale. The model of shared preference has been developed repeatedly and shared preferences

appear to be twice as common as distinct preferences [33], yet there is a continuing emphasis on distinct preferences, probably because most community theory embraces species interactions and remains vague about environmental gradients. Traits and performance currencies could make the above verbal theory more quantitative and rigorous (Box 2).

Prioritizing factors

Many factors (e.g. traits, environmental variables and performance currencies) could influence community structure. However, it is impossible to treat every factor equally and to study each variable and all interaction terms simultaneously. Even three traits and three environmental variables, each studied at five levels, would require a prohibitive number of measurements ($5^{3+3} = 15\,625$ treatments in a complete design). Factors must thus be prioritized using existing knowledge of the study system (Box 1). Without claiming that lower ranked traits and abiotic factors have no effect, we expect them to have less predictive power than do the higher ranked. For fundamental niches, the highest-ranked traits will interact strongly with physical gradients in influencing the

activities that are most crucial for performance and the long-term maintenance of the species.

Similarly, research demands a judgment about which functional traits are most decisive in competition and the interaction milieu, and about which physical gradients those traits interact with most. These functional traits might be the same as those that decide fundamental niche, depending on competition in the particular community (Box 1). In a distinct preference niche organization, the most predictive traits will be those that relate to resource acquisition along the niche dimensions (e.g. beak size and shape). However, in a shared preference niche organization, traits related to competitive dominance ranking, such as height and aggression, will often be most informative.

This process of prioritization produces several questions. For a given system (Box 1), which performance currencies are most predictive of long-term success? For these performance currencies, which traits and environmental variables most affect performance? Which traits modify the effects of the interaction milieu the most? To prioritize factors is to hypothesize about which fundamental and realized niche processes are most important in a given system. Progress of the research program can be thought of as testing and improving those hypotheses by revising or confirming the ranking list. These hypotheses can be objectively tested using measures of predictive power, such as r^2 (Box 2).

An additional approach to dealing with the many potential factors to explore depends on the fact that, often, many separate traits or environmental variables can be reduced to one or two axes of variation that capture a large proportion of the original variation in traits, because of allocation and life-history tradeoffs. For example, a study [14] of >2500 plant species at 175 sites showed that a single axis of variation explained almost 75% of the variation in six leaf-trait dimensions (Figure 1e). Between prioritization and reduction, we are optimistic that the many potential factors can be reduced to a manageable level.

Contrast with other approaches

How does the functional trait approach compare with other community ecology approaches? Three common approaches (mainstream empirical studies of species interactions, community-matrices and neutral theory) stand in strong contrast to what we propose.

Past empirical studies of species interactions covers a range of work, some of which fits well into the functional trait research program [5,27,30,38,40–42]. However, we suggest that much of this work differs from the functional trait-based approach in subtle but important ways. First, many empirical studies have traditionally been nomenclatural in nature, studying typically two–four species with no measurement of the traits that distinguish them. Second, when studies are conducted at multiple sites, the variation among sites has usually been treated as noise or, more recently, as an example of 'historical contingency' with little effort to find systematic variation in performance and outcome as a function of explicit environmental factors, such as temperature, that vary between sites.

Finally, most empirical studies rely on ANOVA with a focus on statistical significance, whereas we emphasize predictive power measured by effect sizes and r^2 (Box 2)

Meanwhile, the dominant paradigm over the past 40 years for theoretical ecologists is based on population dynamics built up into community matrices (paralleling the emphasis on pairwise species interactions). This approach is sensible, but, with hindsight, population dynamics are most successful in modeling only one- or few-species systems. Larger numbers of species lead to modeling challenges, such as chaotic dynamics and difficult parameterization [20].

Population dynamics could move in directions that incorporate our four themes [7,24], but has generally moved in the opposite direction. Thus, the most-discussed population-dynamic community model of the past few years, neutral theory [43–45], is explicitly predicated on an assumption that the differences in traits between species and the environmental variation along gradients have no effect on population dynamics, diametrically opposite to what we propose.

Two less-dominant paradigms (community resource models and macroecology) have some overlap with the functional trait approach. Consumer resource models (CRM) [1,12,46–49] avoid the proliferation of pairwise interaction coefficients and approach a 'milieu' concept of competition. They use measurable numbers (the slope of impact vectors and R^*, defined as the external resource concentration level below which a species cannot sustain its population size) to predict community structure. Recent CRM work [12] emphasizes gradients and niches as central organizing principles. Specifically, CRM explores gradients in nutrient availability, along which R^* delimits the fundamental niche, while the impact vector converts this to and delimits the realized niche. As such, CRM can be thought of as a specific example of the functional trait research program (Box 1), hypothesizing that resource uptake and survival at low resource levels are the most important factors in the system; one can test for which systems these prioritization hypotheses are true [47]. It is not clear how CRM would be applied to gradients of nonconsumable factors, such as temperature, that we believe to be important (but see [12]). Thus, CRM is limited to systems in which its mechanism of resource competition dominates [47], whereas the functional traits approach lays out a more general research program. The two approaches also differ on what types of variable should be measured. R^* functions like our performance currency, but is measured differently; it is a highly abstract, integrative measure incorporating the state of an environmental variable at which a population dynamic measure reaches a particular level (growth rate is zero). By contrast, we believe that traits, performance currencies and the environment are three distinct factors that should be measured independently, using concrete morphological and physiological features of individuals for the first two. Work has been done on how traits (*sensu* our definition) such as root allocation correlate with R^* [12]. We suggest that our approach will be more operational and predictive and will apply to a broader range of systems, but hope that this will be evaluated empirically.

Macroecology [2,11,20] shares similar goals to the functional trait program, seeking to find general rules for the field of community ecology, and pursues this aim in similar ways by comparing data across many species and sites and by emphasizing functional relationships between variables. However, the mainstream of macroecology has usually focused on only one trait (body size, but see [50]), has not traditionally focused on performance currencies (but see [51,52]), tends not to focus on environmental variables (except when exploring latitudinal and productivity gradients in diversity), and arguably deemphasizes niches and the competitive milieu in the pursuit of pattern over process. We hope that macroecology will begin to incorporate our four themes of traits, performance currencies, environmental variables and the competitive milieu.

Limitations and benefits of functional trait-focused community ecology

Where the goal is to understand a single species or pair of species at a single site (e.g. for conservation), the focus on population demographics and on pairwise species interactions with strong competitor or predator species can be more productive than a trait-focused approach. Where the goal is a more mechanistic understanding of communities comprised of many species, especially in relation to physical geography, a functional-traits-on-gradients approach will be more successful. Sometimes, it will be important to add other factors, such as dispersal between communities [53] and extreme events [53,54], to either approach.

Our main argument has been that a focus on functional traits and gradients (Box 3) opens a path to faster progress in community ecology, but there are other benefits. An emphasis on functional relationships between quantitative variables (Box 2) feeds rapidly into the identification of general patterns and, hence, prediction. Ecologists must make predictive statements to help policy makers make informed decisions [55]. The functional trait approach should also facilitate the synthesis between community ecology and ecosystem ecology. This artificial dichotomy is often regretted [56], but rarely bridged. Mapping from morphological and physiological traits through performance currencies to communities can build links to an ecosystem-based view. Similarly, a focus on quantitative traits will enable an extension into the more historical aspects of community ecology, including community assembly [57], phylogenetic structure [13] and trait evolution [58].

Why now?

A research focus that highlights how functional traits are distributed across gradients, especially in the light of what characterizes the fundamental and realized niche, has been around in some fashion for >100 years (e.g. [25,59–61]) and probably seems obvious. In spite of this, its importance to community ecology is routinely overlooked in favor of population dynamic models of species interactions. Here, we are calling for a return to the trait and environment-focused route. The fact that authors are publicly decrying the state of community ecology [2,3]

Box 3. Future research directions

Go beyond 'How many species and why?' to ask 'How much variation in traits and why?'
From a trait-centered perspective, it is natural to see a community as a frequency distribution or histogram of trait values [15,69], but we know little about the distribution of traits within and between communities. Although suitable data have begun to accumulate [5,42,58,70–72], many questions remain. Do some communities have distinctly narrower trait ranges than others? How are the traits dispersed within a community [42]?

Go beyond 'In what environments does a species occur?' to ask 'What traits and environmental variables are most important in determining fundamental niche?'
Current habitat modeling approaches [26,73,74] seek only correlation between environment and species presence, which ignores the mapping from fundamental to realized niche and has serious limits [75]. Ecologists should measure the fundamental niche of organisms either in the laboratory [64] or in gardens [76]. We can then begin to develop a mechanistic, predictive theory of the fundamental niche.

Go beyond 'What are the most important niche dimensions?' to ask 'What traits are most decisive in translating from fundamental niche to realized niche?'
Which traits are most important in deciding outcomes in a competitive milieu and how does this vary for different types of organisms and communities? Based on present evidence, adulthood body size is the single most important trait of a species [11]. It has a strong influence on competitive dominance, on predator–prey interactions [77], and on physiological rates [78] across many types of organism.

Go beyond 'How does population dynamics determine abundance?' to ask 'How does the performance of species in the interaction milieu determine their ranking of abundance or biomass?'
As a matter of logic, abundance of a species is the product of its population dynamics; however, fast population growth potential is rarely a good guide to the abundance of a species in mixed communities. Performance in a fundamental niche setting is sometimes a good predictor of abundance [59,66,79], but the interaction milieu can modify this in currently unknown ways [79,80].

Go beyond 'How does space affect population dynamics?' to ask 'How do environmental gradients affect community structuring?'
The current interest in dispersal and landscape structure should not be pursued in idealized landscapes without environmental gradients. Such gradients must strongly affect the causes and consequences of dispersal as well as the nature of species interactions [66,79].

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suggests that the time is ripe to get back to species characterized by their traits located in a heterogeneous environment. This is especially true for two reasons. First, remote sensing, geographical information technology and the accumulation of worldwide data sets are providing community ecologists with the tools to reinvent the field. Second, the threat of global warming demands the ability to predict the effects of a changing environment on the biosphere. Approaches that ignore the environment or focus on a few species at a time cannot address this question. The functional trait-focused approach, with its emphasis on environmental gradients, traits across many

species and physiologically derived performance currencies, promises a better prospect of understanding how global warming will affect the biosphere.

Acknowledgements

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