

IDEA AND PERSPECTIVE

A structured and dynamic framework to advance traits-based theory and prediction in ecology

Colleen T. Webb,^{1,2*} Jennifer A. Hoeting,³ Gregory M. Ames,² Matthew I. Pyne² and N. LeRoy Poff^{1,2}

¹*Department of Biology, Colorado State University, Fort Collins, CO 80524, USA*

²*Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80524, USA*

³*Department of Statistics, Colorado State University, Fort Collins, CO 80524, USA*

*Correspondence: E-mail: ctwebb@lamar.colostate.edu

Abstract

Predicting changes in community composition and ecosystem function in a rapidly changing world is a major research challenge in ecology. Traits-based approaches have elicited much recent interest, yet individual studies are not advancing a more general, predictive ecology. Significant progress will be facilitated by adopting a coherent theoretical framework comprised of three elements: an underlying trait distribution, a performance filter defining the fitness of traits in different environments, and a dynamic projection of the performance filter along some environmental gradient. This framework allows changes in the trait distribution and associated modifications to community composition or ecosystem function to be predicted across time or space. The structure and dynamics of the performance filter specify two key criteria by which we judge appropriate quantitative methods for testing traits-based hypotheses. Bayesian multilevel models, dynamical systems models and hybrid approaches meet both these criteria and have the potential to meaningfully advance traits-based ecology.

Keywords

Bayesian multilevel models, dynamical systems models, dynamics, environmental gradient, performance filter, quantitative methods, structure, trait distribution, traits-based approaches.

Ecology Letters (2010) 13: 267–283

INTRODUCTION

Ecologists have long struggled with the challenge of predicting changes in species composition and associated changes in ecosystem function across space and through time. A promising avenue for addressing this challenge is to use traits-based approaches, i.e. characterizing organisms in terms of their multiple biological attributes such as physiological, morphological, or life history traits. These approaches are applicable to a range of systems because they are taxon independent and because traits can be linked directly to the environment, thus facilitating mechanistic prediction across environmental gradients (McGill *et al.* 2006; Westoby & Wright 2006; Green *et al.* 2008).

Traits-based approaches have a long history in community ecology (e.g. Grime 1977; Southwood 1977; Connell 1978). Many of these early papers focused on developing conceptual models of how qualitatively described life history traits vary along environmental selection gradients. These efforts were followed by traits-based approaches that sought to develop more quantitative frameworks to

model trait–environment relations to predict species presence/absence (e.g. Keddy 1992; Weiher & Keddy 1995) or abundance (e.g. Chesson *et al.* 2002). More recently, there has been a revival of interest in the development of traits-based approaches spurred by the desire to bridge the historical gap between community and ecosystem ecology (McGill *et al.* 2006; Enquist *et al.* 2007; Green *et al.* 2008). Currently, ecologists are increasingly emphasizing the need to predict how communities and ecosystem function will respond to rapid environmental change, including climate change (e.g. Thuiller *et al.* 2007; Morin & Lechowicz 2008). Traits-based approaches are well suited to this challenge. The recent advances in quantitative traits-based approaches have been touted as both bringing a predictive basis to community ecology and providing stronger theoretical linkages between community and ecosystem ecology. Such hopeful claims for the potential of traits include moving toward a ‘new synthesis of evolutionary, community and ecosystem perspectives’ (Tilman 2001) and even uncovering potential laws in ecology (McGill *et al.* 2006).

Not surprisingly, the potential of traits-based approaches has stimulated interest in reanalysing existing trait datasets and in collecting new data to test many scientifically and socially relevant ecological questions (for examples, see Kolar & Lodge 2001; Norberg *et al.* 2001; Chesson *et al.* 2002; Loreau *et al.* 2003; Naeem & Wright 2003; McGill *et al.* 2006; Olden *et al.* 2006; Shipley *et al.* 2006; Savage *et al.* 2007; Cornwell & Ackerly 2009; Kearney & Porter 2009). The rapid increase in the application of traits-based approaches in the last decade is impressive, as are the many associated conceptual advances in analysing complex trait data. However, despite this progress, we argue that this cumulative body of work cannot be viewed as comprising a coherent foundation for advancing a predictive, traits-based ecology. We suggest that traits-based ecology is at a critical juncture where further advances require an intentionally coherent and integrative framework that can transparently support hypothesis formulation and data collection. We also propose that such a framework should guide development of quantitative approaches that can appropriately analyse the implicit structure of trait data, as this will allow for maximum justifiable inference and prediction. Such a framework should integrate across the many fields that bear on traits-based approaches, including community ecology, ecosystem ecology, evolutionary biology, quantitative genetics, statistics and dynamical systems. Further, it should reveal the underlying commonality of traits-based approaches in community and ecosystem ecology, two active areas of traits-based research. A wide variety of methods and approaches have been developed in these arenas to answer different types of questions, and the numerous traits-based studies arguably give the cumulative impression of an ad hoc collection of system-specific examples, rather than a body of literature organized around unifying principles.

Our goal here is to articulate the shared conceptual foundation among traits-based approaches in ecology, in order to develop a more integrative, theoretical and multi-dimensional framework for advancing this field. Central to this framework is the general proposition that a more transparent traits-based theory is needed, one that can support hypothesis testing and prediction. To achieve this, we argue that trait–environment linkages are best conceptualized in an explicitly structured fashion where trait distributions within communities or ecosystems respond dynamically to environmental gradients across space or time. The hierarchically structured and dynamic nature of the trait–environment relationship necessarily constrains the mathematical or statistical structure of quantitative approaches that are appropriately suited to support rigorous hypothesis testing and prediction, a fact not widely appreciated or reflected in the current traits literature. We argue that new model development is needed to fully exploit

the power of traits-based approaches. Ultimately, we aim to develop a framework that will broadly engage ecologists by linking the underlying concepts of trait–environment relationships to quantitative approaches that can illuminate the fundamental principles of a predictive traits-based ecology.

THE CONCEPTUAL FOUNDATION: ENVIRONMENTAL FILTERING OF TRAIT DISTRIBUTIONS

Here, we frame a conceptual foundation for traits-based approaches, one that explicitly unites questions about community and ecosystem ecology and that can be mapped directly to available and developing quantitative methods for trait data. We follow McGill *et al.* (2006) in using ‘trait’ to mean a well-defined, measurable property of organisms, usually measured at the individual level and used comparatively across species. A ‘functional trait’ (our focus here) is one that strongly influences an organism’s performance or fitness. As discussed below, trait-based approaches based on the functional trait concept have a strong grounding in evolutionary biology and quantitative genetics (Lande 1976, 1979; Turelli & Barton 1994).

Our conceptual foundation consists of three primary elements: trait distributions, performance filters and environmental gradients (see Table 1). First, the trait distribution is initially derived from the pool of possible traits of individual organisms. The contributing pool can be described by its functional trait distribution, which is a statistical distribution describing the frequency or probability of occurrence within the pool for each value or category of trait (Fig. 1). Because traits are defined at the individual level, the trait distribution incorporates both intraspecific variation and community composition. Trait distributions may be univariate, describing only one relevant trait, or multivariate, describing multiple and potentially interacting traits.

Second, the performance of a trait is an expression of its fitness in a given environment, i.e. the local environment acts as a ‘performance filter’ to eliminate traits with inadequate local fitness. A well-established tenet of evolutionary biology is that organismal performance is a function of the environment in which it is measured. For example, a plant with high water use efficiency will have high performance in a xeric setting but a neutral or low performance in a mesic setting. Thus, the performance filter reflects a mechanistic relationship or linkage between the trait(s) and the environment. Most simply, this relationship can be quantified empirically in a regression framework. Alternatively, a description of the performance filter could be based more mechanistically on first-principles understanding of trait response to the environment. By

Table 1 Glossary of terms

Term	Definition
Trait distribution	Statistical distribution describing the frequency or probability of occurrence within the pool of possible traits for each value or category of trait
Performance filter	Function relating performance to trait values and the environment (as performance is a function of the environment in which it is measured). May consist of multiple, correlated traits and drivers
Environmental gradient	Values that the environmental driver(s) take on in space and/or time
Structured	In this context, an approach that recognizes the role of the environment in filtering the trait distribution
Dynamic	In this context, an approach that takes into account changes in the trait distribution (or biodiversity) over time and/or space
PBM	Phenomenological Bayesian multilevel models
FDM	First principles dynamical systems models
FBM	First principles Bayesian multilevel models

eliminating traits that do not match environmental conditions from the available trait pool, the performance filter determines the distribution of traits in a particular location

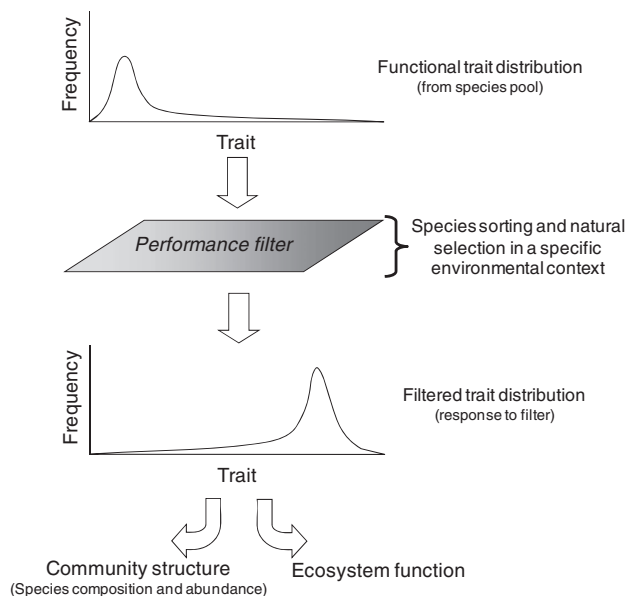


Figure 1 Relationship between trait distributions and performance filters. The functional trait distribution (for a continuous trait) is drawn from the contributing pool of individuals, and in this example, individuals with low trait values occur with high frequency. The functional trait distribution is filtered by the environment based on performance (the match between the trait and the environment) via natural selection and/or ecological sorting at a particular space/time location. In this example, the performance filter favours individuals with higher values of the trait and the resulting filtered trait distribution is shifted towards higher trait values. The filtered trait distribution can then be used to predict changes in either ecosystem function or species composition and abundance. This figure shows a single application of the performance filter, but in reality the performance filter is applied continually or iteratively in space or time.

in space or time (Fig. 1). For example, in a xeric environment the filtered trait distribution will consist of mainly water efficient individuals. At the level of individuals, environmental filtering occurs through the process of natural selection, because traits are associated with individuals within species. Thus the filtering process acting on a trait distribution is closely analogous to quantitative genetics theory in evolutionary biology where natural selection filters the trait distribution within a population (e.g. Lande 1976). In our conceptual foundation, we apply this analogy not only to individuals within populations but we extend it to include the distribution of traits and the filtering process both at the population and at the species level within a whole community. In other words, at the community level environmental filtering also occurs in the form of ecological or species sorting processes.

A key point to recognize is that the performance filter has an explicitly hierarchical or ordered structure: the environment acts to filter the trait(s) and thus creates a filtered trait distribution that can be applied broadly to ecological questions (Fig. 1). In other words, a catalogue of species traits theoretically allows for a back calculation from the filtered trait distribution to potential species composition and abundance. Likewise, a mechanistic understanding of the trait–ecosystem function relationship allows the same type of back calculation from the filtered trait distribution to estimates of ecosystem function.

Despite the fundamental importance of performance filters, scant empirical evidence exists to judge the functional form they may take. A mature traits-based approach should address this question. Are performance filters relatively simple with a single optimal value or are they complex with multiple optima and minima (Marks & Lechowicz 2006; Violle *et al.* 2007)? Can ecological performance generally be predicted by a single or just a few traits, or are many traits required? Are particular types of traits (e.g. physiological, life history) the best predictors? These questions about the nature of the trait–environment relationship mirror the

adaptive topography debate in evolutionary biology (Fisher 1930; Wright 1931), like other recent ecological debates (Tilman 2004; Hubbell 2006).

A third element of our conceptual foundation is the ‘projection’ of the performance filter across some environmental gradient(s) in space or time to make predictions. In other words, because trait performance varies with environmental context (Fig. 2a), the trait–environment relationship can be used to predict the filtered trait distribution at different points in space and time. The more mechanistically based the trait–environment relationship, the more confidently it can be projected along environmental gradients that extend beyond the range of empirical data used to define the performance filter.

For example, if the trait in Fig. 2 is water use efficiency (illustrated in Fig. 2 as transpiration cost, with lower values indicating greater efficiency), performance would be high in a water-limited environment (Fig. 2b) and there would be a strong filter for this trait (Fig. 2c). By contrast, in a more intermediate environment where neither low nor high water use efficiency is favoured (Fig. 2d), the filtered trait distribution would deviate little from the available trait pool (Fig. 2e). Importantly, a nonlinear performance filter can result in differential filtering along this gradient, producing a surprising disconnect between our intuition about traits and the way that performance filters play out across environmental gradients. This disconnect may be magnified when aggregation of traits from the individual to species to community level occurs, as illustrated in Fig. 2f and g, because community level derived performance filters may be inaccurate. We discuss the interpretation of Fig. 2f and g and the implications of this nonlinearity for data collection in the Data constraints section.

Our conceptual foundation of trait distributions, performance filters and projection across environmental gradients offers a general and coherent basis for developing traits-based theory and unifying varying approaches to empirical traits-based studies.

Translating the conceptual foundation into a quantitative framework: structure and dynamics

Simple hierarchical structure and dynamics are the two properties of the conceptual foundation that are central to translating the foundation into a framework that can support quantitative analysis and prediction in traits-based studies, as depicted in Fig. 3. A hierarchically structured environment–trait relationship (i.e. the performance filter) is straightforward for ‘response traits’ (*sensu* Díaz & Cabido 2001), which capture organisms’ reactions to environmental conditions and thus do not directly translate into an ecosystem process (e.g. tolerance to toxins or response to habitat change). The structure is more subtle for ‘effects

traits’ (*sensu* Díaz & Cabido 2001; see Suding *et al.* 2008), which actually induce a change in environmental conditions. For example, photosynthetic rate varies in response to light energy and translates into plant production that creates biomass that can create shade and reduce available light energy. Effects traits incorporate the feedback of organisms on their environment, and this is a vital component of many ecosystem studies. A hierarchical structure still exists for effects traits, but this feedback can modify the environmental gradient over which the performance filter acts and thus alter expected trait distributions.

Predicting filtered trait distributions based on projection of the performance filter across an environmental gradient implies a dynamic process, i.e. the trait distribution changes in space or time. Understanding these trait dynamics is of particular interest because, in contrast to the environmental changes that most species and ecosystems have historically experienced, current global change is occurring over relatively short evolutionary time scales and large spatial scales, resulting in strong selection for rapid changes in species composition. Indeed, several studies report surprisingly rapid changes in community composition and functional diversity in response to changes in the local environment (Tilman & Downing 1994; Pfisterer & Schmid 2002; Pounds *et al.* 2006). Therefore, it is critical that any framework intended to better explain the response of species composition/abundance and ecosystem function to environmental change should be able to address the effects of accompanying changes in the underlying trait distribution over time and/or space.

Specifying a quantitative framework to support traits-based prediction

The structured and dynamic properties of the conceptual foundation (Figs 1–3) provide specific criteria by which quantitative methods can be identified for robust hypothesis testing. Basically, quantitative methods should explicitly incorporate both a description of the performance filter (e.g. structured trait–environment relationship) and a technique for projecting the filter across environmental gradients to predict changes in the trait distribution (dynamics). Additionally, the methods should be able to incorporate the feedback of organisms to the environment when needed (i.e. via effects traits).

Incorporating these criteria necessitates the formulation of a quantitative framework that incorporates the conceptual scientific foundation illustrated in Fig. 3. The value of this framework is that it generates an explicit relationship between the results of a given empirical study and the more general predictions of the underlying conceptual foundation of a dynamic, environmental filtering process across space and time. This structured quantitative framework therefore

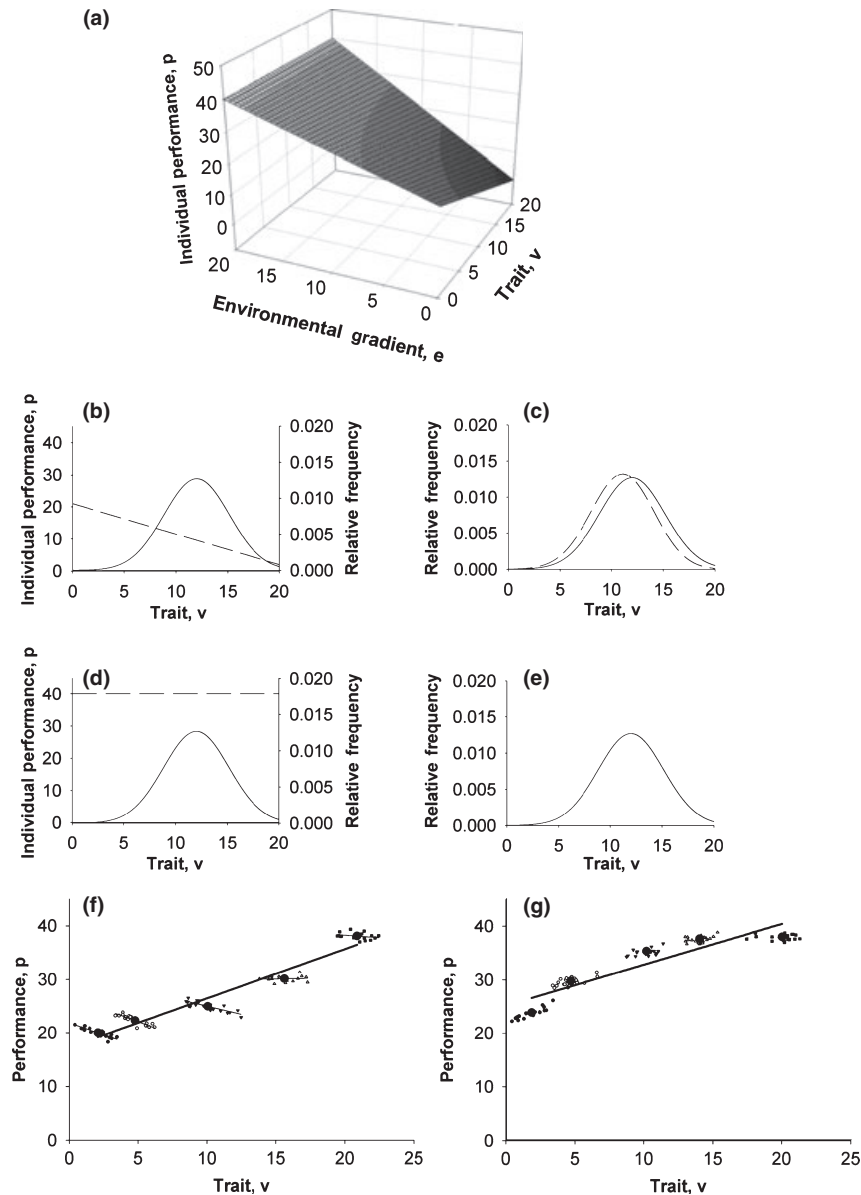


Figure 2 The performance filter can interact with the environmental gradient. (a) The performance filter that describes the relationship between traits and individual performance can change as a function of the environmental gradient resulting in a surface relating traits and environment to individual performance. Here, an illustrative surface is described by the function $p = -\frac{20-e}{20}v + 2e + 20$. (b) The trait distribution (solid line, associated with the relative frequency y -axis) and performance filter (dashed line, $p = -\frac{20-e}{20}v + 22$, associated with the individual performance y -axis) at location 1 on the environmental gradient ($e = 1$). (c) The original trait distribution (solid line) and the filtered trait distribution (dashed line) resulting from application of the performance filter in (b) over one generation. (d) The trait distribution (solid line, associated with the relative frequency y -axis) and performance filter (dashed line, $p = 40$, associated with the individual performance y -axis) at a second location on the environmental gradient ($e = 20$). (e) The original trait distribution (solid line) and the filtered trait distribution (dashed line) resulting from application of the performance filter in (d). The two distributions are indistinguishable from one another because the performance filter is flat. (f) Demonstration of specification bias. The performance filter measured at the individual and community levels for the surface in (a). Individual level: small symbols and associated regression lines indicate the performance filters measured at the individual level within a community at different points along the environmental gradient ($e = 1, 5, 10, 15, 20$ from left to right). Community level: large, filled circles represent the mean performance and mean trait value. The community level regression line is in the opposite direction to the performance at the individual level (specification bias). (g) Demonstration of aggregation bias: the performance filter measured at the individual and community level (similar to the function in (a), but with positive slope in the Trait direction). Symbols as in (f). The community level regression line suggests a stronger correlation than the observed data (aggregation bias).

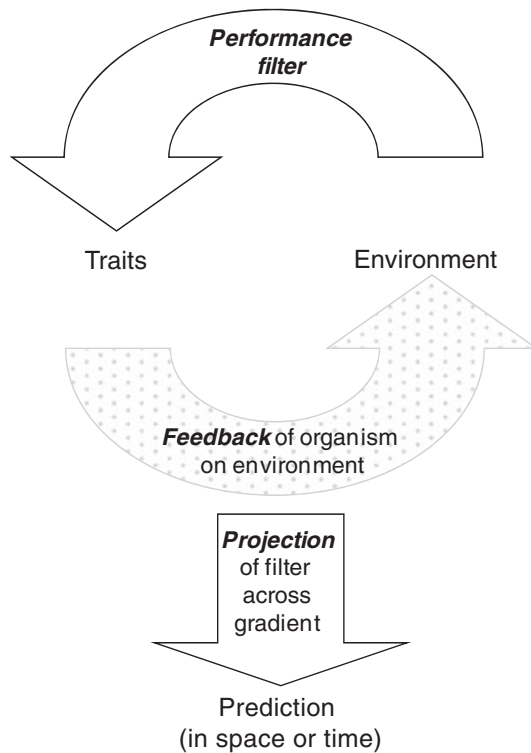


Figure 3 The multilevel quantitative framework reflects the hierarchical, structured action of the performance filter on traits (solid curved arrow) and can incorporate feedback of effects traits back to the environment (dotted curved arrow). This trait–environment relationship or performance filter is projected across an environmental gradient by statistical or mathematical models to predict the changes or dynamics of trait distributions through space or across time.

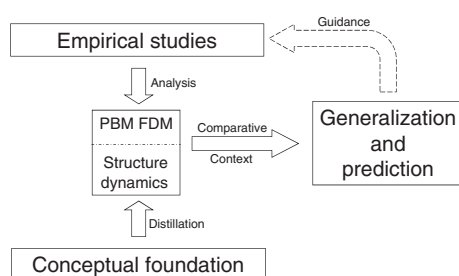


Figure 4 The quantitative framework maps empirical studies to a traits-based conceptual foundation. The conceptual foundation can be distilled to two key components: structure and dynamics. Appropriate quantitative methods, such as phenomenological Bayesian multilevel models (PBM) and first principles dynamical systems models (FDM) incorporate both structure and dynamics in a quantitative framework. When empirical studies are analysed using such methods, they can be linked to the conceptual foundation and in a comparative context can thus result in greater generalization and development of predictive traits-based ecological theory.

acts as a kind of Rosetta stone, i.e. it provides a critical intermediate step that allows empirical data to be translated into coherent examples that are consistent with the underlying conceptual foundation and theory (Fig. 4). This quantitative framework thus enables creation of comparable measures of performance filters and dynamics that allows for a comparative approach across study systems. For example, a better understanding of how the bounds on ecosystem functioning are set by different trait distributions, performance filters and environmental gradients would enhance our ability to confidently predict ecosystem processes and states under altered or novel conditions. The ability to translate and integrate diverse studies into a comparative framework is needed to advance traits-based ecology.

QUANTITATIVE APPROACHES FOR TRAITS-BASED ANALYSES

A variety of quantitative approaches have been used to relate traits and environmental variables via performance to the response of interest (e.g. species composition and abundances, ecosystem function). These include permutation tests (Legendre *et al.* 1997; Dray & Legendre 2008), basic regression or general linear models (Reich *et al.* 2003), statistical mechanics models (Shipley *et al.* 2006), Bayesian multilevel models (Gelman *et al.* 2004; Latimer *et al.* 2004, 2006; Gelfand *et al.* 2005, 2006) and dynamical systems models (Norberg *et al.* 2001; Chesson *et al.* 2002; Loreau *et al.* 2003; Savage *et al.* 2007). The methods that best reflect our conceptual foundation by naturally incorporating both a structured performance filter and projecting it dynamically are statistical mechanics models, Bayesian multilevel models and dynamical systems models. These methods, while mathematically sophisticated, are still maturing. They have great appeal because they both incorporate the complex and extensive information contained within a trait distribution and accurately describe or predict how such distributions change along environmental gradients.

Although lacking appropriate structure or dynamics, traditional statistical approaches remain useful in reducing the complexity of trait data sets (Bernhardt-Römermann *et al.* 2008). For example, principle components analysis reduces the number of traits/environmental drivers used in dynamical systems by removing highly correlated traits or drivers that do not contribute unique information to the analysis. General linear models provide insight into which environmental drivers and traits are important players in the performance filter, and such models can be used for prediction as long as the limits on inference are correctly acknowledged. In fact, there has been a substantial effort to identify correlations between plant traits along environmental gradients that could inform the traits and environ-

mental drivers needed within a traits-based framework (Wright *et al.* 2004; Westoby & Wright 2006; Reich *et al.* 2007). However, we view these traditional statistical methods as being mostly appropriate for exploratory data analysis in a traits-based approach (see Box 1). We note in particular that basic linear regression methods do not include dynamics allowing predictions over space and time because they ignore the interaction between the filter and environmental gradient (unlike Fig. 2) by assuming a constant performance filter.

Here, we focus on Bayesian multilevel models and dynamical systems models. We do not consider statistical mechanics models such as that of Shipley *et al.* (2006) because they lack a clear mechanistic linkage of traits and environment (performance filter) (Marks & Muller-Landau 2007; Roxburgh & Mokany 2007; Shipley *et al.* 2007). Frequentist methods are available to analyse some of the models proposed below, but for many of the models

considered here, Bayesian methods afford a general framework incorporating both parameter estimation and improved estimates of uncertainty. Bayesian multilevel models have traditionally been applied to answer species composition and abundance questions (often across spatial gradients), whereas dynamical systems models have traditionally been applied to answer ecosystem function questions (often in the context of temporal change). Below, we describe each method in more detail and propose an integrated approach with many of the benefits and few of the detriments of the original methods. One size will not fit all, and the choice of quantitative approach will vary to some degree with study system, information content of the trait data available and, of course, the biological question. Nonetheless, the methods we propose here meet an important requirement of consistency with the conceptual foundation. In Box 1, we explore a conceptual example to demonstrate how decisions regarding quantitative approaches might be made.

Box 1 Where to begin with a structured and dynamic traits-based approach? A conceptual example

Motivation

In order to illustrate how a dataset might be analysed using the structured and dynamic traits-based approach, we present a conceptual example. Here, we consider a hypothetical study conducted in a grassland community, where specific traits and environmental drivers can be measured and subjected to the analytical procedures shown in Table 2 and Fig. 5. (The A, B and C below correspond to columns A, B and C in Table 2). The main goal of the study is to predict changes in species abundance and distribution, as well as ecosystem function, under climate change. The hypothetical example offered here can be applied to any number of other ecosystem types.

Data

Consider greenhouse data where a number of traits are measured at the species level for multiple species of annual and perennial grasses that are important contributors to community structure and ecosystem function. Biomass of these species, a measure of performance, is also available from field measurements taken across multiple years. Temporal environmental data are available from climate stations close to where the biomass estimates were made. Ideally, data on traits, performance and environmental drivers would be collected at the same time and at the same location, and trait data should be measured at the individual level and include individual level variability. However, in this example, species level trait data are all that are available, both from the greenhouse experiments and from the literature. Reich *et al.* (2003) provide an example of such data with 14 traits measured for 34 species. Examples of similar data sets for other systems can be found in the literature (e.g. Wright *et al.* 2004; Poff *et al.* 2006; Craine *et al.* 2007).

Data choices and pre-analysis

In this example, traits that are thought to mechanistically contribute to performance were measured. Within the group of 14 traits, many traits are correlated with one another and mostly fall into categories related to relative growth rate (RGR), photosynthetic rate and respiration rate (Reich *et al.* 2003). Principle components analysis (PCA) can be used to eliminate traits that are highly intercorrelated and reduce the number of traits used in the analysis. Similarly, a large number of potential environmental variables are also available from the climate stations and from various GIS layers. Again, correlation analysis or PCA can be used to reduce this large set of environmental variables to a smaller set of mechanistic drivers including for example, average (or extreme) temperature during the growing season and early season precipitation totals.

Box 1 *continued*

For an initial pass, we start by choosing traits that are known to correlate well with performance from other studies. So here, we start with relative growth rate (RGR), an aggregate trait that provides proof-of-concept. Once the ability to predict performance using RGR and the environmental variables has been established, more highly mechanistic, component traits (e.g. photosynthetic rate and respiration rate), can be incorporated.

Part A. Phenomenological Bayesian multilevel models (PBM) analysis

Following pre-analysis, we expect PBM may be the next step in two situations: (1) for prediction within the current data range or (2) where mechanisms or trait response to environmental variables are poorly understood. A multinomial model is appropriate for this example because parameters regulating RGR (or the component traits) for all species in the community are estimated simultaneously, and some competitive interactions are implicitly incorporated due to the constraints applied by multinomial assumptions. If we have adequate, *a priori* knowledge of trait–environment linkages, we can implement a multivariate version of the type of multinomial PBM described in Table 2, column A with output similar to Fig. 5a and d to predict the filtered trait distribution (i.e. the biomass distribution associated with RGR values). PBM predictions are phenomenological and inference is usually restricted to the data range used. However, assuming we lack sufficient confidence in the trait–environment linkages that relate to performance, we can generate sets of traits and drivers hypothesized to be important and use model selection techniques (e.g. Akaike Information Criterion) to determine the most appropriate choice from our model set. In our own laboratory, we have used data similar to this conceptual example and a model selection approach to predict the temporal trajectory in biomass for each trait value in a grassland community over a twenty-five year period using RGR and three environmental drivers (unpublished data). Following this proof of concept, the next step is to add an additional layer to the PBM in which component-specific traits (e.g. photosynthetic rate and respiration rate) are used to predict the aggregate RGR.

Part B. First principles dynamical systems model (FDM) analysis

FDM can be used directly following pre-analysis if the traits and drivers important in the system are well known. Otherwise PBM and model selection can be valuable steps in establishing which traits and drivers are related and predictive of performance. In our conceptual example, FDM is a logical step to follow the PBM analysis since we are interested in exploring our mechanistic understanding of the system and because we want to project how the system would behave outside the measured range of parameter values. In this example, we want to predict changes in biomass or species richness under different climate change scenarios. Here, the traits and drivers identified using PBM are combined in a mechanistic performance filter, where photosynthetic rate and respiration rate are related to performance along an environmental gradient driven by predicted changes in average temperature and early season precipitation under climate change scenarios. The form of the performance filter (e.g. linear, saturating, nonlinear) is based on the ecophysiological literature describing the relationship between photosynthesis, respiration and temperature and water availability. Using a multivariate version of the approach described in Table 2, column B, we could generate predictions for the temporal trajectory in biomass for each combination of trait values (photosynthetic rate and respiration rate) under climate change scenarios (such as the output described in Fig. 5b and e). Like PBM, model selection can be used to test different hypotheses about the shape of the mechanistic relationship.

Part C. First principles Bayesian multilevel models (FBM) analysis

FBM can be used directly following pre-analysis if traits, drivers *and* their mechanistic relationship are all well known. A likely outcome is that FBM is used as a final step following either PBM or FDM (or their sequential application), because traits-based problems can be complex and require several layers of investigation. We expect that FBM can be used for either prediction or mechanistic exploration of systems, but the possibility of inferring prediction beyond the range of the data needs further support (see discussion in text). In our conceptual example, we would use photosynthetic rate, respiration rate, average temperature and early season precipitation in a multivariate version of the model described in Table 2, column C. As noted in Table 2 column C and in contrast with the FDM model described above in Box 1 part B, we would need to use discretized versions of the first principles models in order to be able to fit the resulting model. We would use the same type

Box 1 *continued*

of performance function (e.g. based on ecophysiological relationships) described above for FDM. This approach would provide similar results to the PBM and FDM in terms of biomass predictions, but it could do so under climate change scenarios while still providing credible intervals (similarly to Fig. 5c and f).

Interpretations for community and ecosystem ecology

As with any analytical approach, standard methods for validation should be applied before making valid inference. Once a validated trait distribution is available, the final step in many cases will be to relate it back to species distribution and abundance or to ecosystem function. In our conceptual example, this is straightforward. Because each species has a unique combination of photosynthetic rate and respiration rate, species richness (i.e. Shannon's index) can be directly calculated from the filtered trait distribution. Using the PBM approach, we can predict temporal changes in this trait-inferred species richness over some period (as we have done in our own, unpublished research using RGR alone) and thus potentially rank the relative contribution of each trait and driver to these changes. From an ecosystem perspective, the changes in the size of the trait distribution can naturally be interpreted as changes in total biomass. For many of these species, rates of carbon or nitrogen fixation are known (or the correlation of C and N fixation with photosynthetic rate), so total, or at least relative, changes in carbon and nitrogen fixation could also be predicted based on the changes in the trait distribution. The potential for aggregation bias to affect these results should be acknowledged since the data were collected at the species level.

Bayesian multilevel models for species composition and abundance

Bayesian multilevel models (sometimes called Bayesian hierarchical models, Gelman *et al.* 2004; Gelman & Hill 2007) offer an attractive framework for making probability-based inferences about the relationship between traits and environment. Bayesian models have been used to estimate mechanistically important trait values from traits that are less directly informative but easier to measure (McCarthy *et al.* 2008); to estimate extinction risk based on traits, but without an environmental component (Williams *et al.* 2005); to estimate the performance filter (Billheimer *et al.* 1997, 2001; Johnson *et al.* 2006; Kühn *et al.* 2006); and to investigate the impact of environmental factors on abundance (Ver Hoef & Frost 2003; Thogmartin *et al.* 2004; Diez & Pulliam 2007; Murray *et al.* 2008). More sophisticated models encompass all three components of Fig. 3 by relating traits to the environment and predicting how the spatial distribution of traits would translate into the presence/absence of plant species (Latimer *et al.* 2004, 2006; Gelfand *et al.* 2005, 2006; Dorrough & Scroggie 2008). In studies that estimate the performance filter, it is described phenomenologically using traditional statistical methods (e.g. linear regression) to estimate the relationship between trait data and environmental variables within a Bayesian multilevel framework (see Table 2, column A, for model structure, the associated schematic example shown in Fig. 5a for hypothetical results, and Box 1 part A).

An attractive feature of such phenomenological Bayesian multilevel models (PBM) is that they can simultaneously

estimate both the parameters associated with the performance filter (e.g. estimate the relationship between traits and environment) and project the filter (e.g. predict the estimate of the trait distribution over time or space) (Table 2 and Fig. 5d). Because PBM estimate parameters and provide prediction simultaneously, they provide automatic estimates of uncertainty for all parameters. In contrast, most non-Bayesian approaches use a two-step procedure that ignores uncertainty in the initial regression relationship when it is projected. Estimates of uncertainty are particularly important when observed data on traits and environmental variables are acquired from different sources with different levels of observation error.

A second significant advantage specific to PBM is that they can be broadly applied, because they do not require *a priori* knowledge of the mechanisms that relate traits and environmental variables and define the performance filter. The multilevel nature of Bayesian modelling means that the model can still naturally reflect known causal hierarchies in the data (e.g. metabolic rate is affected by ambient temperature, not vice versa). Further, PBM can easily incorporate synergies among multiple traits and multiple environmental drivers, and they have already been shown to provide accurate predictions for real systems (Gelfand *et al.* 2005, 2006).

A disadvantage of the PBM approach is that the models can be so closely tied to the observed data that they perform poorly when making predictions outside this range. This is not necessarily due to overfitting which can be overcome through improved statistical modelling, but is due to the fact that the phenomenological Bayesian models are not based on sound ecological theory. In comparison, mathematical models based

Table 2 Comparison of proposed quantitative methods and their relationship to the performance filter and its projection. The examples presented could provide results such as shown in Fig. 5

A. Phenomenological Bayesian multilevel models (PBM)	B. First principles dynamical systems models (FDM)	C. First principles Bayesian multilevel models (FBM)
Describing changes in the trait distribution		
1. Use a likelihood to relate an observed response that measures the frequency of the trait to the probability of observing the response. E.g. $Y_{i,t} \sim \text{Multinomial}(p_{i,b}, N)$ where $Y_{i,t}$ = observed relative abundance of plants of type i at time t $p_{i,t}$ = the probability of observing plants of type i at time t (further described in A2) N = the total number of plants	1. Use differential equations to relate the performance filter to a measure of the changes in the frequency of the trait over time. E.g. $\frac{dC_i}{dt} = C_i f(x_i, E)$ $\frac{dE}{dt} = g(E)$ where $C_i(t)$ = predicted abundance of plants of type i at time t (similar to $Y_{i,t}$ in A1 and C1) $\frac{dC_i}{dt}$ = change in the abundance of plants of type i over time $f(x_i, E)$ = performance filter (further described in B2) $g(E)$ = function that describes changes in the environmental driver, $E(t)$, such as a function fit to environmental driver data	1. Use a likelihood to relate an observed response that measures the frequency of the trait to the probability of observing the response (similar to A1). E.g. $Y_{i,t} \sim \text{Multinomial}(p_{i,b}, N)$ where $Y_{i,t}$ = observed relative abundance of plants of type i at time, t $p_{i,t}$ = the probability of observing plants of type i at time t (further described in C2) N = the total number of plants
Performance filter		
2. Observed trait and environmental covariates are related to the probability of observing the response. This is the performance filter and is usually described using linear or logistic regression. E.g. $p_{i,t} = \beta_0 + \beta_1 x_i + \beta_2 E_i + \beta_3 x_i E_i + \epsilon$ where β = parameters of the regression x_i = trait for type i , e.g. water use efficiency E_i = environmental covariate/driver, e.g. soil moisture $x_i E_i$ = interactions between the trait and the environment ϵ = error term	2. Observed traits and environmental data are related to per capita performance in a mechanistic function. Other relevant factors, such as growth rate or competitive effects, can also be included in the per capita performance function. E.g. $f(x_i, E) = r \left(\frac{x_i}{x_i + 1/E} \right)$ where x_i = trait for type i , e.g. water use efficiency (where large x_i signifies high efficiency) E = environmental driver/covariate e.g. soil moisture r = other relevant factor, e.g. per capita growth rate	2. Observed trait and environmental covariates are related to the probability of observing the response. This incorporates the performance filter and is basically a discretized version of the change in the abundance of plants of type i over time, $\frac{dC_i}{dt}$. Thus this contains aspects of A2 and B2 by including both the mathematical model for abundance within the statistical model which allows for data-driven parameter fitting. See also Box 1, part C. E.g. $p_{i,t} = \beta u_i + \epsilon_i$ where β = fitted parameter of the model u_i = discretized version of $\frac{dC_i}{dt}$ (described in B1 and B2) using Runga-Kutta or other standard discretization algorithms. Environmental covariates, such as E_i , can be incorporated instead of using an equation such as $\frac{dE}{dt}$ ϵ_i = error term

Table 2 continued

A. Phenomenological Bayesian multilevel models (PBM)	B. First principles dynamical systems models (FDM)	C. First principles Bayesian multilevel models (FBM)
<p>Prior knowledge</p> <p>3. Prior distributions on parameters and error term are defined that may incorporate previously collected data or expert opinion. E.g. $\beta \sim \text{Normal}(0, \sigma^2)$ could be an uninformative prior for any of the βs. A similar prior could be used for ϵ.</p>	<p>3. No prior information is incorporated.</p>	<p>3. Prior distributions on parameters and error terms are defined that may incorporate previously collected data or expert opinion. E.g. $\beta \sim \text{Normal}(0, \sigma^2)$ could be an uninformative prior for β. A similar prior could be used for ϵ_t and any other parameters that are estimated (similar to A3).</p>
<p>Prediction method</p> <p>4. Model fitting using Markov chain Monte Carlo (MCMC; Givens & Hoeting 2005) allows estimation of βs and credible intervals. Prediction is possible by calculating $p_{i,t}$ for different E_t within the observed range of E_t.</p>	<p>4. Prediction occurs through numerical estimation of the solution of $\frac{dC}{dt}$ and $\frac{dE}{dt}$ for each of the i types using a standard numerical analysis algorithm. The solution estimates how C_i changes through time given the changes in the environmental driver, E.</p>	<p>4. Model fitting using Markov chain Monte Carlo (MCMC; Givens & Hoeting 2005) allows estimation of parameters, such as τ, and credible intervals. Prediction is possible by calculating $p_{i,t}$ for different values of E_t of interest. The use of a model based on first principles allows for model predictions based on E_t values outside the observed range of E_t (compare to A4).</p>

on first principles (e.g. underlying mechanistic relationships) can in principle be used to predict under future environmental conditions outside the range of observed data.

Dynamical systems approaches and ecosystem function

Dynamical systems models offer an attractive framework for incorporating a mechanistic performance filter derived from first principles (e.g. Norberg *et al.* 2001; Chesson *et al.* 2002; Falster & Westoby 2003; Loreau *et al.* 2003; Tilman 2004; McGill & Brown 2007; Savage *et al.* 2007; Vincent & Vincent 2009). This is particularly true in ecosystem function applications where the relationship between trait data and environmental variables is frequently gained from experimental manipulations that allow for strong inference about mechanism. In contrast to PBM, a sequential, two-step approach is used in applying dynamical systems models to traits. In step 1, either phenomenological relationships (e.g. Craine *et al.* 2002; Reich *et al.* 2003) or, more appropriately for mechanistic inferences, first principles can be used to characterize the performance filter (Enquist *et al.* 2007). See Table 2 column B and Box 1 part B. A schematic of a mechanistic performance filter is shown in Fig. 5b. In step 2, dynamical systems approaches (i.e. comprised of ordinary differential equations) project the performance filter temporally (Norberg *et al.* 2001; Chesson *et al.* 2002; Loreau *et al.* 2003; Savage *et al.* 2007) as illustrated in Table 2 column B and Fig. 5e. Dynamical systems models so far have used mechanisms derived solely from first principles (first principles dynamical systems models; FDM) and are highly theoretical.

The greatest strength of FDM is the ability to explicitly incorporate mechanistic performance filters describing relationships among traits and their response to the environment. This approach allows the performance filter mechanism to be projected outside the original data range to generate predictions. This characteristic also allows for hypothesis generation even in the absence of observed data required for model validation. Further, analytical results produced by FDM can provide important insights into long standing ecological questions and theory. For example, analytical results show that negative correlation among traits helps maintain system biomass and biodiversity because optimal values for all traits cannot be obtained, inducing larger trait variances that allow for a relatively rapid response to environmental changes (Savage *et al.* 2007).

The promise of FDM approaches to employ performance mechanisms developed from first principles to predict current data from natural systems is high (Enquist *et al.* 2007); however, their ability to be projected into the future to generate accurate predictions remains to be validated. Finally, FDM approaches do not generate measures of uncertainty like Bayesian multilevel models, although

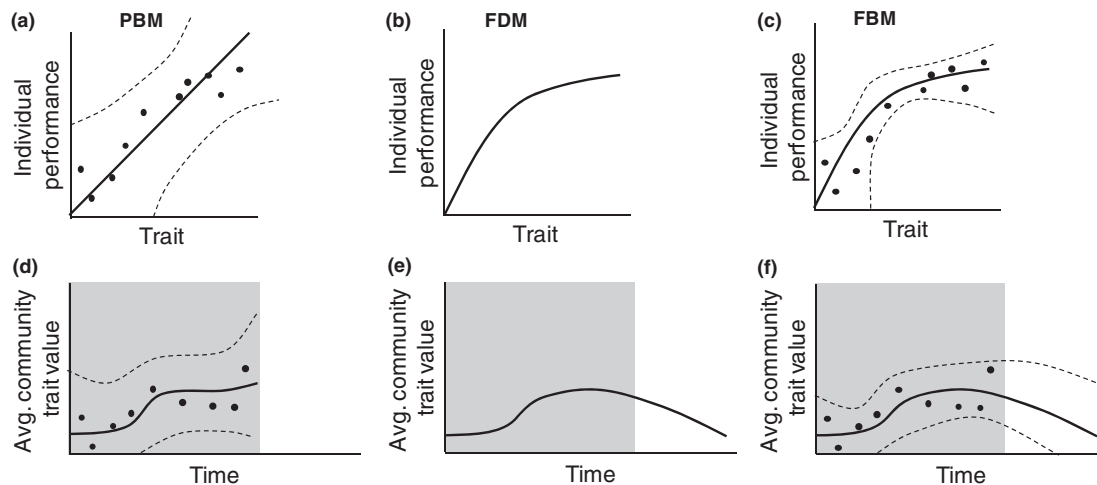


Figure 5 Examples of hypothetical performance filters (a–c) determined at the individual level for each of three modelling approaches. In (d)–(f), the performance filter is applied to the trait distribution across an implicit temporal environmental gradient. This results in a filtered trait distribution, the mean of which is depicted as it varies over time for each of three modelling approaches. In the figures, the solid line represents the main model prediction and dotted lines represent hypothetical credible intervals. Points represent data for individuals (a, c) and mean trait values for the whole community (d, f). These models produce a prediction of the entire filtered trait distribution, but only the mean is shown here for convenience. Other aspects of the trait distribution, such as the variance, can also be predicted (not shown). Shaded grey areas indicate the range of the data. These hypothetical graphs are similar to what we would expect from example models like those described in Table 2. (a) A linear regression model describes the performance filter in a PBM. The regression model has credible intervals, but they are larger than in (c) because the underlying regression model is inaccurate. (b) A saturating function based on first principles describes the performance filter in a FDM, but it lacks credible intervals. (c) A saturating function based on first principles (as in (b)) describes the performance filter in a FBM. The saturating function has tighter credible intervals than (a) because the first principles performance filter is more appropriate to the data. (d) A PBM with an underlying linear regression model for the performance filter produces predictions only within the range of the original environmental data. In this example, relatively large credible intervals occur because the performance filter is inaccurate, and the linear model predicts increasing average trait values within a community over time. (e) A FDM with an underlying saturating function produces predictions through the entire time period, but without credible intervals. The first principles model predicts decreasing average trait values beyond the data range. (f) FBM with an underlying saturating function (as in (e)) produces predictions and credible intervals through the entire time period, with an improved fit within the original data range compared to (d). The predicted downward trend in response outside the data range is captured with credible intervals, but these are increased because prediction is less strongly data-driven in this area.

sensitivity analysis can be used to quantify how model predictions are impacted by changes in parameter values (Webb *et al.* 2006).

An integrative approach: Bayesian multilevel models with a first principles mechanism

The problem of developing a rigorous theoretical framework for traits-based approaches is non-trivial. PBM and FDM both show promise in addressing this problem, but their strengths and weakness differ. While PBM and FDM have traditionally been applied to different biological research themes, there is no fundamental justification for this division. Both approaches reflect the conceptual framework common to predictive community and ecosystem ecology based on traits; they encompass a similar perspective on environmental filtering of traits and projection of this performance filter; and they require similar types

of data. A melded or hybrid approach that balances the strengths and weaknesses of these two techniques would maintain both uncertainty estimates and explicit mechanisms while capturing spatial and temporal dynamics in a process-based framework.

In principle, Bayesian multilevel models can allow for the incorporation of first principles mechanisms and can be used to predict spatial and/or temporal dynamics as described in Table 2 column C, Fig. 5c and f, and Box 1 part C. In traditional PBM, the performance filter is described phenomenologically using traditional statistical methods (e.g. linear regression). In contrast, a first principles Bayesian multilevel models (FBM) estimates the performance filter using a mechanistic model. In other applications, this has been referred to as using a deterministic process model within a multilevel (hierarchical) statistical model (Cressie *et al.* 2009). A FBM combines the strengths of the theoretical mathematical models with

observed data. This melded approach offers an exciting opportunity for modelling trait-related data. FBM have not been implemented, to our knowledge to address traits-based questions, although they have been used to address other community ecology problems (Johns & Mehl 2006; Hooten & Wikle 2008). For example, Hooten & Wikle (2008) modelled the spread of the invasive Eurasian Collared-Dove (*Streptopelia decaocto*) by using a Bayesian approach to estimate parameters from data for an underlying reaction-diffusion partial differential equation model. The model produced estimates of the spread of the dove over time and space as well as parameter estimates to relate this spread to human population density. A variety of underlying mechanistic models could be considered, ranging from a simple univariate independent distribution over species and time (e.g. Norberg *et al.* 2001) to a more complex model motivated by the work of Savage *et al.* (2007). A FBM does not have to include only a mechanistic model of the performance filter. In many applications, it makes sense to use some combination of mechanistic and phenomenological models (Newman *et al.* 2006; Ogle & Barber 2008).

Application of deterministic process models to traits-based problems requires sophisticated statistical algorithms for parameter estimation (e.g. variants of Markov chain Monte Carlo algorithms, Givens & Hoeting 2005; Chapters 7 and 8) as well as some model simplifications (e.g. discretization of the dynamical systems component). Discretization is a necessary step in order to fit the data to the underlying first principles model. A challenge of this approach is that discretization or estimation of solutions of the underlying mechanistic, mathematical model necessarily involves some error. How to incorporate this error into uncertainty estimates in a Bayesian modelling framework is an open area of research in statistics and mathematics (Bortz & Nelson 2006).

The melding of PBM and FDM into a hybrid FBM has strong appeal because it allows incorporation of uncertainty estimates for the parameters used to describe the mechanistic process and because the mechanistic performance filter could more confidently be projected beyond the range of data (Fig. 5f). Application of these types of models present some technical challenges, but their promise merits further development.

Data constraints

PBM, FDM and FBM all naturally reflect the conceptual foundation of the trait approach. However, their utility and appropriate application is practically constrained by the balance between the types of data required by each method and the types of data that are available. It is these types of data constraints that have aligned PBM with species

composition and abundance questions and FDM with ecosystem function questions.

Data constraints strongly limit our ability to build realistic performance filters, but they affect filter projection less because projection is usually an inherent aspect of the statistical or mathematical approach. Both PBM and FDM have similar data requirements for constructing performance filters: a set of trait data, environmental data and performance data on ecosystem functioning or species presence/absence (or abundance). These types of trait and environmental data sets can be collected experimentally (e.g. Grime & Hunt 1975; Buchwalter *et al.* 2008), but are labour intensive. Hence, it is not uncommon for researchers to use trait, environment and performance data collected at different times and places (see Box 1 for an example). Dealing with this type of data misalignment is a technical challenge for quantitative methods, but Bayesian models have been developed to address these data misalignment problems (Banerjee *et al.* 2003).

Linking the performance value of individual traits to specific environmental drivers is the main element in constructing performance filters, ideally in a mechanistic fashion. The relationship between an organism and its environment can depend on both abiotic factors and biotic factors, such as natural enemies, mutualists and competitors (e.g. Janzen 1970; Frost *et al.* 1995; Tylianakis *et al.* 2008). Trait-based approaches make use of both abiotic and biotic environmental drivers and can incorporate complex ecological interactions such as functional complementarity and correlations among drivers or traits (Norberg *et al.* 2001; Savage *et al.* 2007).

While the quantitative methods described here are appropriate for simple (single optimum) or complex (many optima) performance filters, our ability to determine which type of filter occurs in a system depends on the quality of available data. Many easy-to-measure traits (e.g. Cornelissen *et al.* 2003; Wright *et al.* 2004) may not completely capture performance or may interact with other, unmeasured traits (Marks & Lechowicz 2006; Violle *et al.* 2007). Thus, there is strong potential for performance filters to appear simplified when they are not or to appear complex and disjoint because underlying connections among traits and environmental drivers are missing from the analysis. Over-interpretation of performance filters could be misleading. However, Bayesian approaches are currently being developed to relate easy-to-measure traits to more complete measures of performance (McCarthy *et al.* 2008). Such approaches may be one solution to these potential problems.

Data are often observed at the community level instead of the individual level. This data constraint can lead to the problems of specification and aggregation bias. Specification bias occurs when the trend in the relationship between the

trait and the performance is in the wrong direction because the performance filter is measured at the community level instead of the individual level. This is demonstrated in Fig. 2f where there is a positive trend between trait and performance at the community level, while a negative relationship is observed at the individual level. Aggregation bias occurs when associations based on aggregate data do not reflect individual heterogeneity. Aggregation bias can cause scientists to falsely conclude there are highly significant correlations. This is demonstrated in Fig. 2g where there is greater variability in individual performance than in the observed community performance. With specification and aggregation bias, prediction of the average response across the gradient can be qualitatively accurate; however, prediction of the variance in individual responses will be inaccurate. Prediction of the variance can be quite important because trait variance reflects biodiversity. See Shea & Chesson (2002) and Huxman *et al.* (2004) for discussions of similar issues in other areas of ecology.

Aggregation bias also occurs when trait data are collected at the species level. Furthermore, one of the main strengths of a traits-based approach, that it gets away from species distinctions, is compromised when trait data are collected solely at the species level. In addition to aggregation bias, application of traits-based approaches at the species level ignores the potential effects of natural selection on the community or ecosystem response. This implication may be particularly important in situations where evolution can occur at ecologically relevant rates in response to climate change (Reznick & Ghalambor 2001; Finney *et al.* 2002; Parmesan & Yohe 2003).

CONCLUSIONS

Traits-based approaches are clearly a useful way to analyse data, as evidenced by the burgeoning literature in this area over the last few years. However, a more articulated conceptual foundation and coherent theoretical framework is needed to unify and advance this active and promising area of ecological research. The absence of a formal treatment of traits-based theory in major ecology textbooks speaks to this lack of coherence. Development of a more coherent theoretical framework is needed to support hypothesis generation, appropriate inference and prediction in traits-based ecology.

A necessary first step is to recognize that traits-based approaches widely employed in divergent fields of study have a common foundation. In particular, the artificial divide between species composition/abundance and ecosystem function studies disappears when these historically divergent domains are integrated under a shared conceptual framework that describes the spatial and temporal dynamics of trait distributions and their environmental filtering. This unifying

framework indicates that traits-based approaches should not continue to develop independently in these two areas.

The promise of a predictive traits-based ecology can only be realized by confronting a coherent conceptual foundation with the full range of relevant empirical analyses to allow for consistent analysis and comparison. We believe our conceptual framework of trait distributions, performance filters and environmental gradients can act as a kind of Rosetta stone to allow specific (and varied) empirical examples to be translated into a common currency that can be gauged for consistency with expectations from traits-based theoretical constructs. Such a common translator is crucial if we want to advance our understanding of how trait-level processes scale up through an ecological hierarchy from individuals to ecosystems and thus realize the full potential of traits-based ecology.

Achieving this potential will require new analytical approaches because implementation of current techniques results in a tradeoff. On the one hand, PBM generate desirable estimates of uncertainty in predictions, but their general reliance on phenomenological performance filters precludes confident projection outside the original data. On the other hand, FDM do incorporate mechanistic performance filters that support more confident projection, but they fail to provide estimates of uncertainty. We believe a hybrid FBM that both incorporates a mechanistic performance filter and affords estimates of uncertainty holds great promise for advancing a more conceptually rigorous, predictive traits-based ecology.

Traits-based approaches and theory are still developing. While they have great promise, they also have non-trivial limitations that cannot be dismissed. From a practical standpoint, the type and quality of data available will often constrain what can be accomplished analytically. More fundamental constraints must also be noted. First, back calculation from the trait distribution to species abundance and distribution, and possibly ecosystem function as well, is unlikely to be an easy, straightforward process. The more species contributing to the trait distribution and the greater the trait redundancy among species, the more indeterminate this back calculation will be. Thus, the number and type of traits and their relation to one another (and to the environment) should be carefully considered in conducting traits analyses. Second, much of the conceptual foundation of the traits-based approach rests on niche tradeoff arguments (e.g. Tilman 1982) and hence, it does not test alternative hypotheses such as neutral theory or a mix of stochastic and deterministic processes as proposed by Hubbell (2001). However, adding stochastic effects to niche based modelling, particularly FDM approaches, can potentially account for neutral processes (Lande *et al.* 2003; Tilman 2004).

Despite these growing pains, we can glimpse a number of important issues that a mature traits-based theory will

address. For example, what functional forms do performance filters take? Can they be captured as a linear relationship or are they more complex? How many and what types of traits and environmental drivers are needed to understand these performance filters? Do performance filters that are relevant on ecological timescales provide any insight into adaptive topographies that are relevant on evolutionary time scales? How similar are performance filters constructed at the individual level to those constructed at the community level? What are the best ways to relate performance filters and trait distributions to community abundance and distribution or ecosystem function? How far can mechanistic performance filters reasonably be projected (e.g. using uncertainty estimates)?

Furthermore, traits-based approaches can provide insight into active areas of debate, such as the role of biodiversity in ecosystem function. Many data appropriate for traits-based analyses have been collected as part of biodiversity-ecosystem function studies. Theoretical work, using mostly FDM, has begun to address these questions using the conceptual framework outlined here. Ecologists have proposed that trait diversity may be a better predictor of species distributions or ecosystem function than biodiversity itself (Norberg *et al.* 2001). If so, what underlying mechanisms generally control trait diversity? What is the relative importance of temporal sampling effects (Norberg *et al.* 2001; Chesson *et al.* 2002), functional complementarity and correlations with suboptimal traits (Savage *et al.* 2007)? Trait-based approaches can also be used to address these types of questions in a metapopulation or open population context (Norberg *et al.* 2001; Loreau *et al.* 2003; Savage *et al.* 2007).

The interest among ecologists in advancing traits-based theory and analysis is great, in no small part because the questions that can be addressed are important and pressing. Here, we have offered a perspective that can contribute to more rapid and coherent progress in the promising arena of traits-based ecology.

ACKNOWLEDGEMENTS

All authors gratefully acknowledge the financial support for this work including NSF Grant DEB-0618097 for CTW, NSF Grant EID-0914489 for JAH and NSF-IGERT 53-3005 for GMA and MIP. We would like to thank Justin Wright, Joseph von Fischer and three anonymous reviewers for their helpful comments on earlier versions of this manuscript.

REFERENCES

Banerjee, S., Carlin, B.P. & Gelfand, A.E. (2003). *Hierarchical Modeling and Analysis for Spatial Data*. Chapman & Hall/CRC Press, Boca Raton, FL, pp. 175–216.

- Bernhardt-Römermann, M., Römermann, C., Nuske, R., Parth, A., Klotz, S., Schmidt, W. *et al.* (2008). On the identification of the most suitable traits for plant functional trait analyses. *Oikos*, 117, 1533–1541.
- Billheimer, D., Cardoso, T., Freeman, E., Guttorp, P., Ko, H. & Silkey, M. (1997). Natural variability of benthic species in the Delaware Bay. *J. Environ. Ecol. Stat.*, 4, 9–115.
- Billheimer, D., Guttorp, P. & Fagan, W.F. (2001). Statistical interpretation of species composition. *J. Am. Stat. Assoc.*, 96, 1205–1214.
- Bortz, D.M. & Nelson, P.W. (2006). Model selection and mixed-effects modeling of HIV infection dynamics. *Bull. Math. Biol.*, 68, 2005–2025.
- Buchwalter, D.B., Cain, D.J., Martin, C.A., Xie, L., Luoma, S.N. & Garland, T. Jr (2008). Aquatic insect ecophysiological traits reveal phylogenetically based differences in dissolved cadmium susceptibility. *Proc. Natl Acad. Sci. USA*, 105, 8321–8326.
- Chesson, P., Pacala, S. & Neuhauser, C. (2002). Environmental niches and ecosystem functioning. In: *The Functional Consequences of Biodiversity: Empirical Progress and Theoretical Extensions* (eds Kinzig, A.P., Pacala, S. & Tilman, D.). Princeton University Press, Princeton, NJ, pp. 213–245.
- Connell, J.H. (1978). Diversity in tropical rain forests and coral reefs. *Science*, 199, 1302–1310.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E. *et al.* (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.*, 51, 335–380.
- Cornwell, W.K. & Ackerly, D.D. (2009). Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecol. Monogr.*, 79, 109–126.
- Craine, J.M., Tilman, D., Wedin, D., Reich, P., Tjoelker, M. & Knops, J. (2002). Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. *Funct. Ecol.*, 16, 563–574.
- Cressie, N.A.C., Calder, C.A., Clark, J.S., Ver Hoef, J.M. & Wikle, C.K. (2009). Accounting for uncertainty in ecological analysis: the strengths and limitations of hierarchical statistical modeling. *Ecol. Appl.*, 19, 553–570.
- Díaz, S. & Cabido, M. (2001). Vive la difference: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.*, 16, 646–655.
- Diez, J.M. & Pulliam, H.R. (2007). Hierarchical analysis of species distributions and abundance across environmental gradients. *Ecology*, 88, 3144–3152.
- Dorrrough, J. & Scroggie, M.P. (2008). Plant responses to agricultural intensification. *J. Appl. Ecol.*, 45, 1274–1283.
- Dray, S. & Legendre, P. (2008). Testing the species traits–environment relationships: the fourth-corner problem revisited. *Ecology*, 89, 3400–3412.
- Enquist, B.J., Kerkhoff, A.J., Stark, S.C., Swenson, N.G., McCarthy, M.C. & Price, C.A. (2007). A general integrative model for scaling plant growth, carbon flux, and functional trait spectra. *Nature*, 449, 218–222.
- Falster, D.S. & Westoby, M. (2003). Plant height and evolutionary games. *Trends Ecol. Evol.*, 18, 337–343.
- Finney, B.P., Gregory-Eaves, I., Douglas, M.S.V. & Smol, J.P. (2002). Fisheries productivity in the northeastern Pacific Ocean over the past 2,200 years. *Nature*, 416, 729–733.
- Fisher, R.A. (1930). *The Genetical Theory of Natural Selection*. Oxford University Press, London.

- Frost, T.M., Carpenter, S.R., Ives, A.R. & Kratz, T.K. (1995). Species compensation and complementarity in ecosystem function. In: *Linking Species and Ecosystems* (eds Jones, G.C. & Lawton, J.H.). Chapman & Hall, New York, pp. 224–239.
- Gelfand, A.E., Schmidt, A.M., Wu, S., Silander, J.A. Jr, Latimer, A. & Rebelo, A.G. (2005). Modeling species diversity through species level hierarchical modeling. *J. R. Stat. Soc., Ser. C (Appl. Stat.)*, 54 (1), 1–20.
- Gelfand, A.E., Silander, J.A. Jr, Wu, S., Latimer, A., Lewis, P.O., Rebelo, A.G. *et al.* (2006). Explaining species distribution patterns through hierarchical modeling. *Bayesian Anal.*, 1, 41–92.
- Gelman, A. & Hill, J. (2007). *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press, New York.
- Gelman, A., Carlin, J.B., Stern, H.S. & Rubin, D.B. (2004). *Bayesian Data Analysis*, 2nd edn. Chapman & Hall/CRC, New York.
- Givens, G.H. & Hoeting, J.A. (2005). *Computational Statistics*. John Wiley & Sons, New York.
- Green, J.L., Bohannan, B.J.M. & Whitaker, R.J. (2008). Microbial biogeography: from taxonomy to traits. *Science*, 320, 1039–1043.
- Grime, J.P. (1977). Evidence for existence of 3 primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.*, 111, 1169–1194.
- Grime, J.P. & Hunt, R. (1975). Relative growth-rate: its range and adaptive significance in a local flora. *J. Ecol.*, 63, 393–422.
- Hooten, M. & Wikle, C. (2008). A hierarchical Bayesian non-linear spatio-temporal model for the spread of invasive species with application to the Eurasian Collared-Dove. *Environ. Ecol. Stat.*, 15, 59–70.
- Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ, P. 375.
- Hubbell, S.P. (2006). Neutral theory and the evolution of ecological equivalence. *Ecology*, 87, 1387–1398.
- Huxman, T.E., Smith, M.D., Fay, P.A., Knapp, A.K., Shaw, M.R., Loik, M.E. *et al.* (2004). Convergence across biomes to a common rain-use efficiency. *Nature*, 429, 651–654.
- Janzen, D.H. (1970). Herbivores and number of tree species in tropical forests. *Am. Nat.*, 104, 501–528.
- Johns, C.J. & Mehl, C.H. (2006). A dynamic spatial model for chronic wasting disease in Colorado. *J. Data Sci.*, 4, 21–37.
- Johnson, D.S., Hoeting, J.A. & Poff, N.L. (2006). Biological monitoring: a Bayesian model for multivariate compositional data. In: *Bayesian Statistics and its Applications* (eds Upadhyay, S.K., Singh, U. & Dey, D.K.). Anamaya Publishers, New Delhi, pp. 270–289.
- Kearney, M. & Porter, W. (2009). Mechanistic niche modeling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.*, 12, 334–350.
- Keddy, P.A. (1992). Assembly and response rules: two goals for predictive community ecology. *J. Veg. Sci.*, 3, 157–164.
- Kolar, C.S. & Lodge, D.M. (2001). Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.*, 16, 199–204.
- Kühn, I., Bierman, S.M., Durka, W. & Klotz, S. (2006). Relating geographical variation in pollination types to environmental and spatial factors using novel statistical methods. *New Phytol.*, 172, 127–139.
- Lande, R. (1976). Natural selection and random genetic drift in phenotypic evolution. *Evolution*, 30, 314–334.
- Lande, R. (1979). Quantitative genetic analysis of multivariate evolution applied to brain: body size allometry. *Evolution*, 33, 402–416.
- Lande, R., Engen, S. & Saether, B.-E. (2003). *Stochastic Population Dynamics in Ecology and Conservation*. Oxford University Press, Oxford, P. 224.
- Latimer, A.M., Silander, J.A. Jr, Gelfand, A.E., Rebelo, A.G. & Richardson, D.M. (2004). Quantifying threats to biodiversity from invasive alien plants and other factors: a case study from the Cape Floristic Region. *South Afr. J. Sci.*, 100, 81–86.
- Latimer, A.M., Wu, S., Gelfand, A.E. & Silander, J.A. Jr (2006). Building statistical models to analyze species distributions. *Ecol. Appl.*, 16, 33–50.
- Legendre, P., Galzin, R. & Harmelin-Vivien, M.L. (1997). Relating behavior to habitat: solutions to the fourth-corner problem. *Ecology*, 78, 547–562.
- Loreau, M., Mouquet, N. & Gonzales, A. (2003). Biodiversity as spatial insurance in heterogeneous landscapes. *Proc. Natl Acad. Sci. USA*, 100, 12765–12770.
- Marks, C.O. & Lechowicz, M.J. (2006). Alternative designs and the evolution of functional diversity. *Am. Nat.*, 167, 55–66.
- Marks, C.O. & Muller-Landau, H.C. (2007). Comment on 'From plant traits to plant communities: a statistical mechanistic approach to biodiversity'. *Science*, 316, 1425c.
- McCarthy, M.A., Citroen, R. & McCall, S.C. (2008). Allometric scaling and Bayesian priors for annual survival of birds and mammals. *Am. Nat.*, 172, 216–222.
- McGill, B.J. & Brown, J.S. (2007). Evolutionary game theory and adaptive dynamics of continuous traits. *Annu. Rev. Ecol. Evol. Syst.*, 38, 403–435.
- McGill, B.J., Enquist, B., Weiher, E. & Westoby, M. (2006). Rebuilding ecology from functional traits. *Trends Ecol. Evol.*, 21, 178–185.
- Morin, X. & Lechowicz, M.J. (2008). Contemporary perspectives on the niche that can improve models of species range shifts under climate change. *Biol. Lett.*, 4, 573–576.
- Murray, L.D., Ribic, C.A., Thogmartin, W.E. & Knutson, M.G. (2008). Accuracy assessment of predictive models of grassland bird abundances in the prairie hardwood Transition Bird Conservation Region. *Condor*, 110, 747–755.
- Naeem, S. & Wright, J.P. (2003). Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecol. Lett.*, 6, 567–579.
- Newman, K.B., Buckland, S.T., Lindley, S.T., Thomas, L. & Fernández, C. (2006). Hidden process models for animal population dynamics. *Ecol. Appl.*, 16, 74–86.
- Norberg, J., Swaney, D.P., Dushoff, J., Lin, J., Casagrandi, R. & Levin, S.A. (2001). Phenotypic diversity and ecosystem functioning in changing environments: a theoretical framework. *Proc. Natl Acad. Sci. USA*, 98, 11376–11381.
- Ogle, K. & Barber, J.J. (2008). Bayesian data-model integration in plant physiological and ecosystem ecology. *Prog. Bot.*, 69, 281–311.
- Olden, J.D., Poff, N.L. & Bestgen, K.R. (2006). Life-history strategies predict fish invasions and extirpations in the Colorado River Basin. *Ecol. Monogr.*, 76, 25–40.
- Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.
- Pfisterer, A.B. & Schmid, B. (2002). Diversity-dependent production can decrease the stability of ecosystem functioning. *Nature*, 416, 84–86.
- Poff, N.L., Olden, J.D., Viera, N.K.M., Finn, D.S., Simmons, M.P. & Kondratieff, B.C. (2006). Functional trait niches of North

- American lotic insects: traits-based ecological applications in light of phylogenetic relationships. *J. North Am. Benthol. Soc.*, 25, 730–755.
- Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N. *et al.* (2006). Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature*, 439, 161–167.
- Reich, P.B., Buschena, C., Tjoelker, M.G., Wrage, K., Knops, J., Tilman, D. *et al.* (2003). Variation in growth rate and ecophysiology among 34 grassland and savanna species under contrasting N supply: a test of functional group differences. *New Phytol.*, 157, 617–631.
- Reich, P.B., Wright, I.J. & Lusk, C.H. (2007). Predicting leaf physiology from simple plant and climate attributes: a global GLOPNET analysis. *Ecol. Appl.*, 17, 1982–1988.
- Reznick, D.N. & Ghilambor, C.K. (2001). The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica*, 112, 183–198.
- Roxburgh, S.H. & Mokany, K. (2007). Comment on ‘From plant traits to plant communities: a statistical mechanistic approach to biodiversity’. *Science*, 316, 1425b.
- Savage, V.M., Webb, C.T. & Norberg, J. (2007). A general multi-trait-based framework for studying the effects of biodiversity on ecosystem functioning. *J. Theor. Biol.*, 247, 213–229.
- Shea, K. & Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.*, 17, 170–176.
- Shipley, B., Vile, D. & Garnier, E. (2006). From plant traits to plant communities: a statistical mechanistic approach to biodiversity. *Science*, 314, 812–814.
- Shipley, B., Vile, D. & Garnier, E. (2007). Response to comments on ‘From plant traits to plant communities: a statistical mechanistic approach to biodiversity’. *Science*, 316, 1425d.
- Southwood, T.R.E. (1977). Habitat, the template for ecological strategies? *J. Anim. Ecol.*, 46, 337–365.
- Suding, K.N., Lavorel, S., Chapin, F.S. III, Cornelissen, J.H.C., Díaz, S., Garnier, E. *et al.* (2008). Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Glob. Change Biol.*, 14, 1125–1140.
- Thogmartin, W.E., Sauer, J.R. & Knutson, M.G. (2004). A hierarchical spatial model of avian abundance with application to Cerulean Warblers. *Ecol. Appl.*, 14, 1766–1779.
- Thuiller, W., Albert, C., Araújo, M.B., Berry, P.M., Cabeza, M., Guisan, A. *et al.* (2007). Predicting global change impacts on plant species’ distributions: future challenges. *Perspect. Plant Ecol. Evol. Syst.*, 9, 137–152.
- Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ, p. 296.
- Tilman, D. (2001). An evolutionary approach to ecosystem functioning. *Proc. Natl Acad. Sci. USA*, 98, 10979–10980.
- Tilman, D. (2004). Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proc. Natl Acad. Sci. USA*, 101, 10854–10861.
- Tilman, D. & Downing, J.A. (1994). Biodiversity and stability in grasslands. *Nature*, 367, 363–365.
- Turelli, M. & Barton, N.H. (1994). Genetic and statistical-analyses of strong selection on polygenic traits—what, me normal? *Genetics*, 138, 913–941.
- Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.*, 11, 1351–1363.
- Ver Hoef, J.M. & Frost, K.J. (2003). A Bayesian hierarchical model for monitoring harbor seal changes in Prince William Sound, Alaska. *Environ. Ecol. Stat.*, 10, 201–219.
- Vincent, T.L.S. & Vincent, T.L. (2009). Predicting relative abundance using evolutionary game theory. *Evol. Ecol. Res.*, 11, 265–294.
- Vielle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. *et al.* (2007). *Let the concept of trait be functional!* *Oikos*, 116, 882–892.
- Webb, C.T., Brooks, C.P., Gage, K.L. & Antolin, M.F. (2006). Classic flea-borne transmission does not drive plague epizootics in prairie dogs. *Proc. Natl Acad. Sci. USA*, 103, 6236–6241.
- Weiherr, E. & Keddy, P.A. (1995). Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos*, 74, 159–164.
- Westoby, M. & Wright, I.J. (2006). Land-plant ecology on the basis of functional traits. *Trends Ecol. Evol.*, 21, 261–267.
- Williams, N.G., Morgan, J.W., McDonnell, M.J. & McCarthy, M.A. (2005). Plant traits and local extinctions in natural grasslands along an urban–rural gradient. *J. Ecol.*, 93, 1203–1213.
- Wright, S. (1931). Evolution in Mendelian populations. *Genetics*, 16, 97–159.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F. *et al.* (2004). The worldwide leaf economics spectrum. *Nature*, 428, 821–827.

Editor, Jordi Bascompte

Manuscript received 22 June 2009

First decision made 2 August 2009

Second decision made 30 November 2009

Manuscript accepted 28 December 2009