

Revisiting the Holy Grail: using plant functional traits to understand ecological processes

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ABSTRACT

One of ecology's grand challenges is developing general rules to explain and predict highly complex systems. Understanding and predicting ecological processes from species' traits has been considered a 'Holy Grail' in ecology. Plant functional traits are increasingly being used to develop mechanistic models that can predict how ecological communities will respond to abiotic and biotic perturbations and how species will affect ecosystem function and services in a rapidly changing world; however, significant challenges remain. In this review, we highlight recent work and outstanding questions in three areas: (i) selecting relevant traits; (ii) describing intraspecific trait variation and incorporating this variation into models; and (iii) scaling trait data to community- and ecosystem-level processes. Over the past decade, there have been significant advances in the characterization of plant strategies based on traits and trait relationships, and the integration of traits into multivariate indices and models of community and ecosystem function. However, the utility of trait-based approaches in ecology will benefit from efforts that demonstrate how these traits and indices influence organismal, community, and ecosystem processes across vegetation types, which may be achieved through meta-analysis and enhancement of trait databases. Additionally, intraspecific trait variation and species interactions need to be incorporated into predictive models using tools such as Bayesian hierarchical modelling. Finally, existing models linking traits to community and ecosystem processes need to be empirically tested for their applicability to be realized.

Key words: community assembly, ecological modelling, intraspecific variation, leaf economics spectrum, functional diversity, response traits, effect traits.

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I. INTRODUCTION

Ecologists have a long tradition of grouping organisms based on function (Raunkiaer, 1934; Root, 1967; Grime, 1974). A renewed interest in this approach came in the late 1990s when a number of ecologists sought to understand how the functional traits of species could predict community response to environmental change and the effects of changes in community composition on ecosystem processes (Diaz & Cabido, 1997; Lavorel *et al.*, 1997; Chapin *et al.*, 2000). Lavorel & Garnier (2002) developed a conceptual framework by distinguishing traits that predict how species respond to environmental factors (response traits) from traits that affect ecosystem processes (effect traits). They argued that understanding and predicting community processes from species traits, rather than species identity, was a ‘Holy Grail’ in ecology. While empirical tests of this framework were slow to appear (Suding & Goldstein, 2008), the formalization of the leaf economic spectrum (LES) spurred an increased focus on trait-based methodological approaches. The LES shows that relationships exist among several key traits across a broad range of species and different climates (Reich, Walters & Ellsworth, 1997; Wright *et al.*, 2004), and that simple predictors (specific leaf area, SLA) may link to hard-to-measure ecological processes (e.g. growth rate).

Whether or not traits matter to community ecology is closely related to whether or not the niche matters, as niche differentiation can be defined as differential performance along environmental gradients with respect to organismal traits (Chase & Leibold, 2003). Opinions regarding the relative importance of the niche, and hence traits, to community dynamics fall loosely into three camps. The first argues that trait differences among individuals are largely irrelevant at the community level compared to factors such as demographic stochasticity (e.g. Neutral Theory: Hubbell, 2001). The second argues that traits are relevant to individuals, but the complexity of biotic and abiotic interactions precludes us from scaling individual processes to the community level (e.g. Lawton, 1999). The final camp argues that traits provide a path forward to a unified theory of community ecology by providing a taxon-independent means for generalizing the structure and/or functioning of communities that is based on functional traits rather

than species identity (e.g. ; Westoby & Wright, 2006; McGill *et al.*, 2006a). While the impact of stochasticity on community structure is largely undisputed, it has been shown that Neutral Theory cannot, by itself, explain observed species distributions in many systems (McGill, 2003; McGill, Maurer & Weiser, 2006b). Furthermore, many recent studies have demonstrated that traits within communities and regional species pools explain a large amount of variance in community structure (e.g. de Bello *et al.*, 2012; Edwards, Lichtman & Klausmeier, 2013) and function (e.g. Sutton-Grier & Megonigal, 2011). These studies demonstrate that traits can scale up to influence community structure and, thus, provide optimism that it will be possible to develop general, predictive rules in community ecology as we refine our understanding of which traits are important in a given environment, how traits are distributed within and among species, and how those traits relate to mechanisms driving community dynamics and function (Fig. 1).

While trait-based ecology (TBE) has made significant strides over the past decade, a number of critical issues must be addressed before we can have confidence in the framework’s ability to deliver on its significant promise. This review highlights recent work and outstanding questions in three areas: (i) selecting relevant traits; (ii) describing intraspecific trait variation and incorporating this variation into models; and (iii) scaling trait data to community- and ecosystem-level processes. While this review focuses on plants, similar TBE movements are occurring in animal and microbial ecology (e.g. Litchman *et al.*, 2007; Haddad *et al.*, 2008; Bokhorst *et al.*, 2012; Fierer, Barberán & Laughlin, 2014; Pedley & Dolman, 2014).

II. SELECTING RELEVANT TRAITS

(1) Simplifying plant communities: functional groups *versus* functional traits

Over time, there have been major shifts in how trait variation is measured and utilized, particularly with respect to applications in community ecology. Shortcomings in the predictive power of TBE have ironically stemmed from one of its fundamental tenets—species can be grouped



Example traits	Organismal processes	Community processes	Ecosystem processes
Leaf chemistry and longevity	Carbon balance Disease resistance Growth rate	Competition Herbivory Succession	Decomposition Nutrient cycling Productivity
Leaf and stem hydraulic traits	Drought tolerance	Competition and facilitation	Hydrology Precipitation patterns
Fine root traits	Soil resource uptake Growth rate	Competition and facilitation Community invasibility	Decomposition Soil development

Fig. 1. Functional traits can be used to understand a wide range of ecological processes occurring at organismal, community, and ecosystem scales. Examples are given here of how leaf, stem, and fine root traits influence a variety of ecological processes.

according to their responses to and effects on abiotic and biotic conditions (Lavorel & Garnier, 2002). Historically, ecologists have attempted to capture ecological processes within communities (e.g. assembly, response to abiotic factors) by measuring the distribution and responses of species groups based on characteristics such as life history, life form, photosynthetic pathways or other functional traits (Lavorel *et al.*, 1997; Lavorel & Garnier, 2002; Lavorel *et al.*, 2007). If such groups are assumed to function similarly, community-to global-scale processes could be modelled without the collection of detailed trait data for many species.

While numerous studies have found significant relationships between ecosystem functions and traditional plant functional group classifications like the grass–forb–legume approach (reviewed in Díaz & Cabido, 2001), categorical groups mask variability, and may underestimate the important role that functional diversity plays in maintaining key ecosystem functions like productivity and nutrient cycling (Wright *et al.*, 2006). For example, studies have shown that not all C₄ perennial grasses or C₃ annual forbs respond similarly to disturbance or resource fluctuations (Badgery *et al.*, 2005; Firn *et al.*, 2010; Firn, Prober & Buckley, 2012; Han, Buckley & Firn, 2012). Further evidence of the inability of categorical functional groups to predict species responses to environmental change are emerging from the field of invasion ecology, as native and invasive species from similar functional groups respond differently to environmental variation (Funk, 2008; Firn *et al.*, 2010, 2012; Han *et al.*, 2012). Simple categorical functional groups can also be low in number in ecosystems like grasslands, meaning that correlative relationships between simple functional groups and changes in ecosystem function may be statistically significant because variability is reduced and not necessarily because groups are responding in a common way to perturbations.

Given limited abilities of traditional functional groups to capture and represent trait variation, there has been a shift away from describing and predicting community and ecosystem dynamics with functional categories of species and towards the use of continuous trait distributions (Westoby & Wright, 2006; Lavorel *et al.*, 2007). Interspecific differences in continuous traits have been linked to environmental gradients (e.g. Wright & Westoby, 1999; Wright *et al.*, 2005), demographic responses (Poorter & Markesteijn, 2008), and ‘major axes of variation’ describing suites of co-varying traits indicative of broader ecological strategies (e.g. Díaz *et al.*, 2004; Wright *et al.*, 2004). Still, trait effects on ecosystem-, landscape- and global-scale processes depend on the combined traits of co-occurring species, and are likely to be driven disproportionately by traits of the most abundant species (mass ratio hypothesis, Grime, 1998). These realizations have led to the quantification and use of aggregated trait attributes of the community [e.g. community-weighted mean (CWM)] and indices of community diversity to reveal broad patterns and explain more of the variation in trait–environment relationships (see Section IV.1, Díaz *et al.*, 2007a; Vileger, Mason & Mouillot, 2008). Meanwhile, alternative methods of classifying species into ecologically relevant functional groups based on numerous functional traits have continued to develop, often utilizing methods in cluster analysis (e.g. Grime *et al.*, 1997; Pillar & Sosinski, 2003; Aubin *et al.*, 2009; Fry, Power & Manning, 2014); however, identification of consistent groups and demonstrations of their utility in predictive models remain sparse and equivocal (e.g. Louault *et al.*, 2005; Müller *et al.*, 2007; Larson *et al.*, 2015).

(2) Trait selection

Deciding which traits to measure is one of the most difficult aspects of TBE. It is often difficult to know, *a*

priori, the mechanism(s) responsible for driving a particular community- or ecosystem-level process, much less the organismal trait(s) most closely linked to the mechanism. Compounding the problem is that many traits relevant to a particular mechanism are difficult or expensive to measure, especially for enough individuals to accurately characterize the trait distributions of a community, or even populations within the community. Fortunately, these 'hard' traits are often strongly correlated with more easily or cheaply measured 'soft' traits (Hodgson *et al.*, 1999). If certain traits are relevant to multiple plant responses and effects, it may be possible to identify a set of soft but multifaceted traits which predict a substantial portion of the variation in plant function and ecological processes (Fig. 1). Soft traits for many species can now be acquired from global databases like TRY (Kattge *et al.*, 2011) and BioFlor (www.biolflor.de). A recent study of 222 plant species found that soft traits sourced from the TRY database (i.e. seed mass, wood density, and leaf traits) were strong predictors of a range of life-history strategies (Adler *et al.*, 2013). Despite these advances, our understanding of which traits most strongly influence plant and ecosystem function reflects a bias towards leaf traits and databases like TRY generally do not account for site-level differences including species interactions, trait variation, and environmental variation.

(a) Response traits

Plant traits reflect adaptations to abiotic and biotic factors and, thus, can be used to describe and predict species responses to changes in these factors. In this framework, trait variation is assumed to be linked to variation in organismal responses to different factors (e.g. abiotic stress or competition), which scales up to influence demographic responses and species abundances (Suding, Goldberg & Hartman, 2003). The particular response traits of interest will depend on the specific combination of abiotic and biotic factors in a vegetation community. Which traits are linked to specific environmental changes has been the subject of previous reviews (Lavorel *et al.*, 2007), although empirical demonstrations of trait–response linkages remain relatively rare. Here, we briefly review key aspects of functional variation across species and their potential relevance to species responses in light of abiotic and biotic factors.

Plant growth rate is considered a key trait differentiating ecological strategies within communities (e.g. Grime, 1977; Reich, 2014). In general, growth rate has been shown to be positively associated with shade tolerance and negatively associated with drought tolerance (Suding *et al.*, 2003). Rapid growth has also been shown to be more prevalent in productive (e.g. Grime & Hunt, 1975), high-nutrient communities (Wright & Westoby, 1999), suggesting that it provides some fitness advantage when resources are not limiting. In some cases, however, rapid growth can allow plants to escape resource limitation in low, pulse-resource systems (e.g. among invasive species; Funk, 2013). Plant relative growth rate (RGR, the rate of dry mass addition per unit dry mass) has been recognized as a strong predictor of

species' potential for success and the most useful measure of plant growth (Grime & Hunt, 1975; Grime, 1977; Hunt & Cornelissen, 1997). Unfortunately, it is also difficult and time-consuming to measure. However, RGR is a 'synthetic' trait summarizing the outcome of several processes (e.g. photosynthesis, respiration, nutrient allocation, life-history strategies) that are tied to other measurable traits, such as leaf nitrogen (N) concentration, photosynthetic rate, tissue density, and SLA. A small number of soft traits, such as SLA or wood density, can explain a large portion of the variation in RGR across a large range of herbaceous and woody plant species (Hunt & Cornelissen, 1997; Walker & Langridge, 2002; Poorter *et al.*, 2008; Nguyen *et al.*, 2014).

In addition, terrestrial plants exhibit a consistent trade-off among these growth-related traits, such that high SLA is often linked to higher leaf N concentration and photosynthetic rate at the expense of tissue density and longevity. Consequently, soft traits like SLA or plant tissue density may also serve to represent functional strategies of nutrient acquisition and conservation, across a wide range of taxa and ecosystem types (Walker & Langridge, 2002; Díaz *et al.*, 2004; Wright *et al.*, 2004). While these trade-offs may not be exhibited in all species or plant systems (e.g. wetlands and grasslands: Wright & Sutton-Grier, 2012; Funk & Cornwell, 2013), the ubiquity of these trade-offs across many environmental and disturbance gradients, coupled with their strong relationship to important demographic rates (Donohue *et al.*, 2010), suggests that these traits are associated with mechanisms determining plant success in response to different abiotic and biotic factors (reviewed in Reich, 2014). As such, LES traits present a good starting point in the selection of traits for plant systems.

While great progress has been made in understanding the function of LES traits, our understanding of how other traits relate to plant and community responses is limited. Root traits are notoriously difficult to measure, although there is some evidence that an economic axis for roots exists as well, with slow-growing species having low root elongation rates, low specific root length (SRL), high root diameter, and low nutrient concentration (Freschet *et al.*, 2010; Liu *et al.*, 2010; Larson & Funk, 2016). In arid and semi-arid ecosystems, responses to changes in water availability may be better predicted from root traits such as root depth or elongation rate than from leaf traits (Nicotra, Babicka & Westoby, 2002; Padilla & Pugnaire, 2007). Furthermore, the traits most closely linked to plant performance for a given species may change depending on the environment. For example, a study of the annual species *Polygonum persicaria* found that leaf-level water-use efficiency was correlated with plant fitness in water-limited habitats while root biomass allocation was more closely linked to fitness in moist environments (e.g. Heschel *et al.*, 2004). Recent work also suggests that leaf and stem hydraulic traits (e.g. wood density; Cornwell & Ackerly, 2010) are correlated with traits from the LES (reviewed in Reich, 2014), but these traits are rarely incorporated into empirical tests and additional data are needed to determine

if the LES can adequately capture plant response to changes in water availability. Lastly, traits influencing regeneration processes (i.e. dispersal/colonization, resprouting, germination, emergence) also have significant implications for population dynamics and community composition (Zeiter, Stampfli & Newbery, 2006; Donohue *et al.*, 2010; Aicher, Larios & Suding, 2011; Flores-Moreno & Moles, 2013; Pakeman & Eastwood, 2013), but are not well represented in trait-based theoretical frameworks.

Although mean trait values for species are typically used in predictive models, there is growing evidence that species vary in their phenotypic responses to changing abiotic and biotic factors (i.e. phenotypic plasticity, see Section III), which contributes to functional variation within communities (e.g. Funk, 2008; Ashton *et al.*, 2010; Firn *et al.*, 2012; Siebenkäs, Schumacher & Roscher, 2015; Larson & Funk, 2016). Although empirical links between phenotypic plasticity and performance or fitness are still rare across species (van Kleunen & Fischer, 2005; Firn *et al.*, 2012), if plasticity is adaptive it could be an important metric related to population, species, and community responses to environmental change (reviewed in Berg & Ellers, 2010; Nicotra *et al.*, 2010; Valladares *et al.*, 2014). For example, leaf trait plasticity has been linked to productivity and plant growth in response to both nitrogen availability and cutting (da Silveira Pontes *et al.*, 2010) as well as temperature and water availability (Liancourt *et al.*, 2015). Ultimately, while belowground traits, regenerative traits, and intraspecific trait variation have long been recognized as key (albeit difficult) components to incorporate into models (Weiher *et al.*, 1999), their inclusion in empirical tests is still relatively rare, and represents an important area for future research.

Through their influence on plant response to abiotic and biotic factors, response traits can be used to identify ecological processes structuring plant populations and communities (Fig. 1; Dorrrough, Ash & McIntyre, 2004; McIntyre, 2008; Mayfield & Levine, 2010; Butterfield & Callaway, 2013; Gross *et al.*, 2015). For example, Gross *et al.* (2009) used patterns of SLA to determine that community structure in a subalpine grassland was influenced by facilitation in water-limited areas and competition in more mesic areas. In a study of soil disturbance in a lake-plain prairie, Suding *et al.* (2003) found that traits conferring tolerance to shade, drought, and defoliation were better predictors of abundance patterns following disturbance than was competitive ability, a frequently measured response. Other studies have shown that multiple traits can interact to influence community patterns. For example, Maire *et al.* (2012) found that, despite differences in nutrient strategy among species (niche differences), traits associated with competitive ability (e.g. height) were better predictors of abundance across grazing and nutrient treatments in a grassland community. Gross *et al.* (2015) found that while native and invasive species differed in traits (SLA and height), they had similar responses to grazing and competition because different trait combinations generated similar success to these factors. These last two examples demonstrate that

using a diverse set of traits may be important to differentiate ecological processes acting on community assembly. Selection of the performance metric is also important because growth, survival, and reproductive measures will have different relationships with community-level processes (e.g. abundance) as environmental conditions change (Gross *et al.*, 2007, 2009). More studies are needed that examine how traits relate to plant performance across different environments; this will be critical if we are to predict plant and community responses in a changing world (Meinzer, 2003).

(b) *Effect traits*

For functional traits to provide a comprehensive theoretical framework in ecology, we must also understand how trait composition and diversity influence ecosystem functioning (Fig. 1; Lavorel & Garnier, 2002). Effect traits alter abiotic and biotic processes corresponding to a wide range of ecosystem functions, and have been the subject of recent review (Eviner & Chapin, 2003; de Bello *et al.*, 2010; Garnier & Navas, 2012). However, while our understanding of effect traits has improved in the wake of the framework laid out by Lavorel & Garnier (2002), predictive models have lagged behind those incorporating response traits (Suding *et al.*, 2008). In addition to their predictive role in species and community responses to environmental variation, links between LES traits and ecosystem function have been best characterized. The effects of RGR, SLA, and leaf N are particularly well studied, with evidence suggesting positive relationships between these traits and primary productivity, litter decomposition rates (see below), plant-available soil N, N turnover rates, and palatability to herbivores, and negative relationships with soil C and N retention (e.g. De Deyn, Cornelissen & Bardgett, 2008; Lavorel & Grigulis, 2012; Loranger *et al.*, 2012; Grigulis *et al.*, 2013). When community-scale analogues of LES traits are considered, similar patterns emerge. Canopy N and leaf area index (LAI) tend to scale positively with SLA and leaf N values, and have also been tied to aboveground net primary productivity (ANPP; Reich, 2012).

The influence of leaf tissue chemistry and structure on decomposition rate is among the most studied aspects of trait influence (de Bello *et al.*, 2010), and traits associated with the LES have been shown to influence decomposition rates in several studies (Santiago, 2007; Cornwell *et al.*, 2008; Bakker, Carreño-Rocabado & Poorter, 2011). Species on the 'fast return' end of the LES (rapid growth, thin leaves, high nutrient concentrations, and high rates of photosynthesis) decompose more quickly than species on the 'slow return' end of the LES (slow growth, thicker, tougher, more recalcitrant leaves with more defences and lower rates of photosynthesis), suggesting that the suite of coordinated structural and chemical leaf traits maximizing photosynthesis also has important implications for nutrient cycling (Santiago, 2007) and the global carbon cycle (Cornwell *et al.*, 2008). However, the effects of the plant community on biogeochemical cycles will likely require more than singular LES traits. For example,

Sutton-Grier, Wright & Richardson (2012) determined that different plant traits had strong effects on plant biomass N (water-use efficiency) *versus* denitrification (e.g. belowground biomass, root porosity), and the traits that maximized one N removal pathway were largely orthogonal to traits that maximized the other. This suggests that multiple species, exhibiting a diversity of traits, may have complex effects on ecosystem functions.

Although plant traits are an important predictor of decomposition, biotic and abiotic factors are also important drivers. For example, in a restored riparian wetland, Sutton-Grier *et al.* (2012) determined that environmental factors including soil organic matter and soil N had approximately the same amount of explanatory power as plant traits. Variation in external factors such as precipitation, grazing, or land use can also exert strong indirect influences on ecosystem function by driving shifts in plant community composition and community-weighted trait means which result in indirect effects on decomposition (Santiago, Schuur & Silvera, 2005; Garibaldi, Semmartin & Chaneton, 2007; Bakker *et al.*, 2011). Similarly, the net influence of plant traits on soil chemistry not only depends on direct effects *via* the quality and quantity of plant litter and exudates, but on indirect effects of these inputs on soil biota (e.g. Orwin *et al.*, 2010; de Vries *et al.*, 2012), whose properties may explain >70% of the variation in N cycling processes (Grigulis *et al.*, 2013). Consequently, models of decomposition will need to identify and incorporate traits as well as critical feedback mechanisms through which biotic and abiotic factors will influence decomposition.

Given the association of LES traits with gas and water exchange, it is likely that these attributes also drive climatic and hydrologic processes (Reich *et al.*, 2014). However, despite their potential utility in earth–atmospheric models (e.g. Van Bodegom *et al.*, 2012; Verheijen *et al.*, 2015) and the understanding that vegetation drastically influences water cycles (e.g. Huxman *et al.*, 2005), demonstrations of theorized trait–effect links are still relatively sparse. High leaf hydraulic conductance and leaf vein density, which are often linked to rapid carbon assimilation, have been predicted to increase evapotranspiration, canopy vapour flux, and precipitation dynamics in historic and current climate models (Boyce *et al.*, 2009; Brodrribb, Feild & Sack, 2010; Lee & Boyce, 2010). Ollinger *et al.* (2008) also found that high canopy N was associated with greater shortwave surface albedo and CO₂ uptake capacity, suggesting LES implications for surface temperatures and atmospheric CO₂ concentrations, respectively. However, the effect of vegetation on carbon budgets will depend not only on the assimilation of carbon, but its subsequent fate in plant–soil interactions, and more work is needed to map the net influence of functional traits on earth–atmosphere fluxes (perhaps using tools such as structural equation modelling, see Section IV.2).

Beyond the LES, plant height is another important axis of plant trait variation (Westoby *et al.*, 2002; Díaz *et al.*, 2004, 2016). Despite its potential to influence a range of ecosystem functions *via* effects on abiotic properties such

as moisture (e.g. Gross *et al.*, 2008), light (e.g. Violle *et al.*, 2009) and standing/litter/microbial biomass (Grigulis *et al.*, 2013), demonstrations are far less frequent than for LES traits (Chapin, 2003; Garnier & Navas, 2012; Lavorel & Grigulis, 2012). Particularly as canopy height becomes easily estimable with remote-sensing data, demonstrated effects of height on ecosystem processes could prove highly valuable in models of ecosystem function at larger scales, making this a key area for interdisciplinary development (Turner, Ollinger & Kimball, 2004).

Our understanding of how root and wood traits influence ecosystem function is less clear compared to other traits (e.g. LES traits), although (as mentioned above) recent studies have suggested that some water-related root and stem traits may align with ‘fast return’ and ‘slow return’ strategies represented by the LES (Chave *et al.*, 2009). For example, lower sapwood density and higher sap flux—which has been positively associated with SLA (O’Grady *et al.*, 2009)—may explain higher evapotranspiration rates observed in an invasive tree species relative to coexisting natives (Swaffer & Holland, 2015). Independent of the LES, root morphological and architectural traits have been shown to influence soil moisture (Gross *et al.*, 2008), soil stability, and erosion (Stokes *et al.*, 2009), with possible impacts on soil structure (Six *et al.*, 2004), leaching and infiltration (De Deyn *et al.*, 2008), and evapotranspiration and climate cycles (Lee *et al.*, 2005). Like foliar traits, there have been relatively few direct tests linking root and wood traits to hydrologic or atmospheric processes, representing a substantial opportunity for research on belowground trait influence. As in leaves, higher density, lignin or dry matter content in roots and wood should slow decomposition and increase soil C storage (Chambers *et al.*, 2000; De Deyn *et al.*, 2008; Klumpp & Soussana, 2009; Freschet, Aerts & Cornelissen, 2012). Unlike foliar tissue, however, root N is not necessarily related to root decomposition rates, which may be complicated by co-occurring effects of substrate chemistry, litter secondary chemistry, or mycorrhizae on root decomposition (Langley, Chapman & Hungate, 2006; Freschet *et al.*, 2012). Quantity and quality of root exudation could also affect soil C and N dynamics, as higher quantities may increase labile C and microbial stimulation (Dijkstra, Hobbie & Reich, 2006; Kaštovská *et al.*, 2015), although the nature of microbial effects may depend on the type of exudate, which is only just beginning to be explored (De Deyn *et al.*, 2008).

Relationships between plant roots and mycorrhizae or N-fixing bacteria should also affect biogeochemical processes. As symbiotic relationships make N and P more available, primary productivity and soil C inputs should generally increase. Furthermore, increased longevity and slower decomposition of colonized roots, along with C immobilization by symbionts, may also increase soil C and N retention (Langley *et al.*, 2006; De Deyn *et al.*, 2008). It is still unclear whether these trends are generalizable, as effects may vary across species of plants, fungi, and/or microbes (Rillig & Mummey, 2006). For example, Cornelissen *et al.* (2001) found plant litter of species associating with ericoid mycorrhizae,

ectomycorrhizae, and arbuscular mycorrhizae to correspond to poor, intermediate, and rapid decomposition rates, respectively. Ecologists are just beginning to understand the wide functional diversity of soil microbial and fungal communities (Van Der Heijden & Scheublin, 2007; McCormack, Lavelle & Ma, 2014); thus, a critical avenue for future research should focus on how traits, plant community composition, and soil biota interact to impact soil carbon dynamics and ecosystem function (e.g. Grigulis *et al.*, 2013).

(c) *Trait selection: future directions*

Moving forward, a main challenge will be identifying which of many traits are likely to be most useful in predicting community and ecosystem dynamics. The initial pool of traits in an analysis will strongly constrain detectable patterns, but including multiple correlated traits in a given model leads to diminishing returns and defeats the purpose of developing a simple way to characterize community and ecosystem function (Laughlin, 2014b). Fortunately, many emerging methods can aid trait selection when many traits or environmental factors may influence species responses. For example, RLQ and fourth corner analyses are ordination and bivariate analyses, respectively, in a multivariate framework which reveal patterns between three data tables containing environmental variables (R), species abundances (L), and species traits (Q) across a range of samples (e.g. plots, sites). Recently, variations in RLQ and fourth corner analyses have been applied to identify objectively the most informative traits as well as their relatedness to environmental variables in multivariate space (e.g. Bernhardt-Römermann *et al.*, 2008; Dray *et al.*, 2014). Using the same type of data, Jamil *et al.* (2013) developed a generalized linear mixed model (GLMM) approach to identify more directly the links between traits, environmental variables, and abundances.

Other models have simultaneously identified traits linked to ecosystem function as well as species responses (Suding *et al.*, 2008). For example, working across a range of sites (e.g. pasture, agricultural, woodland) on the west coast of Scotland, Pakeman (2011) extended RLQ analysis for this purpose, identifying four traits which predicted species distributions across sites based on their relationships with soil/management attributes and ecosystem function parameters. This shortlist included SLA and leaf size, which aligned positively with more fertile, disturbed sites and led to higher rates of decomposition and nutrient cycling, as well as leaf dry matter content (LDMC) and canopy height, which showed opposite associations. This type of multivariate approach could be extended to other types of systems broadly to identify traits linked to both species responses and ecosystem effects. These efforts should also extend beyond the LES to begin identifying traits which may capture less-understood responses and functions (e.g. root architectural traits related to water availability, germination response traits related to regeneration).

A further challenge is that traits, abiotic factors, and species interactions (e.g. competition, facilitation) may interact in non-additive ways to influence community and ecosystem

processes (Suding *et al.*, 2008). For example, while ‘fast return’ LES traits are generally associated with greater herbivore palatability (e.g. Diaz *et al.*, 2004), Loranger *et al.* (2012) found that influences from surrounding plants obscured the predicted trait influence on herbivore damage. Similarly, litter decomposition rates and effects on N cycling may result from non-additive effects of plant traits and soil biota diversity (Hättenschwiler, Tiunov & Scheu, 2005). Consequently, efforts which seek to expand upon our understanding of critical traits must consider abiotic and biotic context as fully as possible and seek to develop models which account for these interactions in a given system, especially across trophic levels (e.g. Lavorel *et al.*, 2013; Pakeman & Stockan, 2014; Deraison *et al.*, 2015). Once key traits are identified and specific hypotheses are generated regarding their links to responses and effects, other statistical approaches such as structural equation modelling can be applied to test how multiple traits ultimately drive community structure (see Section IV.2).

III. INTRASPECIFIC TRAIT VARIATION

Because traits vary across biological, spatial, and temporal scales in a context-dependent manner (e.g. patterns differ for individual traits and species: Siefert *et al.*, 2015), traits need to be accurately characterized within a species or population. Most plant traits are defined and measured on individual plants (e.g. height), on organs within a plant (e.g. leaves), or on populations (e.g. demography; Violle *et al.*, 2007). Ecological studies commonly assign mean trait values to species, justified on the assumption and frequent evidence that more variation occurs between than within species (e.g. Hulshof & Swenson, 2010; Koehler, Center & Cavender-Bares, 2012). However, variation within species can be substantial and both ecologically (e.g. Clark, 2010) and evolutionarily important (e.g. Etterson & Shaw, 2001). For example, Albert *et al.* (2010) measured three traits (maximum vegetative height, LDMC, leaf nitrogen concentration) on 16 co-occurring alpine species with diverse life histories and found approximately 70% of trait variation to occur among species, leaving variation among individuals of a species to account for 30% of trait variation. These values correspond well to a recent global meta-analysis (Siefert *et al.*, 2015). This intraspecific trait variability in natural populations may impact competitive interactions and ultimately community composition (Bolnick *et al.*, 2011), and can influence key ecosystem functions like productivity (Enquist *et al.*, 2015), nutrient cycles (Lecerf & Chauvet, 2008; Madritch & Lindroth, 2015), litter decomposition (Sundqvist, Giesler & Wardle, 2011; Schweitzer *et al.*, 2012), and response to herbivory (Boege & Dirzo, 2004). For example, Madritch & Lindroth (2015) showed using carefully controlled conditions that condensed tannin concentrations varied among aspen genotypes and decreased with increasing nutrient availability. Genotypic variation in leaf chemistry could be directly linked to nutrient cycling *via* herbivore frass and leaf litter N

concentrations. The ‘after-life’ consequences of intraspecific variation in tannin concentrations, a result of both genetic variation and nutrient treatment, influenced the subsequent availability of N to plants.

Population-level studies illustrate the magnitude of intraspecific variation that may be observed as well as the range of functional traits that may vary. For example, studies of species with very large geographic ranges – such as *Pinus sylvestris* and *Quercus virginiana* – have shown substantial between-population variation in leaf nutrient traits (Oleksyn *et al.*, 2003), needle longevity (Reich *et al.*, 2014), seed mass and growth rate/height increment (Reich *et al.*, 2003), hydraulic traits (Martínez-Vilalta *et al.*, 2009), freezing tolerance (Koehler *et al.*, 2012), and leaf morphology (Cavender-Bares *et al.*, 2011). Studies of plant populations have also assessed the degree to which intraspecific trait variation is shaped by genetic variation and phenotypic plasticity, broadly defined as the capacity of an individual to alter their growth in response to disturbance and fluctuating environmental conditions (Valladares, Gianoli & Gomez, 2007). Common garden studies indicate that the substantial intraspecific variation in needle longevity observed with latitude or elevation in *P. sylvestris* and *Picea abies* is more strongly influenced by phenotypic plasticity than genetic variation (Reich *et al.*, 1996). Likewise, studies of foliar phenology in provenance trials of two common European tree species (*Fagus sylvatica* and *Quercus petraea*) suggest that temperature-mediated plasticity is greater than population-based genetic differences or genotypic differences in plasticity (Vitasse *et al.*, 2010). This distinction could have implications for how traits are sampled and used in modelling efforts (see Section III.2).

(1) How is variation in traits distributed across different scales of organization?

Trait variation among repeated organs within a species may be separated into three components (Albert *et al.*, 2011): variation within an individual plant, variation among individuals within a population, and variation among populations. First, at a given point in time, the trait values of organs within a plant might reflect differences in age, environmental conditions, or disturbance history (e.g. herbivory). For example, differences in the sun exposure and age of leaves can lead to marked differences in SLA, $\delta^{13}\text{C}$, and N concentration within a tree crown (Mediavilla & Escudero, 2003; Cavender-Bares, Keen & Miles, 2006; Yan *et al.*, 2012; Legner, Fleck & Leuschner, 2014). Trait values of an individual plant vary across the season due to environmental tracking (*sensu* Bazzaz, 1996) including predictable shifts with phenology (Donohue *et al.*, 2007; McKown *et al.*, 2013) and acclimation to cold temperatures (Wisniewski *et al.*, 1996; Cavender-Bares *et al.*, 2005). Traits also vary with ontogeny from seedlings to adults as plants reach reproductive maturity (Cavender-Bares & Bazzaz, 2000; Lusk & Warton, 2007). Such shifts may reflect, in part, adaptive shifts in traits that accompany changing environments with life stage (Donohue *et al.*, 2010). Second,

trait values may vary among individuals within a population because of both genetic differences among individuals and phenotypic plasticity reflecting environmental conditions, ontogeny, and competition from neighbouring plants (Le Bagousse-Pinguet *et al.*, 2015). Third, trait values may vary among populations of a species, again reflecting both genetic variation and phenotypic plasticity (e.g. Sultan *et al.*, 1998; Sultan, 2001; Donohue *et al.*, 2005).

In addition, patterns of intraspecific variation differ among traits. For instance, Albert *et al.* (2010) found that differences among populations in maximum height (H_{max}) were nearly equal to differences among individuals within populations across several alpine plant species, whereas more variation was observed among individuals within a population than among populations for LDMC. In addition, both the magnitude and patterns of intraspecific variation differed among species, with individuals sampled within a single plot showing two-thirds to less than one third of site-wide variation in LDMC and H_{max} . For organ-level traits, sometimes more variation occurs within individuals than among individuals within populations or between populations. Messier, McGill & Lechowicz (2010) found LDMC to vary more on average within the crown of a tree than among conspecific trees within plots. In the same study, variation in SLA was near equivalent within and among conspecifics within plots.

While interspecific trait variation is typically captured by differences in mean trait values across species, there are also opportunities to integrate metrics of intraspecific variation described above into our understanding of how species differ functionally. For example, phenotypic plasticity can be a critical component of responses to environmental change that differs substantially across species (see Section II.2a). As such, phenotypic plasticity has been explored for its potential to explain differences in ecological strategy and performance between invasive and native species with mixed results (e.g. Funk, 2008; Davidson, Jennions & Nicotra, 2011; Palacio-López & Gianoli, 2011), as well as competitively dominant and non-dominant species (e.g. Ashton *et al.*, 2010; Grassein, Till-Bottraud & Lavorel, 2010). However, while plasticity is often an independent focus of empirical efforts, some evidence suggests that plasticity may tie into our broader understanding of ecological strategies based on mean trait values (Grime & Mackey, 2002). For example, mean plant height represents a major axis of functional variation across species which has also been linked to the extent of aboveground trait plasticity in response to nitrogen or light across several grass and forb species (e.g. Maire *et al.*, 2013; Siebenkäs *et al.*, 2015). Patterns of below-ground trait plasticity across species are less clear (Siebenkäs *et al.*, 2015; Larson & Funk, 2016). There is thus a need for broader testing of the mechanisms underlying interspecific variation in phenotypic plasticity across traits and environmental variables (e.g. Weiner, 2004) and how this variation ultimately informs species and community responses to environmental change. Incorporating metrics of trait plasticity (reviewed in Valladares, Sanchez-Gomez & Zavala, 2006) into trait databases, alongside trait data

that correlate with ecological strategies, would allow us to assess if trait plasticity is an inherent component of ecological strategies across plant community types.

Beyond species, trait variation might be expected to increase hierarchically among clades. However, early opinions were that ecologically important traits are likely to be very labile through evolutionary time (Donoghue, 2008). Empirical studies have begun to determine the extent to which trait values are phylogenetically conserved; for example, seed mass (Moles *et al.*, 2005), wood density (Chave *et al.*, 2006; Kerkhoff *et al.*, 2006), leaf traits (Ackerly & Reich, 1999; Cavender-Bares *et al.*, 2006), xylem traits (Zanne *et al.*, 2010), and disease resistance (Gilbert & Webb, 2007). Additional studies have begun to assess the degree to which phylogeny and functional traits influence community and ecosystem-level processes (Cadotte, Cardinale & Oakley, 2008; Cadotte *et al.*, 2009; Flynn *et al.*, 2011; Cadotte, Dinnage & Tilman, 2012). The early evidence suggests that integrating both metrics can yield highly predictive models (e.g. community assembly; Cadotte, Albert & Walker, 2013).

(2) How does significant variability within species affect our predictions?

How variation is arranged within species influences how we design sampling efforts to capture relevant trait values. How carefully a trait is defined in relation to its environment becomes especially important in standardizing the measurement of traits that are plastic; for example, defining SLA in relation to sun exposure. If high levels of trait differentiation are observed among populations within a study area, sampling methods will need to reflect such differentiation to capture one or more trait values pertinent to the study question.

The nature and scale of the questions being asked is critical. If we are interested in mechanisms of coexistence (internal community dynamics), sampling to capture intraspecific variation is likely to be important. Recent work increasingly supports the importance of individual-level variation for understanding trade-offs among species that enable coexistence of species (Clark *et al.*, 2010). By contrast, if we are interested in ecosystem consequences of plant community composition, capturing the mean and variance of trait values at the species level may provide sufficient resolution for predictive models. Still, intraspecific variation could indirectly influence our ability to model ecosystem effects of plant communities. A critical and timely example is forecasting changes in species distributions in response to climate change. Studies of genetic diversity and local adaptation repeatedly reveal that genotypes and populations within species differ in their sensitivity to climate (e.g. Shaw & Etterson, 2012; Alberto *et al.*, 2013; Ramírez-Valiente, Koehler & Cavender-Bares, 2015). Shifts in species distributions with climate are thus unlikely to be reasonably well predicted without taking this variation into account, making the ecosystem-level consequences (e.g. carbon uptake) difficult to model.

Most traditional approaches used to model collections of species, such as dynamical systems models (e.g. Warner & Chesson, 1985; Tilman, 2004), can be modified to handle some degree of intraspecific variation by including separate classes for each discrete phenotype within a species. Individual-based models (Grimm & Railsback, 2005) go further by tracking every individual in a community. Both of these methods can potentially become cumbersome for speciose communities that include highly variable species. Some studies simplify these issues by incorporating intraspecific variability into standard statistical analyses by using different mean trait values for populations at different locations along a gradient of interest (e.g. Ackerly & Cornwell, 2007; Jung *et al.*, 2010; Violle *et al.*, 2012). These methods can still be somewhat limiting as focusing on the mean trait, even within subpopulations, neglects the effect of extreme values in the tails of the trait distributions, which may have a profound impact on community response to the environment (Bolnick *et al.*, 2011). Ames, Anderson & Wright (2015) found that statistical inference regarding the environmental drivers of trait variation was greatly altered when using regional species means rather than locally measured trait values. There are several modelling approaches that are better suited for incorporating intraspecific variation into models of community dynamics and function.

Bayesian hierarchical models (BHM, Gelman *et al.*, 2004; Gelman & Hill, 2007) incorporate the hierarchical relationships inherent in scaling from the traits of individuals up to the structure/function of the community in which they are embedded (Clark, 2005). In a BHM, a species' trait distributions are explicitly incorporated into one of the levels of the hierarchy, and uncertainty around trait distributions are considered by including prior distributions on the parameters of the trait distributions. Further, the parameters of the trait distribution can be functions of biotic and/or abiotic environmental factors in order to capture changes to the trait distribution that are driven by changing environmental conditions. A major advantage of BHMs is that they allow the user to explore relationships among traits, the environment, and organismal performance without knowing, *a priori*, the mechanisms that relate them (Webb *et al.*, 2010). However, these models are limited to forecasting within the range of the data used to fit them. Thus, BHMs are beneficial in identifying the traits and environmental drivers that are most important in driving the dynamics of a community. Because the trait distributions and their parameters are described explicitly, it is also possible to explore directly the impact of changes in intraspecific trait variation on the dynamics of the species and the community as a whole.

Dynamical systems models have been developed that explicitly describe the temporal dynamics of the community trait distribution in response to environmental forcing for either a single trait (Norberg *et al.*, 2001) or multiple, correlated traits (Savage, Webb & Norberg, 2007). These models use moment closure, a technique that approximates complete distributions using only low-order moments such as means and variances, to describe the whole community trait

distribution as a function of biotic or abiotic environmental factors. A drawback to this approach is that it requires an explicit, known functional relationship between traits, environment, and organismal performance. However, this allows these models to predict changes in the trait distribution that result from environmental forcing outside of the observed range, such as that expected from climate change. An interesting feature of these models is that they aggregate inter- and intraspecific variation into a single community trait distribution. This results in a loss of information about species identity and changes in relative abundances. On the other hand, for cases where the trait(s) are strongly related to an ecosystem function of interest, these models may allow robust prediction of function while ignoring extraneous details of species composition. A more integrative approach incorporates the predictive power of deterministic, dynamical systems models with the ability of Bayesian models to incorporate empirical data and generate measures of uncertainty associated with the model output. These ‘first principles Bayesian multilevel models’ (Webb *et al.*, 2010) embed known mechanistic relationships into a BHM and thereby allow prediction outside of the observed range of data while simultaneously estimating uncertainty (Bayesian credible intervals) associated with those predictions.

IV. SCALING TRAIT–ENVIRONMENT RELATIONSHIPS TO COMMUNITY AND ECOSYSTEM LEVELS

Nearly all traits vary systematically along broad environmental gradients. At the same time, nearly half of the global variation of many traits can be found within individual communities (Wright *et al.*, 2004). Variation in trait values among communities can be used to predict changes in ecosystem functioning under persistent changes in the environment (Suding *et al.*, 2008; Klumpp & Soussana, 2009), while variation within communities can predict the resilience of ecosystem functioning to disturbance (Mori, Furukawa & Sasaki, 2013). Systematic variation in trait distributions along environmental gradients can also reveal environmentally dependent assembly rules (Keddy, 1992; Ackerly & Cornwell, 2007), thereby linking community assembly theory to models of biodiversity–ecosystem functioning (Naeem & Wright, 2003). Trait–environment relationships are becoming increasingly well described with ‘global’ trait–environment relationships assessed for many traits (Wright *et al.*, 2004; Moles *et al.*, 2007, 2009; Zanne *et al.*, 2010), although the current state of knowledge in this area is hugely variable, with some traits, functional indices, and environmental gradients much more intensively studied than others.

(1) Community-level metrics of plant function

Perhaps the simplest measure of community-level functional composition is the community-weighted mean (CWM) trait value, which uses the relative abundances of species

and their trait values to calculate a community aggregated trait value (Violle *et al.*, 2007). Not only does variation in CWM trait values identify shifts in assembly filters along environmental gradients (Ackerly & Cornwell, 2007), it is also perhaps the strongest determinant of biotic effects on ecosystem functioning (Fortune *et al.*, 2009; Lavorel *et al.*, 2011; Laliberté & Tylianakis, 2012) as more abundant species have a disproportionate influence on ecosystem processes (mass ratio hypothesis; Grime, 1998). A simple null hypothesis is that CWM–environment relationships are identical to interspecific trait–environment relationships, at least qualitatively speaking. At the resolution of 1° of latitude and longitude, Swenson *et al.* (2012) found that CWM values of leaf traits, height, seed mass, and wood density based on species occurrences were relatively strongly correlated with annual mean and seasonality of temperature and precipitation in ways that were consistent with expectations based on species trait–environment patterns across much of the Western Hemisphere. However, trait–environment relationships do not always scale linearly from the species to community levels due to interactions between multiple environmental factors (Rosbakh, Römermann & Poschlod, 2015) and assembly processes that may not favour species with intermediate trait values. For example, in one set of woody plant communities, over 80% of traits were found to have linear or context-dependent abundance distributions within communities while only one was unimodal (Cornwell & Ackerly, 2010), thereby producing CWM–environment relationships that differ from expectations based on interspecific patterns. This difference was likely due to coordinated ecological selection on multiple traits that differed from the evolutionary and biogeographic factors that determined trait correlations among species in the regional pool. Research aimed at identifying these processes and the trait–abundance distributions that they generate is essential for improving predictive models of CWM–environment relationships.

Functional diversity indices capture the distribution of trait values within communities and can also demonstrate systematic variation along environmental gradients. Functional diversity can be broken down into three orthogonal components – richness, evenness, and divergence (Mason *et al.*, 2005) – that are represented in various ways by different indices. The range, or functional richness (Villegger *et al.*, 2008), of trait values within a community can be indicative of the intensity of environmental assembly filters (Cornwell, Schilke & Ackerly, 2006), and can have significant effects on ecosystem functioning (Clark *et al.*, 2012; Butterfield & Suding, 2013). The range of trait values is expected to decrease with increasing environmental severity (i.e. environmental filtering), a hypothesis that has been supported for a variety of traits at fine (Cornwell & Ackerly, 2009; Jung *et al.*, 2010; Kooyman, Cornwell & Westoby, 2010) and coarse (Swenson *et al.*, 2012) spatial scales, but not in all cases (Coyle *et al.*, 2014). Species may, for example, use contrasting strategies to deal with stress (e.g. stress avoidance *versus* tolerance; Ludlow, 1989), resulting in divergent traits and greater functional richness. The distribution of trait

values within a community, as described by functional evenness may also vary systematically along environmental gradients, although indirectly: even spacing of trait values may reflect competition (which may be expected to increase with productivity; Grime, 1977) and, consequently, niche partitioning – although this pattern is not consistently supported (Cornwell & Ackerly, 2009; Jung *et al.*, 2010). Which traits exhibit systematic variation in functional richness or evenness along environmental gradients should depend on their roles in community assembly. Traits related to environmental filtering ought to influence functional richness, while those related to competition ought to influence functional evenness.

The trait–environment predictions outlined above follow from relatively simple models of community assembly, although several studies have demonstrated that biotic interactions can strongly alter trait–environment predictions. Trait-based community assembly studies have typically focused on the convergence–divergence paradox which states that species with similar environmental tolerances and requirements – reflected in the similarity of their functional trait values – may experience simultaneous, competing forces: similar species are more likely to co-occur (converge), and thus to compete more strongly (diverge; Weiher, Clarke & Keddy, 1998; Adler *et al.*, 2013). However, there is increasing evidence that using functional divergence (i.e. degree of niche differentiation; Mason *et al.*, 2005; Vileger *et al.*, 2008) to infer whether environmental filtering or competition mechanisms are operating most strongly in communities may be narrow-sighted. This framework overlooks the fact that plants often compete *via* hierarchical differences in traits (fitness differences) rather than *via* limiting similarity (niche differences; Kunstler *et al.*, 2012, 2016). A consequence of competitive hierarchies is a reduction in the range of trait values observed within a community, where species at one end of a trait spectrum are competitively excluded, and functional divergence is not observed. Furthermore, high divergence could result from the success of different strategies dealing with stress (as described above) rather than from competition. This pattern could also be enabled by facilitation, which has been shown to increase the range of trait values in a community through the creation of favourable microenvironments allowing species with otherwise unsuitable trait values to persist (Gross *et al.*, 2009; Butterfield & Briggs, 2011). In a study of alpine plant communities, Schöb, Butterfield & Pugnaire (2012) found that the magnitude of the net effects of competition and facilitation on the CWM, richness, and evenness of trait distributions was proportional to the effects of broad environmental gradients, and that the biotic effects on trait distributions often countered those of the environment. In short, biotic interactions can substantially alter trait–environment relationships in a variety of ways, and a better understanding of the functional trait basis of interaction outcomes is essential for integrating these effects into predictive models of trait–environment relationships (Butterfield & Callaway, 2013).

In addition to single-trait indices, multi-trait indices of functional composition can be used to represent the multi-dimensional nature of the ‘niche’ (Vileger *et al.*, 2008), while other metrics such as dendrogram-based indices (Petchey & Gaston, 2002) combine richness and evenness. However, functional richness—the key indicator of functional spread within communities—could be heavily influenced by rare, outlying species. Abundance-weighted measures of spread, such as functional dispersion (Laliberté & Legendre, 2010) and Rao’s quadratic entropy (Botta-Dukat, 2005) may more accurately predict some ecosystem functions as the traits of dominant species have stronger effects (i.e. mass ratio hypothesis; Grime, 1998). A great deal of research has gone into the mathematical properties and ecological justifications of these different indices (Petchey & Gaston, 2006; Mouchet *et al.*, 2010); however, their relative performance in identifying biotic responses to a wide variety of environmental gradients, as well as biotic effects on various ecosystem processes, are only just beginning to be addressed (McGill, Sutton-Grier & Wright, 2010; Sutton-Grier *et al.*, 2011).

Deciding which indices to apply to a given trait-based question is not a simple task given the potential relevance of many traits and diversity metrics. Single-trait indices may retain more information, as opposed to combining their variation into composite indices. This may mirror the issue of inter- *versus* intraspecific trait variation discussed above, where the variance in trait values may be reduced through aggregation. Single-trait indices may also provide a better understanding of the complexity of responses to environmental gradients, as well as effects on ecosystem processes, and may in fact be necessary for elucidating response–effect patterns in complex landscapes (Butterfield & Suding, 2013) and identifying multiple assembly processes that act simultaneously along environmental gradients (Spasojevic & Suding, 2012). On the other hand, there are examples of patterns that can only be revealed through multi-trait indices, both for community assembly (Vileger, Novack-Gottshall & Mouillot, 2011) and effects on ecosystem processes (Mouillot *et al.*, 2011). Additionally, while most studies have linked functional diversity to single ecosystem processes (e.g. productivity), there is also mounting evidence that multi-trait metrics (e.g. functional divergence and dispersion) may be useful in predicting multiple processes simultaneously (i.e. multifunctionality; Mouillot *et al.*, 2011; Valencia *et al.*, 2015). At this stage in our understanding, it is important to use both single- and multi-trait indices to examine individual and multifunctional responses or effects on ecosystems, since no generalization is yet available as to which indices may be superior for specific questions. However, useful prescriptions for trait selection and aggregation exist (Vileger *et al.*, 2008) that can aid in comparing and contrasting index performance as we move forward.

(2) Applying community-level metrics at global scales

For TBE to be predictive, relationships between response traits and environmental conditions and disturbance regimes

need to be globally consistent. It is currently unknown whether statistical models that link response traits to environmental conditions in one ecosystem can be easily transferred and applied to another ecosystem on another continent. This lack of generality is partly hindered by the lack of a global-scale database of vegetation composition and associated environmental data. Efforts are underway to develop such a database (sPlot, <http://www.idiv-biodiversity.de/sdiv/workshops/workshops-2013/splot>), which will link directly to a global-scale trait database (Kattge *et al.*, 2011). This research will be instrumental for advancing our understanding of how traits vary along the full range of environmental conditions throughout the planet. In the meantime, however, there is a wealth of published trait–environment relationships that can be synthesized through meta-analysis (Gurevitch & Hedges, 2001). Meta-analysis can be used to determine the consistency of trait responses to environmental conditions and disturbance regimes across multiple studies, and can also be used to rank the importance of traits based on their effect sizes and their consistency of response (e.g. Díaz *et al.*, 2007b; Cornwell *et al.*, 2008).

To predict the response of communities to environmental conditions in new sites or times, it will be necessary to identify the critical predictor variables for those new sites and times. The best-resolved trait–environment relationships demonstrate the influence of temperature and precipitation gradients on interspecific variation in trait values. A recent study found that temperature is a stronger predictor of trait variation than is precipitation across a variety of traits (Moles *et al.*, 2014), likely due to the direct effects of temperature on plant function relative to the less proximate relationship between precipitation and soil moisture dynamics. Predictors of water stress that integrate temperature, precipitation, and other factors that influence soil moisture supply are typically better predictors of plant trait spectra than temperature or precipitation alone (Wright *et al.*, 2004). Soil data are becoming better each year, but the quality of soil data varies among countries, and often within countries. Current climate data and future climate projections are available at a global scale as data layers in Geographical Information Systems (Hijmans *et al.*, 2005). The tools for predicting future responses are increasing rapidly, but the accuracy of our predictions will depend heavily on the precision of these future projections. As access to accurate, consistent environmental data improves, predicting changes in community composition can be accomplished using trait-based models that yield a predicted relative abundance for every species in the local pool based on the traits of the species and the relationships between traits and the environment (Laughlin & Laughlin, 2013).

Our ability to predict ecosystem processes under changing environmental conditions is also contingent on our understanding of the relative importance of both abiotic conditions and the effect traits of the community (Díaz *et al.*, 2007a), and how to account for multiple important factors in predictive models. For example, litter decomposition rate

has been shown to be a function of the local climate, the composition of the microbial community, and the physical and chemical traits of the litter (see Section II.2b). Structural equation modelling (SEM) is a useful tool to quantify the unique effects that are attributable to multiple abiotic *versus* biotic components of the ecosystem (Mokany, Ash & Roxburgh, 2008). SEM permits the specification of a network of relationships that are characteristic of complex systems (Grace, 2006). The standardized path coefficients that describe the statistical relationships among variables are similar to partial regression coefficients, and the absolute values of these coefficients can be ranked to compare their impact on an ecosystem process. For example, nitrification potential was shown to be most strongly driven by the direct effects of abiotic soil properties such as pH, temperature, and nitrogen availability, and only weakly driven by the LES traits in the understorey plant community (Laughlin, 2011). In other words, altering the functional composition of leaf traits in this pine forest understorey plant community would have less effect on internal nitrogen cycling than if we altered the abiotic properties of the soil. In another example, SEM was used to discover that ecosystem multifunctionality was driven equally by both the average and the diversity of traits in a dryland community (Valencia *et al.*, 2015). The ability of SEM to parse out the influence of many factors and feedbacks is proving it to be an extremely useful tool for TBE as seen in several recent studies (Mokany *et al.*, 2008; Laughlin, 2011; Laliberté & Tylianakis, 2012; Lavorel *et al.*, 2013; Valencia *et al.*, 2015); multivariate tools such as these will have a critical role in realistic predictions of ecosystem dynamics moving forward.

Finally, in addition to forecasting the future, TBE can also be used to back-cast previous palaeoecological transitions, a very useful approach to predicting changes in the future. For example, the end-Cretaceous mass extinction of plants resulted in a shift towards dominance of plants with lower LMA and higher vein density, which is consistent with a faster growth strategy in the cold and dark impact winter that followed the Chicxulub bolide impact (Blonder *et al.*, 2014). Changes in leaf vein density have also been observed over much longer timescales throughout the Cretaceous (Feild *et al.*, 2011), with the emergence of high vein densities in angiosperms likely corresponding to major shifts in climatic and hydrological processes *via* increased evapotranspiration rates and associated feedbacks (Boyce *et al.*, 2009). Combining information about how traits have responded to previous climate changes with current trait–environment relationships will enhance our ability to predict how traits will respond to future environmental change.

V. CONCLUSIONS

(1) Trait-based ecology can be a powerful approach to explain and predict highly complex systems. While our

understanding of key components of TBE (e.g. response traits, effect traits, functional diversity) has developed continuously since Lavorel & Garnier (2002) introduced their trait-based conceptual framework, many challenges remain.

(2) We have highlighted several exciting areas for future research. The usefulness of traits in predictive models hinges on deepening our understanding of which traits drive ecological processes at organismal, community, and ecosystem scales. While soft traits, such as SLA or wood density, show much promise in explaining some metrics of plant function (e.g. RGR) and species distributions, it remains to be seen if these traits can simultaneously predict multiple ecological processes across diverse community types. We demonstrated that genetic variation and phenotypic plasticity can strongly influence a range of plant functions, but how these two components contribute to intraspecific trait variation and ecological strategies across a range of species needs to be addressed. Furthermore, future work needs to identify how intraspecific trait variation should be quantified and incorporated into models. Our review also highlighted the need to understand how non-additive effects of traits, species interactions, and abiotic factors influence community- and ecosystem-level processes, and how these separate components may be incorporated into cohesive and predictive frameworks. While TBE has seen many recent advances in modelling approaches, we still do not know if algorithms developed in one community can be applied at larger spatial and temporal scales. Progress on all of these questions will be facilitated by improvements in the quality and availability of trait and environmental data.

(3) While this review has focused on how TBE informs our understanding of basic ecological processes, work is underway to apply this framework to conservation and restoration programs (e.g. Funk *et al.*, 2008; Laughlin, 2014a). For example, traits have been used to identify native species from regional species pools that can tolerate certain abiotic conditions or compete with invasive species (Funk & McDaniel, 2010; Kimball *et al.*, 2014), and re-establish critical ecosystem services (e.g. pollination services: Lavorel *et al.*, 2011).

(4) The potential for TBE to improve our understanding of basic and applied ecological processes makes the need for empirical tests of this framework a priority in ecology.

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