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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.

CONTENTS

I. INTRODUCTION

Ecologists have a long tradition of grouping organisms based on function (Grime, 1974; Raunkiaer, 1934; Root, 1967). 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 (Chapin *et al.*, 2000; Díaz & Cabido, 1997; Lavorel *et al.*, 1997). 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. McGill *et al.*, 2006*a*; Westoby & Wright, 2006). 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, 2006*b*). 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. Bokhorst *et al.*, 2012; Fierer, Barberán & Laughlin, 2014; Haddad *et al.*, 2008; Litchman *et al.*, 2007; 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 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.*, 2007; Lavorel & Garnier, 2002; Lavorel *et al.*, 1997). 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 C_4 perennial grasses or C_3 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 (Firn *et al.*, 2010, 2012; Funk, 2008; 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 (Lavorel *et al.*, 2007; Westoby & Wright, 2006). Interspecific differences in continuous traits have been linked to environmental gradients (e.g. Wright *et al.*, 2005; Wright & Westoby, 1999), 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 (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.*, 2007*a*; Villeger, 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. Aubin *et al.*, 2009; Fry, Power & Manning, 2014; Grime *et al.*, 1997; Pillar & Sosinski, 2003); however, identification of consistent groups and demonstrations of their utility in predictive models remain sparse and equivocal (e.g. Larson *et al.*, 2015; Louault *et al.*, 2005; Müller *et al.*, 2007).

(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 BiolFlor (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 empircal 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, 1977; Grime & Hunt, 1975; Hunt & Cornelissen, 1997). Unfortunately, it is also difficult and time-consuming to measure. However,

251 RGR is a ‘synthetic’ trait summarizing the outcome of several processes (e.g.
252 photosynthesis, respiration, nutrient allocation, life-history strategies) that
253 are tied to other measurable traits, such as leaf nitrogen (N) concentration,
254 photosynthetic rate, tissue density, and SLA. A small number of soft traits,
255 such as SLA or wood density, can explain a large portion of the variation in
256 RGR across a large range of herbaceous and woody plant species (Hunt &
257 Cornelissen, 1997; Nguyen *et al.*, 2014; Poorter *et al.*, 2008; Walker &
258 Langridge, 2002).

259 In addition, terrestrial plants exhibit a consistent trade-off among these
260 growth-related traits within the LES, such that high SLA is often linked to
261 higher leaf N concentration and photosynthetic rate at the expense of tissue
262 density and longevity. Consequently, soft traits like SLA or plant tissue
263 density may also serve to represent functional strategies of nutrient
264 acquisition and conservation, across a wide range of taxa and ecosystem
265 types (Díaz *et al.*, 2004; Walker & Langridge, 2002; Wright *et al.*, 2004).
266 While these trade-offs may not be exhibited in all species or plant systems
267 (e.g. wetlands and grasslands: Funk & Cornwell, 2013; Wright & Sutton-Grier,
268 2012), the ubiquity of these trade-offs across many environmental and
269 disturbance gradients, coupled with their strong relationship to important
270 demographic rates (Donohue *et al.*, 2010), suggests that these traits are
271 associated with mechanisms determining plant success in response to
272 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, 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). However, the traits most closely linked to plant performance 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.

296 dispersal/colonization, resprouting, germination, emergence) also have
297 significant implications for population dynamics and community composition
298 (Aicher, Larios & Suding, 2011; Donohue *et al.*, 2010; Flores-Moreno & Moles,
299 2013; Pakeman & Eastwood, 2013; Zeiter, Stampfli & Newbery, 2006), but
300 are not well represented in trait-based theoretical frameworks.

301 Although mean trait values for organisms and species are typically
302 used in predictive models, there is growing evidence that species vary in
303 their phenotypic responses to changing abiotic and biotic factors (i.e.
304 phenotypic plasticity, see Section III), which contributes to functional
305 variation within communities (e.g. Ashton *et al.*, 2010; Firn *et al*., 2012; Funk,
306 2008; Larson & Funk, 2016; Siebenkäs, Schumacher & Roscher, 2015).
307 Although empirical links between phenotypic plasticity and performance or
308 fitness are still rare across species (Van Kleunen & Fischer, 2005; Firn *et al.*,
309 2012), if plasticity is adaptive it could be an important metric related to
310 population, species, and community responses to environmental change
311 (reviewed in Berg & Ellers, 2010; Nicotra *et al.*, 2010; Valladares *et al.*,
312 2014). For example, leaf trait plasticity has been linked to productivity and
313 plant growth in response to both nitrogen availability and cutting (da Silveira
314 Pontes *et al.*, 2010) as well as temperature and water availability (Liancourt
315 *et al.*, 2015). Ultimately, while belowground traits, regenerative traits, and
316 intraspecific trait variation have long been recognized as key (albeit difficult)
317 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; Dorrough, 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 (de Bello *et al.*, 2010; Eviner & Chapin, 2003; 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; Grigulis *et al.*, 2013; Lavorel & Grigulis, 2012; Loranger *et al.*, 2012). 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 (Bakker, Carreño-Rocabado & Poorter, 2011; Cornwell *et al.*, 2008; see for example Santiago, 2007). 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)

387 *versus* denitrification (e.g. belowground biomass, root porosity), and the
388 traits that maximized one N removal pathway were largely orthogonal to
389 traits that maximized the other. This suggests that multiple species,
390 exhibiting a diversity of traits, may have complex effects on ecosystem
391 functions.

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

410 Given the association of LES traits with gas and water exchange, it is
411 likely that these attributes also drive climatic and hydrologic processes
412 (Reich *et al.*, 2014). However, despite their potential utility in earth–
413 atmospheric models (e.g. Van Bodegom *et al.*, 2012; Verheijen *et al.*, 2015)
414 and the understanding that vegetation drastically influences water cycles
415 (e.g. Huxman *et al.*, 2005), demonstrations of theorized trait–effect links are
416 still relatively sparse. High leaf hydraulic conductance and leaf vein density,
417 which are often linked to rapid carbon assimilation, have been predicted to
418 increase evapotranspiration, canopy vapour flux, and precipitation dynamics
419 in historic and current climate models (Boyce *et al.*, 2009; Brodribb, Feild &
420 Sack, 2010; Lee & Boyce, 2010). Ollinger *et al.* (2008) also found that high
421 canopy N was associated with greater shortwave surface albedo and CO_2
422 uptake capacity, suggesting LES implications for surface temperatures and
423 atmospheric CO_2 concentrations, respectively. However, the effect of
424 vegetation on carbon budgets will depend not only on the assimilation of
425 carbon, but its subsequent fate in plant–soil interactions, and more work is
426 needed to map the net influence of functional traits on earth–atmosphere
427 fluxes (perhaps using tools such as structural equation modelling, see
428 Section IV.2).
429 Beyond the LES, plant height is another important axis of plant trait
430 variation (Díaz *et al.*, 2004, 2016; Westoby *et al.*, 2002). Despite its potential
431 to influence a range of ecosystem functions *via* effects on abiotic properties
432 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 improvements in remote-sensing data and techniques, 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; Freschet, Aerts & Cornelissen, 2012; Klumpp & Soussana, 2009). 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 (Freschet *et al.*, 2012; Langley, Chapman & Hungate, 2006). 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 (De Deyn *et al.*, 2008; Langley *et al.*, 2006). 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

479 rates, respectively. Ecologists are just beginning to understand the wide
480 functional diversity of soil microbial and fungal communities (McCormack,
481 Lavely & Ma, 2014; Van Der Heijden & Scheublin, 2007); thus, a critical
482 avenue for future research should focus on how traits, plant community
483 composition, and soil biota interact to impact soil carbon dynamics and
484 ecosystem function (e.g. Grigulis *et al.*, 2013).
485
486 (*c*) *Trait selection: future directions*
487 Moving forward, a main challenge will be identifying which of many
488 traits are likely to be most useful in predicting community and ecosystem
489 dynamics. The initial pool of traits in an analysis will strongly constrain
490 detectable patterns, but including multiple correlated traits in a given model
491 leads to diminishing returns and defeats the purpose of developing a simple
492 way to characterize community and ecosystem function (Laughlin, 2014*b*).
493 Fortunately, many emerging methods can aid trait selection when many
494 traits or environmental factors may influence species responses. For
495 example, RLQ and fourth corner analyses are ordination and bivariate
496 analyses, respectively, in a multivariate framework which reveal patterns
497 between three data tables containing environmental variables (R), species
498 abundances (L), and species traits (Q) across a range of samples (e.g. plots,
499 sites). Recently, variations in RLQ and fourth corner analyses have been
500 applied to identify objectively the most informative traits as well as their
501 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 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. Díaz *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. Deraison *et al.*, 2015; Lavorel *et al.*, 2013; Pakeman & Stockan, 2014). 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 capture and 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

548 commonly assign mean trait values to species, justified on the assumption
549 and frequent evidence that more variation occurs between than within
550 species (e.g. Hulshof & Swenson, 2010; Koehler, Center & Cavender-Bares,
551 2012). However, variation within species can be substantial and both
552 ecologically (e.g. Clark, 2010) and evolutionarily important (e.g. Etterson &
553 Shaw, 2001). For example, Albert *et al.* (2010) measured three traits
554 (maximum vegetative height, LDMC, leaf nitrogen concentration) on 16 co-
555 occurring alpine species with diverse life histories and found approximately
556 70% of trait variation to occur among species, leaving variation among
557 individuals of a species to account for 30% of trait variation. These values
558 correspond well to a recent global meta-analysis (Siefert *et al.*, 2015). This
559 intraspecific trait variability in natural populations may impact competitive
560 interactions and ultimately community composition (Bolnick *et al.*, 2011),
561 and can influence key ecosystem functions like productivity (Enquist *et al.*,
562 2015), nutrient cycles (Lecerf & Chauvet, 2008; Madritch & Lindroth, 2015),
563 litter decomposition (Sundqvist, Giesler & Wardle, 2011; Schweitzer *et al.*,
564 2012), and response to herbivory (Boege & Dirzo, 2004). For example,
565 Madritch & Lindroth (2015) showed using carefully controlled conditions that
566 condensed tannin concentrations varied among aspen genotypes and
567 decreased with increasing nutrient availability. Genotypic variation in leaf
568 chemistry could be directly linked to nutrient cycling *via* herbivore frass and
569 leaf litter N concentrations. The ‘after-life’ consequences of intraspecific

570 variation in tannin concentrations, a result of both genetic variation and
571 nutrient treatment, influenced the subsequent availability of N to plants.
572 Population-level studies illustrate the magnitude of intraspecific
573 variation that may be observed as well as the range of functional traits that
574 may vary. For example, studies of species with very large geographic ranges
575 – such as *Pinus sylvestris* and *Quercus virginiana* – have shown substantial
576 between-population variation in leaf nutrient traits (Oleksyn *et al.*, 2003),
577 needle longevity (Reich *et al.*, 2014), seed mass and growth rate/height
578 increment (Reich *et al.*, 2003), hydraulic traits (Martínez-Vilalta *et al.*, 2009),
579 freezing tolerance (Koehler *et al.*, 2012), and leaf morphology (Cavender-
580 Bares *et al.*, 2011). Studies of plant populations have also assessed the
581 degree to which intraspecific trait variation is shaped by genetic variation
582 and phenotypic plasticity, broadly defined as the capacity of an individual to
583 alter their growth in response to disturbance and fluctuating environmental
584 conditions (Valladares, Gianoli & Gomez, 2007). Common garden studies
585 indicate that the substantial intraspecific variation in needle longevity
586 observed with latitude or elevation in *P. sylvestris* and *Picea abies* is more
587 strongly influenced by phenotypic plasticity than genetic variation (Reich *et*
588 *al.*, 1996). Likewise, studies of foliar phenology in provenance trials of two
589 common European tree species (*Fagus sylvatica* and *Quercus petraea*)
590 suggest that temperature-mediated plasticity is greater than population-
591 based genetic differences or genotypic differences in plasticity (Vitasse *et*

592 *al.*, 2010). This distinction could have implications for how traits are sampled
593 and used in modelling efforts (see Section III.2).
594
595 **(1) How is variation in traits distributed across different scales of**
596 **organization?**
597 Trait variation among repeated organs within a species may be
598 separated into three components (Albert *et al.*, 2011): variation within an
599 individual plant, variation among individuals within a population, and
600 variation among populations. First, at a given point in time, the trait values
601 of organs within a plant might reflect differences in age, environmental
602 conditions, or disturbance history (e.g. herbivory). For example, differences
603 in the sun exposure and age of leaves can lead to marked differences in SLA,
604 $\delta^{13}C$, and N concentration within a tree crown (Cavender-Bares, Keen &
605 Miles, 2006; Legner, Fleck & Leuschner, 2014; Mediavilla & Escudero, 2003;
606 Yan *et al.*, 2012). Trait values of an individual plant vary across the season
607 due to environmental tracking (*sensu* Bazzaz, 1996) including predictable
608 shifts with phenology (Donohue *et al.*, 2007; McKown *et al.*, 2013) and
609 acclimation to cold temperatures (Cavender-Bares *et al.*, 2005; Wisniewski *et*
610 *al.*, 1996). Traits also vary with ontogeny from seedlings to adults as plants
611 reach reproductive maturity (Cavender-Bares & Bazzaz, 2000; Lusk &
612 Warton, 2007). Such shifts may reflect, in part, adaptive shifts in traits that
613 accompany changing environments with life stage (Donohue *et al.*, 2010).
614 Second, trait values may vary among individuals within a population because

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

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

635 While interspecific trait variation is typically captured by differences in
636 mean trait values across species, there are also opportunities to integrate
637 metrics of intraspecific variation described above into our understanding of

638 how species differ functionally. For example, phenotypic plasticity can be a
639 critical component of responses to environmental change that differs
640 substantially across species (see Section II.2*a*). As such, phenotypic plasticity
641 has been explored for its potential to explain differences in ecological
642 strategy and performance between invasive and native species with mixed
643 results (e.g. Davidson, Jennions & Nicotra, 2011; Funk, 2008; Palacio-López &
644 Gianoli, 2011), as well as competitively dominant species and non-dominant
645 species (e.g. Ashton *et al.*, 2010; Grassein, Till-Bottraud & Lavorel, 2010).
646 However, while plasticity is often an independent focus of empirical efforts,
647 some evidence suggests that plasticity may tie into our broader
648 understanding of ecological strategies based on mean trait values (Grime &
649 Mackey, 2002). For example, mean plant height represents a major axis of
650 functional variation across species which has also been linked to the extent
651 of aboveground trait plasticity in response to nitrogen or light across several
652 grass and forb species (e.g. Maire *et al.*, 2013, Siebenkäs *et al.*, 2015).
653 Patterns of below-ground trait plasticity across species are less clear
654 (Siebenkäs *et al.*, 2015; Larson & Funk, 2016). There is thus a need for
655 broader testing of the mechanisms underlying interspecific variation in
656 phenotypic plasticity across traits and environmental variables (e.g. Weiner,
657 2004) and how this variation ultimately informs species and community
658 responses to environmental change. Incorporating metrics of trait plasticity
659 (reviewed in Valladares, Sanchez-Gomez & Zavala, 2006) into trait
660 databases, alongside trait data that correlate with ecological strategies,

661 would allow us to assess if trait plasticity is an inherent component of
662 ecological strategies across plant community types.
663 Beyond species, trait variation might be expected to increase
664 hierarchically among clades. However, early opinions were that ecologically
665 important traits are likely to be very labile through evolutionary time
666 (Donoghue, 2008). Empirical studies have begun to determine the extent to
667 which trait values are phylogenetically conserved; for example, seed mass
668 (Moles *et al.*, 2005), wood density (Chave *et al.*, 2006; Kerkhoff *et al.*, 2006),
669 leaf traits (Ackerly & Reich, 1999; Cavender-Bares *et al.*, 2006), xylem traits
670 (Zanne *et al.*, 2010), and disease resistance (Gilbert & Webb, 2007).
671 Additional studies have begun to assess the degree to which phylogeny and
672 functional traits influence community and ecosystem-level processes
673 (Cadotte, Cardinale & Oakley, 2008; Cadotte *et al.*, 2009; Cadotte, Dinnage &
674 Tilman, 2012; Flynn *et al.*, 2011). The early evidence suggests that
675 integrating both metrics can yield highly predictive models (e.g. community
676 assembly; Cadotte, Albert & Walker, 2013).
677
678 **(2) How does significant variability within species affect our**
679 **predictions?**
680 How variation is arranged within species influences how we design
681 sampling efforts to capture relevant trait values. How carefully a trait is
682 defined in relation to its environment becomes especially important in
683 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; Ramirez-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. Tilman, 2004; Warner & Chesson, 1985), 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 (BHMs, 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

729 which they are embedded (Clark, 2005). In a BHM, a species' trait
730 distributions are explicitly incorporated into one of the levels of the
731 hierarchy, and uncertainty around trait distributions are considered by
732 including prior distributions on the parameters of the trait distributions.
733 Further, the parameters of the trait distribution can be functions of biotic
734 and/or abiotic environmental factors in order to capture changes to the trait
735 distribution that are driven by changing environmental conditions. A major
736 advantage of BHMs is that they allow the user to explore relationships
737 among traits, the environment, and organismal performance without
738 knowing, *a priori*, the mechanisms that relate them (Webb *et al.*, 2010).
739 However, these models are limited to forecasting within the range of the
740 data used to fit them. Thus, BHMs are beneficial in identifying the traits and
741 environmental drivers that are most important in driving the dynamics of a
742 community. Because the trait distributions and their parameters are
743 described explicitly, it is also possible to explore directly the impact of
744 changes in intraspecific trait variation on the dynamics of the species and
745 the community as a whole.
746 Dynamical systems models have been developed that explicitly
747 describe the temporal dynamics of the community trait distribution in
748 response to environmental forcing for either a single trait (Norberg *et al.*,
749 2001) or multiple, correlated traits (Savage, Webb & Norberg, 2007). These
750 models use moment closure, a technique that approximates complete
751 distributions using only low-order moments such as means and variances, to

752 describe the whole community trait distribution as a function of biotic or
753 abiotic environmental factors. A drawback to this approach is that it requires
754 an explicit, known functional relationship between traits, environment, and
755 organismal performance. However, this allows these models to predict
756 changes in the trait distribution that result from environmental forcing
757 outside of the observed range, such as that expected from climate change.
758 An interesting feature of these models is that they aggregate inter- and
759 intraspecific variation into a single community trait distribution. This results
760 in a loss of information about species identity and changes in relative
761 abundances. On the other hand, for cases where the trait(s) are strongly
762 related to an ecosystem function of interest, these models may allow robust
763 prediction of function while ignoring extraneous details of species
764 composition. A more integrative approach incorporates the predictive power
765 of deterministic, dynamical systems models with the ability of Bayesian
766 models to incorporate empirical data and generate measures of uncertainty
767 associated with the model output. These ‘first principles Bayesian multilevel
768 models’ (Webb *et al.*, 2010) embed known mechanistic relationships into a
769 BHM and thereby allow prediction outside of the observed range of data
770 while simultaneously estimating uncertainty (Bayesian credible intervals)
771 associated with those predictions.
772

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

775 Nearly all traits vary systematically along broad environmental
776 gradients. At the same time, nearly half of the global variation of many traits
777 can be found within individual communities (Wright *et al.*, 2004). Variation in
778 trait values among communities can be used to predict changes in
779 ecosystem functioning under persistent changes in the environment (Klumpp
780 & Soussana, 2009; Suding *et al.*, 2008), while variation within communities
781 can predict the resilience of ecosystem functioning to disturbance (Mori,
782 Furukawa & Sasaki, 2013). Systematic variation in trait distributions along
783 environmental gradients can also reveal environmentally dependent
784 assembly rules (Ackerly & Cornwell, 2007; Keddy, 1992), thereby linking
785 community assembly theory to models of biodiversity–ecosystem functioning
786 (Naeem & Wright, 2003). Trait–environment relationships are becoming
787 increasingly well described with 'global' trait–environment relationships
788 assessed for many traits (Moles *et al.*, 2007, 2009; Wright *et al.*, 2004; Zanne
789 *et al.*, 2010), although the current state of knowledge in this area is hugely
790 variable, with some traits, functional indices, and environmental gradients
791 much more intensively studied than others.
792
793 **(1) Community-level metrics of plant function**
794 Perhaps the simplest measure of community-level functional
795 composition is the community-weighted mean (CWM) trait value, which uses
796 the relative abundances of species and their trait values to calculate a
797 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 (Fortunel *et al.*, 2009; Laliberté & Tylianakis, 2012; Lavorel *et al.*, 2011) 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 (although species may not co-occur within 1° grid cells) 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

821 due to coordinated ecological selection on multiple traits that differed from
822 the evolutionary and biogeographic factors that determined trait correlations
823 among species in the regional pool. Research aimed at identifying these
824 processes and the trait–abundance distributions that they generate is
825 essential for improving predictive models of CWM–environment relationships.
826 Functional diversity indices capture the distribution of trait values
827 within communities and can also demonstrate systematic variation along
828 environmental gradients. Functional diversity can be broken down into three
829 orthogonal components – richness, evenness, and divergence (Mason *et al.*,
830 2005) – that are represented in various ways by different indices. The range,
831 or functional richness (Villeger *et al*., 2008), of trait values within a
832 community can be indicative of the intensity of environmental assembly
833 filters (Cornwell, Schwilk & Ackerly, 2006), and can have significant effects
834 on ecosystem functioning (Butterfield & Suding, 2013; Clark *et al.*, 2012).
835 The range of trait values is expected to decrease with increasing
836 environmental severity (i.e. environmental filtering), a hypothesis that has
837 been supported for a variety of traits at fine (Cornwell & Ackerly, 2009; Jung
838 *et al.*, 2010; Kooyman, Cornwell & Westoby, 2010) and coarse (Swenson *et*
839 *al.*, 2012) spatial scales, but not in all cases (Coyle *et al.*, 2014). Species
840 may, for example, use contrasting strategies to deal with stress (e.g. stress
841 avoidance *versus* tolerance; Ludlow, 1989), resulting in divergent traits and
842 greater functional richness. The distribution of trait values within a
843 community, as described by functional evenness may also vary

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

853 The trait–environment predictions outlined above follow from relatively
854 simple models of community assembly, although several studies have
855 demonstrated that biotic interactions can strongly alter trait–environment
856 predictions. Trait-based community assembly studies have typically focused
857 on the convergence–divergence paradox which states that species with
858 similar environmental tolerances and requirements – reflected in the
859 similarity of their functional trait values – may experience simultaneous,
860 competing forces: similar species are more likely to co-occur (converge), and
861 thus to compete more strongly (diverge; Weiher, Clarke & Keddy, 1998;
862 Adler *et al.,* 2013). However, there is increasing evidence that using
863 functional divergence (i.e. degree of niche differentiation; Mason *et al*., 2005;
864 Villeger *et al*., 2008) to infer whether environmental filtering or competition
865 mechanisms are operating most strongly in communities may be narrow-
866 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 multidimensional nature of the

890 ‘niche’ (Villeger *et al.*, 2008), while other metrics such as dendrogram-based
891 indices (Petchey & Gaston, 2002) combine richness and evenness. However,
892 functional richness—the key indicator of functional spread within
893 communities—could be heavily influenced by rare, outlying species.
894 Abundance-weighted measures of spread, such as functional dispersion
895 (Laliberté & Legendre, 2010) and Rao’s quadratic entropy (Botta-Dukat,
896 2005) may more accurately predict some ecosystem functions as the traits
897 of dominant species have stronger effects (i.e. mass ratio hypothesis; Grime,
898 1998). A great deal of research has gone into the mathematical properties
899 and ecological justifications of these different indices (Petchey & Gaston,
900 2006; Mouchet *et al.*, 2010); however, their relative performance in
901 identifying biotic responses to a wide variety of environmental gradients, as
902 well as biotic effects on various ecosystem processes, are only just beginning
903 to be addressed (McGill, Sutton-Grier & Wright, 2010; Sutton-Grier *et al.*,
904 2011).
905 Deciding which indices to apply to a given trait-based question is not a
906 simple task given the potential relevance of many traits and diversity
907 metrics. Single-trait indices may retain more information, as opposed to
908 combining their variation into composite indices. This may mirror the issue of
909 inter- *versus* intraspecific trait variation discussed above, where the variance
910 in trait values may be reduced through aggregation. Single-trait indices may
911 also provide a better understanding of the complexity of responses to
912 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 (Villeger, 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 in 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 (Villeger *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, 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. Cornwell *et al.*, 2008; Díaz *et al.,* 2007*b*).

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

959 between precipitation and soil moisture dynamics. Predictors of water stress
960 that integrate temperature, precipitation, and other factors that influence
961 soil moisture supply are typically better predictors of plant trait spectra than
962 temperature or precipitation alone (Wright *et al.*, 2004). Soil data are
963 becoming better each year, but the quality of soil data varies among
964 countries, and often within countries. Current climate data and future climate
965 projections are available at a global scale as data layers in Geographical
966 Information Systems (Hijmans *et al.*, 2005). The tools for predicting future
967 responses are increasing rapidly, but the accuracy of our predictions will
968 depend heavily on the precision of these future projections. As access to
969 accurate, consistent environmental data improves, predicting changes in
970 community composition can be accomplished using trait-based models that
971 yield a predicted relative abundance for every species in the local pool based
972 on the traits of the species and the relationships between traits and the
973 environment (Laughlin & Laughlin, 2013).

974 Our ability to predict ecosystem processes under changing
975 environmental conditions is also contingent on our understanding of the
976 relative importance of both abiotic conditions and the effect traits of the
977 community (Díaz *et al.*, 2007*a*), and how simultaneously to test and account
978 for multiple important factors in predictive models. For example, litter
979 decomposition rate has been shown to be a function of the local climate, the
980 composition of the microbial community, and the physical and chemical
981 traits of the litter (see Section II.2*b*). 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

1027 understanding of which traits drive ecological processes at organismal,
1028 community, and ecosystem scales. While soft traits, such as SLA or wood
1029 density, show much promise in explaining some metrics of plant function
1030 (e.g. RGR) and species distributions, it remains to be seen if these traits can
1031 simultaneously predict multiple ecological processes across diverse
1032 community types. We demonstrated that genetic variation and phenotypic
1033 plasticity can strongly influence a range of plant functions, but how these
1034 two components contribute to intraspecific trait variation and ecological
1035 strategies across a range of species needs to be addressed. Furthermore,
1036 future work needs to identify how intraspecific trait variation should be
1037 quantified and incorporated into models. Our review also highlighted the
1038 need to understand how non-additive effects of traits, species interactions,
1039 and abiotic factors influence community- and ecosystem-level processes,
1040 and how these separate components may be incorporated into cohesive and
1041 predictive frameworks. While TBE has seen many recent advances in
1042 modelling approaches, we still do not know if algorithms developed in one
1043 community can be applied at larger spatial and temporal scales. Progress on
1044 all of these questions will be facilitated by improvements in the quality and
1045 availability of trait and environmental data.
1046 (3) While this review has focused on how TBE informs our understanding of
1047 basic ecological processes, work is underway to apply this framework to
1048 conservation and restoration programs (e.g. Funk *et al.*, 2008; Laughlin,
1049 2014*a*). 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 traits that may be useful in re-establishing 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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VII. REFERENCES

Ackerly, D. & Reich, P. (1999). Convergence and correlations among leaf size and function in seed plants: A comparative test using independent contrasts. *American Journal of Botany* **86**, 1272–1281.

Ackerly, D. D. & Cornwell, W. K. (2007). A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecology Letters* **10**, 135–145.

Adler, P. B., Salguero-Gomez, R., Compagnoni, A., Hsu, J. S., Ray-Mukherjee, J., Mbeau-Ache, C. & Franco, M. (2013). Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences* **111**, 740–745.

Aicher, R. J., Larios, L. & Suding, K. N. (2011). Seed supply, recruitment, and assembly: Quantifying relative seed and establishment limitation in a plant community context. *The American Naturalist* **178**, 464–477.

Albert, C. H., Grassein, F., Schurr, F. M., Vieilledent, G. & Violle, C. (2011). When and how should intraspecific variability be considered in trait-based plant ecology? *Perspectives in Plant Ecology, Evolution and Systematics* **13**, 217–225.

Albert, C. H., Thuiller, W., Yoccoz, N. G., Soudant, A., Boucher, F., Saccone, P. & Lavorel, S. (2010). Intraspecific functional variability: extent, structure and sources of variation. *Journal of Ecology* **98**, 604–613.

Alberto, F. J., Aitken, S. N., Alía, R., González-Martínez, S. C., Hänninen, H., Kremer, A., Lefèvre, F., Lenormand, T., Yeaman, S., Whetten, R. & Savolainen, O. (2013). Potential for evolutionary responses to climate change – evidence from tree populations. *Global Change Biology* **19**, 1645–1661.

Ames, G. M. , Anderson, S. M. & Wright, J. P. (2015). Multiple environmental drivers structure plant traits at the community level in a pyrogenic system. *Functional Ecology* doi:10.1111/1365-2435.12536.

Ashton, I. W., Miller, A. E., Bowman, W. D. & Suding, K. N. (2010). Niche complementarity due to plasticity in resource use: plant partitioning of chemical N forms. *Ecology* **91**, 3252–3260.

Aubin, I., Ouellette, M. H., Legendre, P., Messier, C. & Bouchard, A. (2009). Comparison of two plant functional approaches to evaluate natural restoration along an old-field – deciduous forest chronosequence. *Journal of Vegetation Science* **20**, 185–198.

Badgery, W., Kemp, D., Michalk, D. & King, W. (2005). Competition for nitrogen between Australian native grass and the introduced weed *Nassella trichotoma*. *Annals of Botany* **96**, 799–809.

Bakker, M. A., Carreño-Rocabado, G. & Poorter, L. (2011). Leaf economics traits predict litter decomposition of tropical plants and differ among land use types. *Functional Ecology* **25**, 473–483.

Bazzaz, F. A. (1996). *Plants in changing environments: linking physiological, population, and community ecology*. Cambridge University Press, Cambridge.

Berg, M. & Ellers, J. (2010). Trait plasticity in species interactions: a driving force of community dynamics. *Evolutionary Ecology* **24**, 617–629.

Bernhardt-Römermann, M., Römermann, C., Nuske, R., Parth, A., Klotz, S., Schmidt, W. & Stadler, J. (2008). On the identification of the most suitable traits for plant functional trait analyses. *Oikos* **117**, 1533–1541.

Blonder, B., Royer, D. L., Johnson, K. R., Miller, I. & Enquist, B. J. (2014). Plant ecological strategies shift across the Cretaceous–Paleogene boundary. *PLOS Biology* **12**, e1001949.

BOEGE, K. & DIRZO, R. (2004). Intraspecific variation in growth, defense and herbivory in *Dialium guianense* (Caesalpiniaceae) mediated by edaphic heterogeneity. *Plant Ecology* **175**, 59–69.

BOKHORST, S., PHOENIX, G. K., BJERKE, J. W., CALLAGHAN, T. V., HUYER-BRUGMAN, F. & BERG, M. P. (2012). Extreme winter warming events more negatively impact small rather than large soil fauna: shift in community composition explained by traits not taxa. *Global Change Biology* **18**, 1152–1162.

BOLNICK, D. I., AMARASEKARE, P., ARAUJO, M. S., BURGER, R., LEVINE, J. M., VOLKER, H. W. R., SCHREIBER, S. J., URBAN, M. C. & VASSEUR, D. A. (2011). Why intraspecific trait variability matters in community ecology. *Trends in Ecology and Evolution* **26**, 183–192.

BOTTA-DUKAT, Z. (2005). Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science* **16**, 533–540.

BOYCE, C. K., BRODRIBB, T. J., FEILD, T. S. & ZWIENIECKI, M. A. (2009). Angiosperm leaf vein evolution was physiologically and environmentally transformative. *Proceedings of the Royal Society B: Biological Sciences* **276**, 1771–1776.

BRODRIBB, T. J., FEILD, T. S. & SACK, L. (2010). Viewing leaf structure and evolution from a hydraulic perspective. *Functional Plant Biology* **37**, 488–498.

BUTTERFIELD, B. J., & BRIGGS , J. M. (2011). Regeneration niche differentiates functional strategies of desert woody plant species. *Oecologia* **165**, 477–487.

Butterfield, B. J., & Callaway, R. M. (2013). A functional comparative approach to facilitation and its context dependence. *Functional Ecology* **27**, 907–917.

Butterfield, B. J. & Suding, K. N. (2013). Single-trait functional indices outperform multi-trait indices in linking environmental gradients and ecosystem services in a complex landscape. *Journal of Ecology* **101**, 9–17.

Cadotte, M., Albert, C. H. & Walker, S. C. (2013). The ecology of differences: assessing community assembly with trait and evolutionary distances. *Ecology Letters* **16**, 1234–1244.

Cadotte, M. W., Cardinale, B. J. & Oakley, T. H. (2008). Evolutionary history and the effect of biodiversity on plant productivity. *Proceedings of the National Academy of Sciences* **105**, 17012–17017.

Cadotte, M. W., Cavender-Bares, J., Tilman, D. & Oakley, T. H. (2009). Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLOS ONE* **4**, e5695.

Cadotte, M. W., Dinnage, R. & Tilman, D. (2012). Phylogenetic diversity promotes ecosystem stability. *Ecology* **93**, S223–S233.

Cavender-Bares, J. & Bazzaz, F. A. (2000). Changes in drought response strategies with ontogeny in *Quercus rubra*: implications for scaling from seedlings to mature trees. *Oecologia* **124**, 8–18.

Cavender-Bares, J., Cortes, P., Rambal, S., Joffre, R., Miles, B. & Rocheteau, A. (2005). Summer and winter sensitivity of leaves and xylem to minimum

freezing temperatures: a comparison of co-occurring Mediterranean oaks that differ in leaf lifespan. *New Phytologist* **168**, 597–611.

CAVENDER-BARES, J., GONZALEZ-RODRIGUEZ, A., PAHLICH, A., KOEHLER, K. & DEACON, N. (2011). Phylogeography and climatic niche evolution in live oaks (*Quercus* series *Virentes*) from the tropics to the temperate zone. *Journal of Biogeography* **38**, 962–981.

CAVENDER-BARES, J., KEEN, A. & MILES, B. (2006). Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. *Ecology* **87**, S109–S122.

CHAMBERS, J. Q., HIGUCHI, N., SCHIMEL, J. P., FERREIRA, L. V. & MELACK, J. M. (2000). Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. *Oecologia* **122**, 380–388.

CHAPIN III, F. S. (2003). Effects of plant traits on ecosystem and regional processes: a conceptual framework for predicting the consequences of global change. *Annals of Botany* **91**, 455–463.

CHAPIN III, F. S., ZAVALETA, E. S., EVINER, V. T., NAYLOR, R. L., VITOUSEK, P. M., REYNOLDS, H. L., HOOPER, D. U., LAVOREL, S., SALA, O. E., HOBBIE, S. E., MACK, M. C. & DÍAZ, S. (2000). Consequences of changing biodiversity. *Nature* **405**, 234–242.

CHASE, J. M. & LEIBOLD, M.A. (2003). *Ecological niches: linking classical and contemporary approaches*. University of Chicago Press, Chicago.

Chave, J., Coomes, D., Jansen, S., Lewis, S., Swenson, N. G. & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters* **12**, 351–366.

Chave, J., Muller-Landau, H. C., Baker, T. R., Easdale, T. A., ter Steege, H. & Webb, C. O. (2006). Regional and phylogenetic variation of wood density across 2456 Neotropical tree species. *Ecological Applications* **16**, 2356–2367.

Clark, C. M., Flynn, D. F. B., Butterfield, B. J. & Reich, P. B. (2012). Testing the link between functional diversity and ecosystem functioning in a minnesota grassland experiment. *PLOS ONE* **7**, e52821.

Clark, J. S. (2005). Why environmental scientists are becoming Bayesians. *Ecology Letters* **8**, 2–14.

Clark, J. S. (2010). Individuals and the variation needed for high species diversity in forest trees. *Science* **327**, 1129–1132.

Clark, J. S., Bell, D., Chu, C., Courbaud, B., Dietze, M., Hersh, M., HilleRisLambers, J., Ibáñez, I., LaDeau, S., McMahon, S., Metcalf, J., Mohan, J., Moran, E., Pangle, L., Pearson, S. *et al*. (2010). High dimensional coexistence based on individual variation: a synthesis of evidence. *Ecological Monographs* **80**, 569–608.

Cornelissen, J., Aerts, R., Cerabolini, B., Werger, M. & van der Heijden, M. (2001). Carbon cycling traits of plant species are linked with mycorrhizal strategy. *Oecologia* **129**, 611–619.

Cornwell, W. K. & Ackerly, D. D. (2009). Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs* **79**, 109–126.

Cornwell, W. K. & Ackerly, D. D. (2010). A link between plant traits and abundance: evidence from coastal California woody plants. *Journal of Ecology* **98**, 814–821.

Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., Hobbie, S. E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H. M., Santiago, L. S., Wardle, D. A., Wright, I. J., Aerts, R. *et al.* (2008). Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* **11**, 1065–1071.

Cornwell, W. K., Schwilk, D. W. & Ackerly, D. D. (2006). A trait-based test for habitat filtering: convex hull volume. *Ecology* **87**, 1465–1471.

Coyle, J. R., Halliday, F. W., Lopez, B. E., Palmquist, K. A., Wilfahrt, P. A. & Hurlbert, A. H. (2014). Using trait and phylogenetic diversity to evaluate the generality of the stress-dominance hypothesis in eastern North American tree communities. *Ecography* **37**, 814–826.

da Silveira Pontes, L., Louault, F., Carrère, P., Maire, V., Andueza, D. & Soussana, J.-F. (2010). The role of plant traits and their plasticity in the response of pasture grasses to nutrients and cutting frequency. *Annals of Botany* **105**, 957–965.

DAVIDSON, A. M., JENNIONS, M. & NICOTRA, A. B. (2011). Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecology Letters* **14**, 419–431.

DE BELLO, F., LAVOREL, S., DÍAZ, S., HARRINGTON, R., CORNELISSEN, J. C., BARDGETT, R., BERG, M., CIPRIOTTI, P., FELD, C., HERING, D., MARTINS DA SILVA, P., POTTS, S., SANDIN, L., SOUSA, J., STORKEY, J., WARDLE, D. & HARRISON, P. (2010). Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation* **19**, 2873–2893.

DE BELLO, F., PRICE, J. N., MÜNKEMÜLLER, T., LIIRA, J., ZOBEL, M., THUILLER, W., GERHOLD, P., GÖTZENBERGER, L., LAVERGNE, S., LEPŠ, J., ZOBEL, K. & PÄRTEL, M. (2012). Functional species pool framework to test for biotic effects on community assembly. *Ecology* **93**, 2263–2273.

DE DEYN, G. B., CORNELISSEN, J. H. & BARDGETT, R. D. (2008). Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters* **11**, 516–531.

DERAISON, H., BADENHAUSSER, I., LOEUILLE, N., SCHERBER, C. & N. GROSS, N. (2015). Functional trait diversity across trophic levels determines herbivore impact on plant community biomass. *Ecology Letters* **18**, 1346-1355.

DE VRIES, F. T., MANNING, P., TALLOWIN, J. R. B., MORTIMER, S. R., PILGRIM, E. S., HARRISON, K. A., HOBBS, P. J., QUIRK, H., SHIPLEY, B., CORNELISSEN, J. H. C., KATTGE, J. & BARDGETT, R. D. (2012). Abiotic drivers and plant traits explain landscape-scale patterns in soil microbial communities. *Ecology Letters* **15**, 1230–1239.

Díaz, S. & Cabido, M. (1997). Plant functional types and ecosystem function in relation to global change. *Journal of Vegetation Science* **8**, 463–474.

Díaz, S. & Cabido, M. (2001). Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution* **16**, 646–655.

Díaz, S., Hodgson, J., Thompson, K., Cabido, M., Cornelissen, J., Jalili, A., Montserrat-Martí, G., Grime, J., Zarrinkamar, F. & Asri, Y. (2004). The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science* **15**, 295–304.

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Prentice, I. C., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P. B. *et al*. (2016). The global spectrum of plant form and function. *Nature* **529**, 167–171.

Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K. & Robson, T. M. (2007*a*). Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences* **104**, 20684–20689.

Díaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D. G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W., Clark, H. & B. D. Cambell, B. D. (2007*b*). Plant trait responses to grazing – a global synthesis. *Global Change Biology* **13**, 313–341.

DIJKSTRA, F. A., HOBBIE, S. E. & REICH, P. B. (2006). Soil processes affected by sixteen grassland species grown under different environmental conditions. *Soil Science Society of America Journal* **70**, 770–777.

DONOGHUE, M. J. (2008). A phylogenetic perspective on the distribution of plant diversity. *Proceedings of the National Academy of Sciences* **105 (Supplement 1),** 11549–11555.

DONOHUE, K., DORN, L., GRIFFITH, C., KIM, E., AGUILERA, A., POLISETTY, C. & SCHMITT, J. (2005). Environmental and genetic influences on the germination of *Arabidopsis thaliana* in the field. *Evolution* **59**, 740–757.

DONOHUE, K., HESCHEL, M. S., CHIANG, G. C. K., BUTLER, C. M. & BARUA, D. (2007). Phytochrome mediates germination responses to multiple seasonal cues. *Plant, Cell and Environment* **30**, 202–212.

DONOHUE, K., RUBIO DE CASAS, R., BURGHARDT, L., KOVACH, K. & WILLIS, C. G. (2010). Germination, postgermination adaptation, and species ecological ranges. *Annual Review of Ecology, Evolution, and Systematics* **41**, 293–319.

DORROUGH, J., ASH, J. &MCINTYRE, S. (2004). Plant responses to livestock grazing frequency in an Australian temperate grassland. *Ecography* **27**, 798-810.

DRAY, S., CHOLER, P., DOLÉDEC, S., PERES-NETO, P. R., THUILLER, W., PAVOINE, S. & TER BRAAK, C. J. F. (2014). Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology* **95**, 14–21.

Edwards, K. F., Lichtman, E. & Klausmeier, C. A. (2013). Functional traits explain phytoplankton community structure and seasonal dynamics in a marine ecosystem. *Ecology Letters* **16**, 56–63.

Enquist, B. J., Norberg, J., Bonser, S. P., Violle, C., Webb, C. T., Henderson, A., Sloat, L. L. & Savage, V. M. (2015). Scaling from traits to ecosystems: developing a general trait driver theory via integrating trait-based and metabolic scaling theories. *Advances in Ecological Research* **52**, 249–318.

Etterson, J. R. & Shaw, R. G. (2001). Constraint to adaptive evolution in response to global warming. *Science* **294**, 151–154.

Eviner, V. T. & Chapin III, F. S. (2003). Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. *Annual Review of Ecology, Evolution, and Systematics* **34**, 455–485.

Feild, T. S., Brodribb, T. J., Iglesias, A., Chatelet, D. S., Baresch, A., Upchurch Jr., G. R., Gomez, B., Mohr, B. A. R., Coiffard, C., Kvacek, J. & Jaramillo, C. (2011). Fossil evidence for Cretaceous escalation in angiosperm leaf vein evolution. *Proceedings of the National Academy of Sciences* **108**, 8363–8366.

Fierer, N., Barberán, A. & Laughlin, D. C. (2014). Seeing the forest for the genes: using metagenomics to infer the aggregated traits of microbial communities. *Frontiers in Microbiology* **5**, 614, doi: 10.3389/fmicb.2014.00614.

FIRN, J., MACDOUGALL, A. S., SCHMIDT, S. & BUCKLEY, Y. M. (2010). Early emergence and resource availability can competitively favour natives over a functionally similar invader. *Oecologia* **163**, 775–784.

FIRN, J., PROBER, S. M. & BUCKLEY, Y. M. (2012). Plastic traits of an exotic grass contribute to its abundance but are not always favorable. *PLOS ONE* **7**, e35870, doi:10.1371/journal.pone.0035870.

FLORES-MORENO, H. & MOLES, A. T. (2013). A comparison of the recruitment success of introduced and native species under natural conditions. *PLOS ONE* **8**, e72509.

FLYNN, D. F., MIROTCHNICK, N., JAIN, M., PALMER, M. I. & NAEEM, S. (2011). Functional and phylogenetic diversity as predictors of biodiversity-ecosystem-function relationships. *Ecology* **92**, 1573–1581.

FORTUNEL, C., GARNIER, E., JOFFRE, R., KAZAKOU, E., QUESTED, H., GRIGULIS, K., LAVOREL, S., ANSQUER, P., CASTRO, C., CRUZ, P., DOLEŽAL, J., ERIKSSON, O., FREITAS, H., GOLODETS, C., JOUANY, C. *ET AL*. (2009). Leaf traits capture the effects of land use changes and climate on litter decomposability of grasslands across Europe. *Ecology* **90**, 598–611.

FRESCHET, G. T., AERTS, R. & CORNELISSEN, J. H. C. (2012). A plant economics spectrum of litter decomposability. *Functional Ecology* **26**, 56–65.

FRESCHET, G. T., CORNELISSEN, J. H. C., VAN LOGTESTIJN, R. S. P. & AERTS, R. (2010). Evidence of the ‘plant economics spectrum’ in a subarctic flora. *Journal of Ecology* **98**, 362–373.

FRY, E. L., POWER, S. A. & MANNING, P. (2014). Trait-based classification and manipulation of plant functional groups for biodiversity–ecosystem function experiments. *Journal of Vegetation Science* **25**, 248–261.

FUNK, J. L. (2008). Differences in plasticity between invasive and native plants from a low resource environment. *Journal of Ecology* **96**, 1162–1174.

FUNK, J. L. (2013). The physiology of invasive plants in low-resource environments. *Conservation Physiology* **1**, doi:10.1093/conphys/cot1026.

FUNK, J. L., CLELAND, E. E., SUDING, K. N. & ZAVALETA, E. S. (2008). Restoration through re-assembly: plant traits and invasion resistance. *Trends in Ecology and Evolution* **23**, 695–703.

FUNK, J. L. & CORNWELL, W. K. (2013). Leaf traits within communities: context may affect the mapping of traits to function. *Ecology* **94**, 1893–1897.

FUNK, J. L. & MCDANIEL, S. (2010). Altering light availability to restore invaded forest: the predictive role of plant traits. *Restoration Ecology* **18**, 865–872.

GARIBALDI, L. A., SEMMARTIN, M. & CHANETON, E. J. (2007). Grazing-induced changes in plant composition affect litter quality and nutrient cycling in flooding Pampa grasslands. *Oecologia* **151**, 650–662.

GARNIER, E. & NAVAS, M.-L. (2012). A trait-based approach to comparative functional plant ecology: concepts, methods and applications for agroecology. A review. *Agronomy for Sustainable Development* **32**, 365–399.

GELMAN, A., CARLIN, J. B., STERN, H. S. & RUBIN, D. B. (2004). *Bayesian Data Analysis, second edition*. Chapman & Hall/CRC, New York.

GELMAN, A. & HILL, J. (2007). *Data Analysis Using Regression and Multillevel/Hierarchical Models*. Cambridge University Press, Cambridge.

GILBERT, G. S. & WEBB, C. O. (2007). Phylogenetic signal in plant pathogen-host range. *Proceedings of the National Academy of Sciences* **104**, 4979–4983.

GRACE, J. B. (2006). *Structural Equation Modeling and Natural Systems*. Cambridge University Press.

GRASSEIN, F., TILL-BOTTRAUD, I. & LAVOREL, S. (2010). Plant resource-use strategies: the importance of phenotypic plasticity in response to a productivity gradient for two subalpine species. *Annals of Botany* **106**, 637–645.

GRIGULIS, K., LAVOREL, S., KRAINER, U., LEGAY, N., BAXENDALE, C., DUMONT, M., KASTL, E., ARNOLDI, C., BARDGETT, R. D., POLY, F., POMMIER, T., SCHLOTER, M., TAPPEINER, U., BAHN, M. & CLÉMENT, J.-C. (2013). Relative contributions of plant traits and soil microbial properties to mountain grassland ecosystem services. *Journal of Ecology* **101**, 47–57.

GRIME, J. P. (1974). Vegetation classification by reference to strategies. *Nature* **250**, 26–31.

GRIME, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* **111**, 1169–1194.

GRIME, J. P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* **86**, 902–910.

Grime, J. P. & Hunt, R. (1975). Relative growth-rate: its range and adaptive significance in a local flora. *Journal of Ecology* **63**, 393–422.

Grime, J. P. & Mackey, J. M. L. (2002). The role of plasticity in resource capture by plants. *Evolutionary Ecology* **16**, 299–307.

Grime, J. P., Thompson, K., Hunt, R., Hodgson, J. G., Cornelissen, J. H. C., Rorison, I. H., Hendry, G. A. F., Ashenden, T. W., Askew, A. P., Band, S. R., Booth, R. E., Bossard, C. C., Campbell, B. D., Cooper, J. E. L., Davison, A. W. *et al*. (1997). Integrated screening validates primary axes of specialisation in plants. *Oikos* **79**, 259–281.

Grimm, V. & Railsback, S. F. (2005). *Individual based modeling and ecology*. Princeton University Press, New Jersey.

Gross, N., Kunstler, G., Liancourt, P., De Bello, F., Suding, K. N. & Lavorel, S. (2009). Linking individual response to biotic interactions with community structure: a trait-based framework. *Functional Ecology* **23**, 1167–1178.

Gross, N., Liancourt, P., Butters, R., Duncan, R. P. & Hulme, P. E. (2015). Functional equivalence, competitive hierarchy and facilitation determine species coexistence in highly invaded grasslands. *New Phytologist* **206**, 175–186.

Gross, N., Robson, T. M., Lavorel, S., Albert, C., Le Bagousse-Pinguet, Y. & Guillemin, R. (2008). Plant response traits mediate the effects of subalpine grasslands on soil moisture. *New Phytologist* **180**, 652–662.

GROSS, N., SUDING, K. N., LAVOREL, S. & ROUMET, C. (2007). Complementarity as a mechanism of coexistence between functional groups of grasses. *Journal of Ecology* **95**, 1296–1305.

GUREVITCH, J. & HEDGES, L. V. (2001). *Meta-analysis. Design and analysis of ecological experiments. Second edition.* Oxford University Press, New York.

HADDAD, N. M., HOLYOAK, M., MATA, T. M., DAVIES, K. F., MELBOURNE, B. A. & PRESTON, K. (2008). Species' traits predict the effects of disturbance and productivity on diversity. *Ecology Letters* **11**, 348–356.

HAN, Y., BUCKLEY, Y. M. & FIRN, J. (2012). An invasive grass shows colonization advantages over native grasses under conditions of low resource availability. *Plant Ecology* **213**, 1117–1130.

HÄTTENSCHWILER, S., TIUNOV, A. V. & SCHEU, S. (2005). Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology, Evolution, and Systematics* **36**, 191–218.

HESCHEL, M. S., SULTAN, S. E., GLOVER, S. & SLOAN, D. (2004). Population differentiation and plastic responses to drought stress in the generalist annual *Polygonum persicaria*. *International Journal of Plant Sciences* **165**, 817–824.

HIJMANS, R. J., CAMERON, S. E., PARRA, J. L., JONES, P. G. & JARVIS, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**, 1965–1978.

HODGSON, J. G., WILSON, P. J., HUNT, R., GRIME, J. P., & THOMPSON, K. (1999). Allocating C-S-R plant functional types: a soft approach to a hard problem. *Oikos* **85**, 282-294.

HUBBELL, S. P. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ.

HULSHOF, C. M. & SWENSON, N. G. (2010). Variation in leaf functional trait values within and across individuals and species: an example from a Costa Rican dry forest. *Functional Ecology* **24**, 217–223.

HUNT, R. & CORNELISSEN, J. H. C. (1997). Components of relative growth rate and their interrelations in 59 temperate plant species. *New Phytologist* **135**, 395–417.

HUXMAN, T. E., WILCOX, B. P., BRESHEARS, D. D., SCOTT, R. L., SNYDER, K. A., SMALL, E. E., HULTINE, K., POCKMAN, W. T. & JACKSON, R. B. (2005). Ecohydrological implications of woody plant encroachment. *Ecology* **86**, 308–319.

JAMIL, T., OZINGA, W. A., KLEYER, M. & TER BRAAK, C. J. F. (2013). Selecting traits that explain species–environment relationships: a generalized linear mixed model approach. *Journal of Vegetation Science* **24**, 988–1000.

JUNG, V., VIOLLE, C., MONDY, C., HOFFMAN, L. & MULLER, S. (2010). Intraspecific variability and trait-based community assembly. *Journal of Ecology* **98**, 1134–1140.

KAŠTOVSKÁ, E., EDWARDS, K., PICEK, T. & ŠANTRŮČKOVÁ, H. (2015). A larger investment into exudation by competitive versus conservative plants is

connected to more coupled plant–microbe N cycling. *Biogeochemistry* **122**, 47–59.

KATTGE, J., DÍAZ, S., LAVOREL, S., PRENTICE, I. C., LEADLEY, P., BÖNISCH, G., GARNIER, E., WESTOBY, M., REICH, P. B., WRIGHT, I. J., CORNELISSEN, J. H. C., VIOLLE, C., HARRISON, S. P., VAN BODEGOM, P. M., REICHSTEIN, M., ENQUIST, B. J., SOUDZILOVSKAIA, N. A., ACKERLY, D. D. *ET AL*. (2011). TRY – a global database of plant traits. *Global Change Biology* **17**, 2905–2935.

KEDDY, P. A. (1992). Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science* **3**, 157–164.

KERKHOFF, A. J., FAGAN, W. F., ELSER, J. J. & ENQUIST, B. J. (2006). Phylogenetic and growth form variation in the scaling of nitrogen and phosphorus in the seed plants. *American Naturalist* **168**, E103–E122.

KIMBALL, S., LULOW, M. E., MOONEY, K. A. & SORENSON, Q. M. (2014). Establishment and management of native functional groups in restoration. *Restoration Ecology* **22**, 81–88.

KLUMPP, K. & SOUSSANA, J.-F. (2009). Using functional traits to predict grassland ecosystem change: a mathematical test of the response-and-effect trait approach. *Global Change Biology* **15**, 2921–2934.

KOEHLER, K., CENTER, A. & CAVENDER-BARES, J. (2012). Evidence for a freezing tolerance - growth rate trade-off in the live oaks (*Quercus* series Virentes) across the tropical-temperate divide. *New Phytologist* **193**, 730–744.

KOOYMAN, R., CORNWELL, W. & WESTOBY, M. (2010). Plant functional traits in Australian subtropical rain forest: partitioning within-community from cross-landscape variation. *Journal of Ecology* **98**, 517–525.

KUNSTLER, G., LAVERGNE, S., COURBAUD, B., THUILLER, W., VIEILLEDENT, G., ZIMMERMANN, N. E., KATTGE, J. & COOMES, D. A. (2012). Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: implications for forest community assembly. *Ecology Letters* **15**, 831–840.

KUNSTLER, G., FALSTER, D., COOMES, D. A., HUI, F., KOOYMAN, R. M., LAUGHLIN, D. C., POORTER, L., VANDERWEL, M., VIEILLEDENT, G., WRIGHT, S. J., AIBA, M., BARALOTO, C., CASPERSEN, J., CORNELISSEN, J. H. C., GOURLET-FLEURY, S. *ET AL*. (2016). Plant functional traits have globally consistent effects on competition. *Nature* **529**, 204–207.

LALIBERTE, E. & LEGENDRE, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology* **91**, 299–305.

LALIBERTÉ, E. & TYLIANAKIS, J. M. (2012). Cascading effects of long-term land-use changes on plant traits and ecosystem functioning. *Ecology* **93**, 145–155.

LANGLEY, J. A., CHAPMAN, S. K. & HUNGATE, B. A. (2006). Ectomycorrhizal colonization slows root decomposition: the post-mortem fungal legacy. *Ecology Letters* **9**, 955–959.

LARSON, J. E. & FUNK, J. L. (2016). Seedling root responses to soil moisture and the identification of a belowground trait spectrum across three growth forms. *New Phytologist* 10.1111/nph.13829

LARSON, J. E., SHELEY, R. L., HARDEGREE, S. P., DOESCHER, P. S. & JAMES, J. J. (2015). Do key dimensions of seed and seedling functional trait variation capture variation in recruitment probability? *Oecologia*, doi: 10.1007/s00442-015-3430-3.

LAUGHLIN, D. C. (2011). Nitrification is linked to dominant leaf traits rather than functional diversity. *Journal of Ecology* **99**, 1091–1099.

LAUGHLIN, D. C. (2014*a*). Applying trait-based models to achieve functional targets for theory-driven ecological restoration. *Ecology Letters* **17**, 771–784.

LAUGHLIN, D. C. (2014*b*). The intrinsic dimensionality of plant traits and its relevance to community assembly. *Journal of Ecology* **102**, 186–193.

LAUGHLIN, D. C. & LAUGHLIN, D. E. (2013). Advances in modelling trait-based plant community assembly. *Trends in Plant Science* **18**, 584–593.

LAVOREL, S., DÍAZ, S., CORNELISSEN, J. H. C., HARRISON, S. P., MCINTYRE, S., PAUSAS, J. G., PEREZ-HARGUINDEGUY, N., ROUMET, C. & URCELAY, C. (2007). Plant functional types: are we getting any closer to the holy grail? In *Terrestrial Ecosystems in a Changing World* (eds J. G. CANADELL, D. PATAKI AND L. PITELKA), pp. 149–164. Springer-Verlag, Berlin Heidelberg.

LAVOREL, S. & GARNIER, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* **16**, 545–556.

LAVOREL, S. & GRIGULIS, K. (2012). How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services. *Journal of Ecology* **100**, 128–140.

LAVOREL, S., GRIGULIS, K., LAMARQUE, P., COLACE, M. P., GARDEN, D., GIREL, J., PELLET, G. & DOUZET, R. (2011). Using plant functional traits to understand the landscape distribution of multiple ecosystem services. *Journal of Ecology* **99**, 135–147.

LAVOREL, S., MCINTYRE, S., LANDSBERG, J. & FORBES, T. D. A. (1997). Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology and Evolution* **12**, 474–478.

LAVOREL ,S., STORKEY, J., BARDGETT, R. D., DE BELLO, F., BERG, M. P., LE ROUX, X., MORETTI, M., MULDER, C., PAKEMAN, R. J., DÍAZ, S. & HARRINGTON, R. (2013). A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. *Journal of Vegetation Science* **25**, 942–948.

LAWTON, J. H. (1999). Are there general laws in ecology? *Oikos* **84**, 177–192.

LE BAGOUSSE-PINGUET, Y., BÖRGER, L., QUERO, J. -L., GARCÍA-GÓMEZ, M., SORIANO, S., MAESTRE, F. T. & GROSS, N. (2015). Traits of neighbouring plants and space limitation determine intraspecific trait variability in semi-arid shrublands. *Journal of Ecology* **103**, 1647–1657.

LECERF, A. & CHAUVET, E. (2008). Intraspecific variability in leaf traits strongly affects alder leaf decomposition in a stream. *Basic and Applied Ecology* **9**, 598–605.

Lee, J.-E. & Boyce, K. (2010). Impact of the hydraulic capacity of plants on water and carbon fluxes in tropical South America. *Journal of Geophysical Research: Atmospheres* **115**, D23123.

Lee, J.-E., Oliveira, R. S., Dawson, T. E. & Fung, I. (2005). Root functioning modifies seasonal climate. *Proceedings of the National Academy of Sciences* **102**, 17576–17581.

Legner, N., Fleck, S. & Leuschner, C. (2014). Within-canopy variation in photosynthetic capacity, SLA and foliar N in temperate broad-leaved trees with contrasting shade tolerance. *Trees* **28**, 263–280.

Liancourt, P., Boldgiv, B., Song, D. S., Spence, L. A., Helliker, B. R., Petraitis, P. S. & Casper, B. B. (2015). Leaf-trait plasticity and species vulnerability to climate change in a Mongolian steppe. *Global Change Biology* **21**, 3489–3498.

Litchman, E., Klausmeier, C. A., Schofield, O. M. & Falkowski, P. G. (2007). The role of functional traits and trade-offs in structuring phytoplankton communities: scaling from cellular to ecosystem level. *Ecology Letters* **10**, 1170–1181.

Liu, G., Freschet, G. T., Pan, X., Cornelissen, J. H. C., Li, Y. & Dong, M. (2010). Coordinated variation in leaf and root traits across multiple spatial scales in Chinese semi-arid and arid ecosystems. *New Phytologist* **188**, 543–553.

Loranger, J., Meyer, S. T., Shipley, B., Kattge, J., Loranger, H., Roscher, C. & Weisser, W. W. (2012). Predicting invertebrate herbivory from plant traits:

evidence from 51 grassland species in experimental monocultures. *Ecology* **93**, 2674–82.

LOUAULT, F., PILLAR, V., AUFRERE, J., GARNIER, E. & SOUSSANA, J.-F. (2005). Plant traits and functional types in response to reduced disturbance in a semi-natural grassland. *Journal of Vegetation Science* **16**, 151–160.

LUDLOW, M. M. (1989). Strategies of response to water stress. Pages 269–281 in K. H. Kreeb, H. Richter, and T. M. Minckley, editors. Structural and functional responses to environmental stress. SPB Academic, The Hague, the Netherlands.

LUSK, C. H. & WARTON, D. I. (2007). Global meta-analysis shows that relationships of leaf mass per area with species shade tolerance depend on leaf habit and ontogeny. *New Phytologist* **176**, 764–774.

MADRITCH, M. D. & LINDROTH, R. L. (2015). Condensed tannins increase nitrogen recovery by trees following insect defoliation. *New Phytologist* **208**, 410–420.

MAIRE, V., GROSS, N., BORGER, L., PROULX, R., WIRTH, C., DA SILVEIRA PONTES, L., SOUSSANA, J.-F. & LOUAULT, F. (2012). Habitat filtering and niche differentiation jointly explain species relative abundance within grassland communities along fertility and disturbance gradients. *New Phytologist* **196**, 497–509.

MAIRE, V., GROSS, N., HILL, D., MARTIN, R., WIRTH, C., WRIGHT, I. J. & SOUSSANA, J.-F. (2013). Disentangling coordination among functional traits using an individual-centred model: Impact on plant performance at intra- and inter-specific levels. *PLOS ONE* **8**, e77372.

Martínez-Vilalta, J., Cochard, H., Mencuccini, M., Sterck, F., Herrero, A., Korhonen, J. F. J., Llorens, P., Nikinmaa, E., Nolè, A., Poyatos, R., Ripullone, F., Sass-Klaassen, U. & Zweifel, R. (2009). Hydraulic adjustment of Scots pine across Europe. *New Phytologist* **184**, 353–364.

Mason, N. W. H., Mouillot, D., Lee, W. G. & Wilson, J. B. (2005). Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos* **111**, 112–118.

Mayfield, M. M. & Levine, J. M. (2010). Opposing effects of competitive exclusion on teh phylogenetic structure of communities. *Ecology Letters* **13**, 1085–1093.

McCormack, M. L., Lavely, E. & Ma, Z. (2014). Fine-root and mycorrhizal traits help explain ecosystem processes and responses to global change. *New Phytologist* **204**, 455–458.

McGill, B. J. (2003). A test of the unified neutral theory of biodiversity. *Nature* **422**, 881–885.

McGill, B. J., Enquist, B. J., Weiher, E. & Westoby, M. (2006*a*). Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* **21**, 178–185.

McGill, B. J., Maurer, B. A. & Weiser, M. D. (2006*b*). Empirical evaluation of neutral theory. *Ecology* **87**, 1411–1423.

McGill, B. M., Sutton-Grier, A. E. & Wright, J. P. (2010). Plant trait diversity buffers variability in denitrification potential over changes in season and soil conditions. *PLOS ONE* **5**, e11618, doi: 10.1371/journal.pone.0011618.

McIntyre, S. (2008). The role of plant leaf attributes in linking land use to ecosystem function in temperate grassy vegetation. *Agriculture, Ecosystems and Environment* **128**, 251-258.

McKown, A. D., Guy, R. D., Azam, M. S., Drewes, E. C. & Quamme, L. K. (2013). Seasonality and phenology alter functional leaf traits. *Oecologia* **172**, 653–665.

Mediavilla, S. & Escudero, A. (2003). Photosynthetic capacity, integrated over the lifetime of a leaf, is predicted to be independent of leaf longevity in some tree species. *New Phytologist* **159**, 203–211.

Meinzer, F. C. (2003). Functional convergence in plant responses to the environment. *Oecologia* **134**, 1–11.

Messier, J., McGill, B. J. & Lechowicz, M. J. (2010). How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters* **13**, 838–848.

Mokany, K., Ash, J. & Roxburgh, S. (2008). Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology* **96**, 884–893.

Moles, A. T., Ackerly, D. D., Tweddle, J. C., Dickie, J. B., Smith, R., Leishman, M. R., Mayfield, M. M., Pitman, A., Wood, J. T. & Westoby, M. (2007). Global patterns in seed size. *Global Ecology and Biogeography* **16**, 109–116.

Moles, A. T., Ackerly, D. D., Webb, C. O., Tweddle, J., Dickie, J. & Westoby, M. (2005). A brief history of seed size. *Science* **307**, 576–580.

Moles, A. T., Perkins, S. E., Laffan, S. W., Flores-Moreno, H., Awasthy, M., Tindall, M. L., Sack, L., Pitman, A., Kattge, J., Aarssen, L. W., Anand, M., Bahn, M., Blonder, B., Cavender-Bares, J., Cornelissen, J. H. C. *et al*. (2014). Which is a better predictor of plant traits: temperature or precipitation? *Journal of Vegetation Science* **25**, 1167–1180.

Moles, A. T., Warton, D. I., Warman, L., Swenson, N. G., Laffan, S. W., Zanne, A. E., Pitman, A., Hemmings, F. A. & Leishman, M. R. (2009). Global patterns in plant height. *Journal of Ecology* **97**, 923–932.

Mori, A. S., Furukawa, T. & Sasaki, T. (2013). Response diversity determines the resilience of ecosystems to environmental change. *Biological Reviews* **88**, 349–364.

Mouchet, M. A., Villéger, S., Mason, N. W. H. & Mouillot, D. (2010). Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology* **24**, 867–876.

Mouillot, D., Villeger, S., Scherer-Lorenzen, M. & Mason, N. W. (2011). Functional structure of biological communities predicts ecosystem multifunctionality. *PLOS ONE* **6**, e17476.

Müller, S. C., Overbeck, G. E., Pfadenhauer, J. & Pillar, V. D. (2007). Plant functional types of woody species related to fire disturbance in forest–grassland ecotones. *Plant Ecology* **189**, 1–14.

NAEEM, S. & WRIGHT, J. P. (2003). Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters* **6**, 567–579.

NGUYEN, H., FIRN, J., LAMB, D. & HERBOHN, J. (2014). Wood density: A tool to find complementary species for the design of mixed species plantations. *Forest Ecology and Management* **334**, 106–113.

NICOTRA, A., BABICKA, N. & WESTOBY, M. (2002). Seedling root anatomy and morphology: an examination of ecological differentiation with rainfall using phylogenetically independent contrasts. *Oecologia* **130**, 136–145.

NICOTRA, A. B., ATKIN, O. K., BONSER, S. P., DAVIDSON, A. M., FINNEGAN, E. J., MATHESIUS, U., POOT, P., PURUGGANAN, M. D., RICHARDS, C. L., VALLADARES, F. & VAN KLEUNEN, M. (2010). Plant phenotypic plasticity in a changing climate. *Trends in Plant Science* **15**, 684–692.

NORBERG, J., SWANEY, D. P., DUSHOFF, J., LIN, J., CASAGRANDI, R. & LEVIN, S. (2001). Phenotypic diversity and ecosystem functioning in changing environments: A theoretical framework. *Proceedings of the National Academy of Sciences* **98**, 11376–11381.

O'GRADY, A. P., COOK, P. G., EAMUS, D., DUGUID, A., WISCHUSEN, J. D. H., FASS, T. & WORLDEGE, D. (2009). Convergence of tree water use within an arid-zone woodland. *Oecologia* **160**, 643–655.

OLEKSYN, J., REICH, P. B., ZYTKOWIAK, R., KAROLEWSKI, P. & TJOELKER, M. G. (2003). Nutrient conservation increases with latitude of origin in European *Pinus sylvestris* populations. *Oecologia* **136**, 220–235.

Ollinger, S. V., Richardson, A. D., Martin, M. E., Hollinger, D. Y., Frolking, S. E., Reich, P. B., Plourde, L. C., Katul, G. G., Munger, J. W., Oren, R., Smith, M.-L., Paw U, K. T., Bolstad, P. V., Cook, B. D., Day, M. C., Martin, T. A., Monson, R. K. & Schmid, H. P. (2008). Canopy nitrogen, carbon assimilation, and albedo in temperate and boreal forests: Functional relations and potential climate feedbacks. *Proceedings of the National Academy of Sciences* **105**, 19336–19341.

Orwin, K. H., Buckland, S. M., Johnson, D., Turner, B. L., Smart, S., Oakley, S. & Bardgett, R. D. (2010). Linkages of plant traits to soil properties and the functioning of temperate grassland. *Journal of Ecology* **98**, 1074–1083.

Padilla, F. M. & Pugnaire, F. I. (2007). Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. *Functional Ecology* **21**, 489–495.

Pakeman, R. J. (2011). Multivariate identification of plant functional response and effect traits in an agricultural landscape. *Ecology* **92**, 1353–1365.

Pakeman, R. J. & Eastwood, A. (2013). Shifts in functional traits and functional diversity between vegetation and seed bank. *Journal of Vegetation Science* **24**, 865–876.

Pakeman, R. J. & Stockan, J. A. (2014). Drivers of carabid functional diversity: abiotic environment, plant functional traits, or plant functional diversity? *Ecology* **95**, 1213–1224.

PALACIO-LÓPEZ, K. & GIANOLI, E. (2011). Invasive plants do not display greater phenotypic plasticity than their native or non-invasive counterparts: a meta-analysis. *Oikos* **120**, 1393–1401.

PEDLEY, S. M. & DOLMAN, P. M. (2014). Multi-taxa trait and functional responses to physical disturbance. *Journal of Animal Ecology* **83**, 1542–1552.

PETCHEY, O. L., & GASTON, K. J. (2002). Functional diversity (FD), species richness and community composition. *Ecology Letters* **5**, 402–411.

PETCHEY, O. L., & GASTON, K. J. (2006). Functional diversity: back to basics and looking forward. *Ecology Letters* **9**, 741–758.

PILLAR, V. D. & SOSINSKI, E. E. (2003). An improved method for searching plant functional types by numerical analysis. *Journal of Vegetation Science* **14**, 323–332.

POORTER, L. & MARKESTEIJN, L. (2008). Seedling traits determine drought tolerance of tropical tree species. *Biotropica* **40**, 321–331.

POORTER, L., WRIGHT, S. J., PAZ, H., ACKERLY, D. D., CONDIT, R., IBARRA-MANRIQUEZ, G., HARMS, K. E., LICONA, J. C., MARTINEZ-RAMOS, M., MAZER, S. J., MULLER-LANDAU, H. C., PENA-CLAROS, M., WEBB, C. O. & WRIGHT, I. J. (2008). Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology* **89**, 1908–1920.

RAMÍREZ-VALIENTE, J.A., KOEHLER, K. & CAVENDER-BARES, J. (2015). Climatic origins predict variation in photoprotective leaf pigments in response to drought and low temperatures in live oaks (Quercus series Virentes). *Tree Physiology*, doi: 10.1093/treephys/tpv032.

RAUNKIAER, C. (1934). *The Life Forms of Plants and Statistical Plant Geography*. Clarendon Press, Oxford.

REICH, P. B. (2012). Key canopy traits drive forest productivity. *Proceedings of the Royal Society B: Biological Sciences***,** rspb20112270.

REICH, P. B. (2014). The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. *Journal of Ecology* **102**, 275–301.

REICH, P. B., BUSCHENA, C., TJOELKER, M. G., WRAGE, K., KNOPS, J., TILMAN, D. & MACHADO, J. L. (2003). Variation in growth rate and ecophysiology among 34 grassland and savanna species under contrasting N supply: A test of functional group differences. *New Phytologist* **157**, 617–631.

REICH, P. B., OLEKSYN, J., MODRZYNSKI, J. & TJOELKER, M. J. (1996). Evidence that longer needle retention of spruce and pine populations at high elevations and high latitudes is largely a phenotypic response. *Tree Physiology* **16**, 643–647.

REICH, P. B., RICH, R. L., LU, X., WANG, Y. P. & OLEKSYN, J. (2014). Biogeographic variation in evergreen conifer needle longevity and impacts on boreal forest carbon cycle projections. *Proceedings of the National Academy of Sciences* **111**, 13703–13708.

REICH, P. B., WALTERS, M. B. & ELLSWORTH, D. S. (1997). From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences* **94**, 13730–13734.

RILLIG, M. C. & MUMMEY, D. L. (2006). Mycorrhizas and soil structure. *New Phytologist* **171**, 41–53.

ROOT, R. B. (1967). The niche exploitation pattern of the blue-gray gnatcatcher. *Ecological Monographs* **37**, 317–350.

ROSBAKH, S., RÖMERMANN, C. & POSCHLOD, P. (2015). Specific leaf area correlates with temperature: new evidence of trait variation at the population, species and community levels. *Alpine Botany* **125**, 79-86.

SANTIAGO, L. S. (2007). Extending the leaf economics spectrum to decomposition: evidence from a tropical forest. *Ecology* **88**, 1126–1131.

SANTIAGO, L. S., SCHUUR, E. A. G. & SILVERA, K. (2005). Nutrient cycling and plant-soil feedbacks along a precipitation gradient in lowland Panama. *Journal of Tropical Ecology* **21**, 461–470.

SAVAGE, V., WEBB, C. T. & NORBERG, J. (2007). A general multi-trait-based framework for studying the effects of biodiversity on ecosystem functioning. *Journal of Theoretical Biology* **247**, 213–229.

SCHÖB, C., BUTTERFIELD, B. J. & PUGNAIRE, F. I. (2012). Foundation species influence trait-based community assembly. *New Phytologist* **196**, 824–834.

SCHWEITZER, J.A., MADRITCH, M.D., FELKER-QUINN, E. & BAILEY, J.K. (2012). From genes to ecosystems: Plant genetics as a link between above- and belowground processes. In *Soil Ecology & Ecosystem Services* (ed D. WALL), pp. 82–97. Oxford University Press, Oxford.

SHAW, R.G. & ETTERSON, J.R. (2012). Rapid climate change and the rate of adaptation: insight from experimental quantitative genetics. *New Phytologist* **195**, 752–765.

Siebenkäs, A., Schumacher, J. & Roscher, C. (2015). Phenotypic plasticity to light and nutrient availability alters functional trait ranking across eight perennial grassland species. *AoB Plants* **7**.

Siefert, A., Violle, C., Chalmandrier, L., Albert, C.H., Taudiere, A., Fajardo, A., Aarssen, L.W., Baraloto, C., Carlucci, M.B., Cianciaruso, M.V., de L. Dantas, V., de Bello, F., Duarte, L.D.S., Fonseca, C.R., Freschet, G.T. *et al*. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters* 18, 1406–1419, doi: 10.1111/ele.12508.

Six, J., Bossuyt, H., Degryze, S. & Denef, K. (2004). A history of research on the link between (micro) aggregates, soil biota, and soil organic matter dynamics. *Soil and Tillage Research* **79**, 7–31.

Spasojevic, M. J. & K. N. Suding. (2012). Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *Journal of Ecology* **100**, 652–661.

Stokes, A., Atger, C., Bengough, A., Fourcaud, T. & Sidle, R. (2009). Desirable plant root traits for protecting natural and engineered slopes against landslides. *Plant and Soil* **324**, 1–30.

Suding, K. N., Goldberg, D. E. & Hartman, K. M. (2003). Relationships among species traits: separating levels of response adn identifying linkages to abundance. *Ecology* **84**, 1–16.

Suding, K. N. & Goldstein, L. J. (2008). Testing the Holy Grail framework: using functional traits to predict ecosystem change. *New Phytologist* **180**, 559–562.

SUDING, K. N., LAVOREL, S., CHAPIN III, F. S., CORNELISSEN, J. H. C., DÍAZ, S., GARNIER, E., GOLDBERG, D., HOOPER, D. U., JACKSON, S. T. & NAVAS, M.-L. (2008). Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology* **14**, 1125–1140.

SULTAN, S. E. (2001). Phenotypic plasticity for fitness components in *Polygonum* species of contrasting ecological breadth. *Ecology* **82**, 328–343.

SULTAN, S. E., WILCZEK, A. M., BELL, D. L. & HAND, G. (1998). Physiological response to complex environments in annual *Polygonum* species of contrasting ecological breadth. *Oecologia* **115**, 564–578.

SUNDQVIST, M. K., GIESLER, R. & WARDLE, D. A. (2011). Within- and across-species responses of plant traits and litter decomposition to elevation across contrasting vegetation types in subarctic. *PLOS ONE* **6**, e27056.

SUTTON-GRIER, A. E. & MEGONIGAL, J. P. (2011). Plant species traits regulate methane production in freshwater wetland soils. *Soil Biology & Biogeochemistry* **43**, 413–420.

SUTTON-GRIER, A. E., WRIGHT, J., MCGILL, B. & RICHARDSON, C. (2011). Environmental conditions influence the plant functional diversity effect on denitrification potential. *PLOS ONE* **6**, e16584, doi:10.1371/journal.pone.0016584.

SUTTON-GRIER, A. E., WRIGHT, J. & RICHARDSON, C. (2012). Different plant traits affect two pathways of riparian nitrogen removal in a restored freshwater wetland. *Plant and Soil* **365**, 41–57.

SWAFFER, B. A. & HOLLAND, K. L. (2015). Comparing ecophysiological traits and evapotranspiration of an invasive exotic,Pinus halepensisin native woodland overlying a karst aquifer. *Ecohydrology* **8**, 230–242.

SWENSON, N. G., ENQUIST, B. J., PITHER, J., KERKHOFF, A. J., BOYLE, B., WEISER, M. D., ELSER, J. J., FAGAN, W. F., FORERO-MONTANA, J., FYLLAS, N., KRAFT, N. J. B., LAKE, J. K., MOLES, A. T., PATINO, S., PHILLIPS, O. L. *ET AL*. (2012). The biogeography and filtering of woody plant functional diversity in North and South America. *Global Ecology and Biogeography* **21**, 798–808.

TILMAN, D. (2004). Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences* **101**, 10854–10861.

TURNER, D. P., OLLINGER, S. V. & KIMBALL, J. S. (2004). Integrating Remote Sensing and Ecosystem Process Models for Landscape- to Regional-Scale Analysis of the Carbon Cycle. *BioScience* **54**, 573–584.

VALENCIA, E., MAESTRE, F. T., BAGOUSSE-PINGUET, Y. L., QUERO, J. L., TAMME, R., BÖRGER, L., GARCÍA-GÓMEZ, M. & GROSS, N. (2015). Functional diversity enhances the resistance of ecosystem multifunctionality to aridity in Mediterranean drylands. *New Phytologist* **206**, 660–671.

VALLADARES, F., SANCHEZ-GOMEZ, D. & ZAVALA, M.A. (2006). Quantitative estimation of
phenotypic plasticity: bridging the gap between the evolutionary concept and its ecological

applications. *Journal of Ecology* **94,** 1103-1116.

VALLADARES, F., GIANOLI, E. & GOMEZ, J. M. (2007). Ecological limits to plant phenotypic plasticity. *New Phytologist* **176**, 749–763.

VALLADARES, F., MATESANZ, S., GUILHAUMON, F., ARAÚJO, M. B., BALAGUER, L., BENITO-GARZÓN, M., CORNWELL, W., GIANOLI, E., VAN KLEUNEN, M., NAYA, D. E., NICOTRA, A. B., POORTER, H. & ZAVALA, M. A. (2014). The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters* **17**, 1351–1364.

VALLADARES, F., SANCHEZ-GOMEZ, D. & ZAVALA, M.A. (2006). Quantitative estimation of phenotypic plasticity: bridging the gap between the evolutionary concept and its ecological applications. *Journal of Ecology* **94,** 1103-1116.

VAN BODEGOM, P., DOUMA, J., WITTE, J., ORDOÑEZ, J., BARTHOLOMEUS, R. & AERTS, R. (2012). Going beyond limitations of plant functional types when predicting global ecosystem–atmosphere fluxes: exploring the merits of traits-based approaches. *Global Ecology and Biogeography* **21**, 625–636.

VAN DER HEIJDEN, M. G. A. & SCHEUBLIN, T. R. (2007). Functional traits in mycorrhizal ecology: their use for predicting the impact of arbuscular mycorrhizal fungal communities on plant growth and ecosystem functioning. *New Phytologist* **174**, 244–250.

VAN KLEUNEN, M. & FISCHER, M. (2005). Constraints on the evolution of adaptive phenotypic plasticity in plants. *New Phytologist* **166**, 49–60.

Verheijen, L. M., Aerts, R., Brovkin, V., Cavender-Bares, J., Cornelissen, J. H. C., Kattge, J. & van Bodegom, P. M. (2015). Inclusion of ecologically based trait variation in plant functional types reduces the projected land carbon sink in an earth system model. *Global Change Biology*, doi: 10.1111/gcb.12871.

Villeger, S., Mason, N. W. H. & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **89**, 2290–2301.

Villeger, S., Novack-Gottshall, P. M. & Mouillot, D. (2011). The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. *Ecology Letters* **14**, 561–568.

Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., Jung, V. & Messier, J. (2012). The return of the variance: intraspecific variability in community ecology. *Trends in Ecology and Evolution* **27**, 244–252.

Violle, C., Garnier, E., Lecoeur, J., Roumet, C., Podeur, C., Blanchard, A. & Navas, M.-L. (2009). Competition, traits and resource depletion in plant communities. *Oecologia* **160**, 747–755.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007). Let the concept of trait be functional! *Oikos* **116**, 882–892.

Vitasse, Y., Bresson, C. C., Kremer, A., Michalet, R. & Delzon, S. (2010). Quantifying phenological plasticity to temperature in two temperate tree species. *Functional Ecology* **24**, 1211–1218.

WALKER, B. H. & LANGRIDGE, J. L. (2002). Measuring functional diversity in plant communities with mixed life forms: A problem of hard and soft attributes. *Ecosystems* **5**, 529–538.

WARNER, R. R. & CHESSON, P. L. (1985). Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *American Naturalist* **125**, 769–787.

WEBB, C. T., HOETING, J. A., AMES, G. M., PYNE, M. I. & POFF, N. L. (2010). A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology Letters* **13**, 267–283.

WEIHER, E., CLARKE, G. D. P. & KEDDY, P. A. (1998). Assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos* **81**, 309–322.

WEIHER, E., VAN DER WERF, A., THOMPSON, K., RODERICK, M., GARNIER, E. & ERIKSSON, O. (1999). Challenging Theophrastus: A common core list of plant traits for functional ecology. *Journal of Vegetation Science* **10**, 609–620.

WEINER, J. (2004). Allocation, plasticity and allometry in plants. *Perspectives in Plant Ecology, Evolution and Systematics* **6**, 207–215.

WESTOBY, M., FALSTER, D. S., MOLES, A. T., VESK, P. A. & WRIGHT, I. J. (2002). Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* **33**, 125–159.

WESTOBY, M. & WRIGHT, I. J. (2006). Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution* **21**, 261–268.

WISNIEWSKI, M., CLOSE, T., ARTLIP, T. & ARORA, R. (1996). Seasonal patterns of dehydrins and 70-kDa heat-shock proteins in bark tissues of eight species of woody plants. *Physiologia Plantarum* **96**, 496–505.

WRIGHT, I. J., REICH, P. B., CORNELISSEN, J. H. C., FALSTER, D. S., GARNIER, E., HIKOSAKA, K., LAMONT, B. B., LEE, W., OLEKSYN, J., OSADA, N., POORTER, H., VILLAR, R., WARTON, D. I. & WESTOBY, M. (2005). Assessing the generality of global leaf trait relationships. *New Phytologist* **166**, 485–496.

WRIGHT, I. J., REICH, P. B., WESTOBY, M., ACKERLY, D. D., BARUCH, Z., BONGERS, F., CAVENDER-BARES, J., CHAPIN, T., CORNELISSEN, J. H. C., DIEMER, M., FLEXAS, J., GARNIER, E., GROOM, P. K., GULIAS, J., HIKOSAKA, K. *ET AL*. (2004). The worldwide leaf economics spectrum. *Nature* **428**, 821–827.

WRIGHT, I. J. & WESTOBY, M. (1999). Differences in seedling growth behaviour among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. *Journal of Ecology* **87**, 85–97.

WRIGHT, J. P., NAEEM, S., HECTOR, A., LEHMAN, C., REICH, P. B., SCHMID, B. & TILMAN, D. (2006). Conventional functional classification schemes underestimate the relationship with ecosystem functioning. *Ecology Letters* **9**, 111–120.

WRIGHT, J. P. & SUTTON-GRIER, A. (2012). Does the leaf economic spectrum hold within local species pools across varying environmental conditions? *Functional Ecology* **26**, 1390–1398.

YAN C.-F., HAN, S.-J., ZHOU, Y.-M., WANG, C.-G., DAI, G.-H., XIAO, W.-F. & LI, M.-H. (2012). Needle-age related variability in nitrogen, mobile carbohydrates, and δ13C within *Pinus koraiensis* tree crowns. *PLOS ONE* **7**, e35076.

ZANNE, A. E., WESTOBY, M., FALSTER, D. S., ACKERLY, D. D., LOARIE, S. R., ARNOLD, S. E. J. & COOMES, D. A. (2010). Angiosperm wood structure: Global patterns in vessel anatomy and their relation to wood density and potential conductivity. *American Journal of Botany* **97**, 207–215.

ZEITER, M., STAMPFLI, A. & NEWBERY, D. M. (2006). Recruitment limitation constrains local species richness and productivity in dry grassland. *Ecology* **87**, 942–51.

Figure legend

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

1925 Figure 1



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

1926