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

3

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26 Running head: Plant functional traits

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30

31 ABSTRACT

32 One of ecology's grand challenges is developing general rules to
33 explain and predict highly complex systems. Understanding and predicting
34 ecological processes from species' traits has been considered a 'Holy Grail'
35 in ecology. Plant functional traits are increasingly being used to develop
36 mechanistic models that can predict how ecological communities will
37 respond to abiotic and biotic perturbations and how species will affect
38 ecosystem function and services in a rapidly changing world; however,
39 significant challenges remain. In this review, we highlight recent work and
40 outstanding questions in three areas: (i) selecting relevant traits, (ii)
41 describing intraspecific trait variation and incorporating this variation into
42 models, and (iii) scaling trait data to community- and ecosystem-level
43 processes. Over the past decade, there have been significant advances in

44 the characterization of plant strategies based on traits and trait
45 relationships, and the integration of traits into multivariate indices and
46 models of community and ecosystem function. However, the utility of trait-
47 based approaches in ecology will benefit from efforts that demonstrate how
48 these traits and indices influence organismal, community, and ecosystem
49 processes across vegetation types, which may be achieved through meta-
50 analysis and enhancement of trait databases. Additionally, intraspecific trait
51 variation and species interactions need to be incorporated into predictive
52 models using tools such as Bayesian hierarchical modelling. Finally, existing
53 models linking traits to community and ecosystem processes need to be
54 empirically tested for their applicability to be realized.

55

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

59

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81 **I. INTRODUCTION**

82 Ecologists have a long tradition of grouping organisms based on
83 function (Grime, 1974; Raunkiaer, 1934; Root, 1967). A renewed interest in
84 this approach came in the late 1990s when a number of ecologists sought to
85 understand how the functional traits of species could predict community
86 response to environmental change and the effects of changes in community
87 composition on ecosystem processes (Chapin *et al.*, 2000; Díaz & Cabido,
88 1997; Lavorel *et al.*, 1997). Lavorel & Garnier (2002) developed a conceptual
89 framework by distinguishing traits that predict how species respond to

90 environmental factors (response traits) from traits that affect ecosystem
91 processes (effect traits). They argued that understanding and predicting
92 community processes from species traits, rather than species identity, was a
93 'Holy Grail' in ecology. While empirical tests of this framework were slow to
94 appear (Suding & Goldstein, 2008), the formalization of the leaf economic
95 spectrum (LES) spurred an increased focus on trait-based methodological
96 approaches. The LES shows that relationships exist among several key traits
97 across a broad range of species and different climates (Reich, Walters &
98 Ellsworth, 1997; Wright *et al.*, 2004), and that simple predictors (specific leaf
99 area, SLA) may link to hard-to-measure ecological processes (e.g. growth
100 rate).

101 Whether or not traits matter to community ecology is closely related to
102 whether or not the niche matters, as niche differentiation can be defined as
103 differential performance along environmental gradients with respect to
104 organismal traits (Chase & Leibold, 2003). Opinions regarding the relative
105 importance of the niche, and hence traits, to community dynamics fall
106 loosely into three camps. The first argues that trait differences among
107 individuals are largely irrelevant at the community level compared to factors
108 such as demographic stochasticity (e.g. Neutral Theory: Hubbell, 2001). The
109 second argues that traits are relevant to individuals, but the complexity of
110 biotic and abiotic interactions precludes us from scaling individual processes
111 to the community level (e.g. Lawton, 1999). The final camp argues that traits
112 provide a path forward to a unified theory of community ecology by

113 providing a taxon-independent means for generalizing the structure and/or
114 functioning of communities that is based on functional traits rather than
115 species identity (e.g. McGill *et al.*, 2006a; Westoby & Wright, 2006). While
116 the impact of stochasticity on community structure is largely undisputed, it
117 has been shown that Neutral Theory cannot, by itself, explain observed
118 species distributions in many systems (McGill, 2003; McGill, Maurer &
119 Weiser, 2006b). Furthermore, many recent studies have demonstrated that
120 traits within communities and regional species pools explain a large amount
121 of variance in community structure (e.g. de Bello *et al.*, 2012; Edwards,
122 Lichtman & Klausmeier, 2013) and function (e.g. Sutton-Grier & Megonigal,
123 2011). These studies demonstrate that traits can scale up to influence
124 community structure and, thus, provide optimism that it will be possible to
125 develop general, predictive rules in community ecology as we refine our
126 understanding of which traits are important in a given environment, how
127 traits are distributed within and among species, and how those traits relate
128 to mechanisms driving community dynamics and function (Fig. 1).

129 While trait-based ecology (TBE) has made significant strides over the
130 past decade, a number of critical issues must be addressed before we can
131 have confidence in the framework's ability to deliver on its significant
132 promise. This review highlights recent work and outstanding questions in
133 three areas: (i) selecting relevant traits, (ii) describing intraspecific trait
134 variation and incorporating this variation into models, and (iii) scaling trait
135 data to community- and ecosystem-level processes. While this review

136 focuses on plants, similar TBE movements are occurring in animal and
137 microbial ecology (e.g. Bokhorst *et al.*, 2012; Fierer, Barberán & Laughlin,
138 2014; Haddad *et al.*, 2008; Litchman *et al.*, 2007; Pedley & Dolman, 2014).

139

140 **II. SELECTING RELEVANT TRAITS**

141 **(1) Simplifying plant communities: functional groups *versus*** 142 **functional traits**

143 Over time, there have been major shifts in how trait variation is
144 measured and utilized, particularly with respect to applications in community
145 ecology. Shortcomings in the predictive power of TBE have ironically
146 stemmed from one of its fundamental tenets—species can be grouped
147 according to their responses to and effects on abiotic and biotic conditions
148 (Lavorel & Garnier, 2002). Historically, ecologists have attempted to capture
149 ecological processes within communities (e.g. assembly, response to abiotic
150 factors) by measuring the distribution and responses of species groups
151 based on characteristics such as life history, life form, photosynthetic
152 pathways or other functional traits (Lavorel *et al.*, 2007; Lavorel & Garnier,
153 2002; Lavorel *et al.*, 1997). If such groups are assumed to function similarly,
154 community- to global-scale processes could be modelled without the
155 collection of detailed trait data for many species.

156 While numerous studies have found significant relationships between
157 ecosystem functions and traditional plant functional group classifications like
158 the grass-forb-legume approach (reviewed in Díaz & Cabido, 2001),

159 categorical groups mask variability, and may underestimate the important
160 role that functional diversity plays in maintaining key ecosystem functions
161 like productivity and nutrient cycling (Wright *et al.*, 2006). For example,
162 studies have shown that not all C₄ perennial grasses or C₃ annual forbs
163 respond similarly to disturbance or resource fluctuations (Badgery *et al.*,
164 2005; Firn *et al.*, 2010; Firn, Prober & Buckley, 2012; Han, Buckley & Firn,
165 2012). Further evidence of the inability of categorical functional groups to
166 predict species responses to environmental change are emerging from the
167 field of invasion ecology, as native and invasive species from similar
168 functional groups respond differently to environmental variation (Firn *et al.*,
169 2010, 2012; Funk, 2008; Han *et al.*, 2012). Simple categorical functional
170 groups can also be low in number in ecosystems like grasslands, meaning
171 that correlative relationships between simple functional groups and changes
172 in ecosystem function may be statistically significant because variability is
173 reduced and not necessarily because groups are responding in a common
174 way to perturbations.

175 Given limited abilities of traditional functional groups to capture and
176 represent trait variation, there has been a shift away from describing and
177 predicting community and ecosystem dynamics with functional categories of
178 species and towards the use of continuous trait distributions (Lavorel *et al.*,
179 2007; Westoby & Wright, 2006). Interspecific differences in continuous traits
180 have been linked to environmental gradients (e.g. Wright *et al.*, 2005; Wright
181 & Westoby, 1999), demographic responses (Poorter & Markesteijn, 2008),

182 and ‘major axes of variation’ describing suites of co-varying traits indicative
183 of broader ecological strategies (e.g. Díaz *et al.*, 2004; Wright *et al.*, 2004).
184 Still, trait effects on ecosystem-, landscape- and global-scale processes
185 depend on the combined traits of co-occurring species, and are likely to be
186 driven disproportionately by traits of the most abundant species (Grime,
187 1998). These realizations have led to the quantification and use of
188 aggregated trait attributes of the community [e.g. community-weighted
189 mean (CWM)] and indices of community diversity to reveal broad patterns
190 and explain more of the variation in trait–environment relationships (see
191 Section IV.1, Díaz *et al.*, 2007a; Villegger, Mason & Mouillot, 2008). Meanwhile,
192 alternative methods of classifying species into ecologically relevant
193 functional groups based on numerous functional traits have continued to
194 develop, often utilizing methods in cluster analysis (e.g. Aubin *et al.*, 2009;
195 Fry, Power & Manning, 2014; Grime *et al.*, 1997; Pillar & Sosinski, 2003);
196 however, identification of consistent groups and demonstrations of their
197 utility in predictive models remain sparse and equivocal (e.g. Larson *et al.*,
198 2015; Louault *et al.*, 2005; Müller *et al.*, 2007).

199

200 **(2) Trait selection**

201 Deciding which traits to measure is one of the most difficult aspects of
202 TBE. It is often difficult to know, *a priori*, the mechanism(s) responsible for
203 driving a particular community- or ecosystem-level process, much less the
204 organismal trait(s) most closely linked to the mechanism. Compounding the

205 problem is that many traits relevant to a particular mechanism are difficult or
206 expensive to measure, especially for enough individuals to accurately
207 characterize the trait distributions of a community, or even populations
208 within the community. Fortunately, these 'hard' traits are often strongly
209 correlated with more easily or cheaply measured 'soft' traits (Hodgson *et al.*,
210 1999). If certain traits are relevant to multiple plant responses and effects, it
211 may be possible to identify a set of soft but multifaceted traits which predict
212 a substantial portion of the variation in plant function and ecological
213 processes (Fig. 1). Soft traits for many species can now be acquired from
214 global databases like TRY (Kattge *et al.*, 2011) and BioFlor (www.biolflor.de).
215 A recent study of 222 plant species found that soft traits sourced from the
216 TRY database (i.e. seed mass, wood density, and leaf traits) were strong
217 predictors of a range of life-history strategies (Adler *et al.*, 2013). Despite
218 these advances, our understanding of which traits most strongly influence
219 plant and ecosystem function reflects a bias towards leaf traits and
220 databases like TRY generally do not account for site-level differences
221 including species interactions, trait variation, and environmental variation.

222

223 (a) *Response traits*

224 Plant traits reflect adaptations to abiotic and biotic factors and, thus,
225 can be used to describe and predict species responses to changes in these
226 factors. In this framework, trait variation is assumed to be linked to variation
227 in organismal responses to different factors (e.g. abiotic stress or

228 competition), which scales up to influence demographic responses and
229 species abundances (Suding, Goldberg & Hartman, 2003). The particular
230 response traits of interest will depend on the specific combination of abiotic
231 and biotic factors in a vegetation community. Which traits are linked to
232 specific environmental changes has been the subject of previous reviews
233 (Lavorel *et al.*, 2007), although empirical demonstrations of trait-response
234 linkages remain relatively rare. Here, we briefly review key aspects of
235 functional variation across species and their potential relevance to species
236 responses in light of abiotic and biotic factors.

237 Plant growth rate is considered a key trait differentiating ecological
238 strategies within communities (e.g. Grime, 1977; Reich, 2014). In general,
239 growth rate has been shown to be positively associated with shade tolerance
240 and negatively associated with drought tolerance (Suding *et al.*, 2003). Rapid
241 growth has also been shown to be more prevalent in productive (e.g. Grime
242 & Hunt, 1975), high-nutrient communities (Wright & Westoby, 1999),
243 suggesting that it provides some fitness advantage when resources are not
244 limiting. In some cases, however, rapid growth can allow plants to escape
245 resource limitation in low, pulse-resource systems (e.g. among invasive
246 species; Funk, 2013). Plant relative growth rate (RGR, the rate of dry mass
247 addition per unit dry mass) has been recognized as a strong predictor of
248 species' potential for success and the most useful measure of plant growth
249 (Grime, 1977; Grime & Hunt, 1975; Hunt & Cornelissen, 1997).
250 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

273 traits present a good starting point in the selection of traits for plant
274 systems.

275 While great progress has been made in understanding the function of
276 LES traits, our understanding of how other traits relate to plant and
277 community responses is limited. Root traits are notoriously difficult to
278 measure, although there is some evidence that an economic axis for roots
279 exists as well, with slow-growing species having low root elongation rates,
280 specific root length (SRL), high root diameter, and low nutrient concentration
281 (Freschet *et al.*, 2010; Liu *et al.*, 2010; Larson & Funk, 2016). In arid and
282 semi-arid ecosystems, responses to changes in water availability may be
283 better predicted from root traits such as root depth or elongation rate than
284 from leaf traits (Nicotra, Babicka & Westoby, 2002; Padilla & Pugnaire, 2007).
285 However, the traits most closely linked to plant performance may change
286 depending on the environment. For example, a study of the annual species
287 *Polygonum persicaria* found that leaf-level water-use efficiency was
288 correlated with plant fitness in water-limited habitats while root biomass
289 allocation was more closely linked to fitness in moist environments (e.g.,
290 Heschel *et al.*, 2004). Recent work also suggests that leaf and stem hydraulic
291 traits (e.g. wood density; Cornwell & Ackerly, 2010) are correlated with traits
292 from the LES (reviewed in Reich, 2014), but these traits are rarely
293 incorporated into empirical tests and additional data are needed to
294 determine if the LES can adequately capture plant response to changes in
295 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

318 in empirical tests is still relatively rare, and represents an important area for
319 future research.

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

341 of the performance metric is also important because growth, survival, and
342 reproductive measures will have different relationships with community-level
343 processes (e.g. abundance) as environmental conditions change (Gross *et*
344 *al.*, 2007, 2009). More studies are needed that examine how traits relate to
345 plant performance across different environments; this will be critical if we are
346 to predict plant and community responses in a changing world (Meinzer,
347 2003).

348

349 (b) *Effect traits*

350 For functional traits to provide a comprehensive theoretical framework
351 in ecology, we must also understand how trait composition and diversity
352 influence ecosystem functioning (Fig. 1; Lavorel & Garnier, 2002). Effect
353 traits alter abiotic and biotic processes corresponding to a wide range of
354 ecosystem functions, and have been the subject of recent review (de Bello *et*
355 *al.*, 2010; Eviner & Chapin, 2003; Garnier & Navas, 2012). However, while
356 our understanding of effect traits has improved in the wake of the framework
357 laid out by Lavorel & Garnier (2002), predictive models have lagged behind
358 those incorporating response traits (Suding *et al.*, 2008). In addition to their
359 predictive role in species and community responses to environmental
360 variation, links between LES traits and ecosystem function have been best
361 characterized. The effects of RGR, SLA, and leaf N are particularly well
362 studied, with evidence suggesting positive relationships between these traits
363 and primary productivity, litter decomposition rates (see below), plant-

364 available soil N, N turnover rates, and palatability to herbivores, and
365 negative relationships with soil C and N retention (e.g. De Deyn, Cornelissen
366 & Bardgett, 2008; Grigulis *et al.*, 2013; Lavorel & Grigulis, 2012; Loranger *et*
367 *al.*, 2012). When community-scale analogues of LES traits are considered,
368 similar patterns emerge. Canopy N and leaf area index (LAI) tend to scale
369 positively with SLA and leaf N values, and have also been tied to
370 aboveground net primary productivity (ANPP; Reich, 2012).

371 The influence of leaf tissue chemistry and structure on decomposition
372 rate is among the most studied aspects of trait influence (de Bello *et al.*,
373 2010), and traits associated with the LES have been shown to influence
374 decomposition rates in several studies (Bakker, Carreño-Rocabado & Poorter,
375 2011; Cornwell *et al.*, 2008; see for example Santiago, 2007). Species on the
376 'fast return' end of the LES (rapid growth, thin leaves, high nutrient
377 concentrations, and high rates of photosynthesis) decompose more quickly
378 than species on the 'slow return' end of the LES (slow growth, thicker,
379 tougher, more recalcitrant leaves with more defences and lower rates of
380 photosynthesis), suggesting that the suite of coordinated structural and
381 chemical leaf traits maximizing photosynthesis also has important
382 implications for nutrient cycling (Santiago, 2007) and the global carbon cycle
383 (Cornwell *et al.*, 2008). However, the effects of the plant community on
384 biogeochemical cycles will likely require more than singular LES traits. For
385 example, Sutton-Grier, Wright & Richardson (2012) determined that different
386 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 CO₂
422 uptake capacity, suggesting LES implications for surface temperatures and
423 atmospheric CO₂ 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

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

440 Our understanding of how root and wood traits influence ecosystem
441 function is less clear compared to other traits (e.g. LES traits), although (as
442 mentioned above) recent studies have suggested that some water-related
443 root and stem traits may align with ‘fast return’ and ‘slow return’ strategies
444 represented by the LES (Chave *et al.*, 2009). For example, lower sapwood
445 density and higher sap flux—which has been positively associated with SLA
446 (O’Grady *et al.*, 2009)—may explain higher evapotranspiration rates
447 observed in an invasive tree species relative to coexisting natives (Swaffer &
448 Holland, 2015). Independent of the LES, root morphological and architectural
449 traits have been shown to influence soil moisture (Gross *et al.*, 2008), soil
450 stability, and erosion (Stokes *et al.*, 2009), with possible impacts on soil
451 structure (Six *et al.*, 2004), leaching and infiltration (De Deyn *et al.*, 2008),
452 and evapotranspiration and climate cycles (Lee *et al.*, 2005). Like foliar
453 traits, there have been relatively few direct tests linking root and wood traits
454 to hydrologic or atmospheric processes, representing a substantial
455 opportunity for research on belowground trait influence. As in leaves, higher

456 density, lignin or dry matter content in roots and wood should slow
457 decomposition and increase soil C storage (Chambers *et al.*, 2000; De Deyn
458 *et al.*, 2008; Freschet, Aerts & Cornelissen, 2012; Klumpp & Soussana, 2009).
459 Unlike foliar tissue, however, root N is not necessarily related to root
460 decomposition rates, which may be complicated by co-occurring effects of
461 substrate chemistry, litter secondary chemistry, or mycorrhizae on root
462 decomposition (Freschet *et al.*, 2012; Langley, Chapman & Hungate, 2006).
463 Quantity and quality of root exudation could also affect soil C and N
464 dynamics, as higher quantities may increase labile C and microbial
465 stimulation (Dijkstra, Hobbie & Reich, 2006; Kaštovská *et al.*, 2015), although
466 the nature of microbial effects may depend on the type of exudate, which is
467 only just beginning to be explored (De Deyn *et al.*, 2008).

468 Relationships between plant roots and mycorrhizae or N-fixing bacteria
469 should also affect biogeochemical processes. As symbiotic relationships
470 make N and P more available, primary productivity and soil C inputs should
471 generally increase. Furthermore, increased longevity and slower
472 decomposition of colonized roots, along with C immobilization by symbionts,
473 may also increase soil C and N retention (De Deyn *et al.*, 2008; Langley *et*
474 *al.*, 2006). It is still unclear whether these trends are generalizable, as effects
475 may vary across species of plants, fungi and/or microbes (Rillig & Mummey,
476 2006). For example, Cornelissen *et al.* (2001) found plant litter of species
477 associating with ericoid mycorrhizae, ectomycorrhizae, and arbuscular
478 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 Lavelly & 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-

502 Römermann *et al.*, 2008; Dray *et al.*, 2014). Using the same type of data,
503 Jamil *et al.* (2013) developed a generalized linear mixed model (GLMM)
504 approach to identify more directly links between traits, environmental
505 variables, and abundances.

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

522 A further challenge is that traits, abiotic factors, and species
523 interactions (e.g. competition, facilitation) may interact in non-additive ways
524 to influence community and ecosystem processes (Suding *et al.*, 2008). For

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

540

541 **III. INTRASPECIFIC TRAIT VARIATION**

542 Because traits vary across biological, spatial, and temporal scales in a
543 context-dependent manner (e.g. patterns differ for individual traits and
544 species: Siefert *et al.*, 2015), traits need to be accurately characterized
545 within a species or population. Most plant traits are defined and measured on
546 individual plants (e.g. height), on organs within a plant (e.g. leaves), or on
547 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 $\delta^{13}\text{C}$, 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.2a). 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,

684 defining SLA in relation to sun exposure. If high levels of trait differentiation
685 are observed among populations within a study area, sampling methods will
686 need to reflect such differentiation to capture one or more trait values
687 pertinent to the study question.

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

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

726 Bayesian hierarchical models (BHMs, Gelman *et al.*, 2004; Gelman &
727 Hill, 2007) incorporate the hierarchical relationships inherent in scaling from
728 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 (Klump
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

798 variation in CWM trait values identify shifts in assembly filters along
799 environmental gradients (Ackerly & Cornwell, 2007), it is also perhaps the
800 strongest determinant of biotic effects on ecosystem functioning (Fortune et
801 al., 2009; Laliberté & Tylianakis, 2012; Lavorel et al., 2011) as more
802 abundant species have a disproportionate influence on ecosystem processes
803 (mass ratio hypothesis; Grime, 1998). A simple null hypothesis is that CWM-
804 environment relationships are identical to interspecific trait-environment
805 relationships, at least qualitatively speaking. At the resolution of 1° of
806 latitude and longitude, Swenson et al. (2012) found that CWM values of leaf
807 traits, height, seed mass, and wood density based on species occurrences
808 (although species may not co-occur within 1° grid cells) were relatively
809 strongly correlated with annual mean and seasonality of temperature and
810 precipitation in ways that were consistent with expectations based on
811 species trait-environment patterns across much of the Western Hemisphere.
812 However, trait-environment relationships do not always scale linearly from
813 the species to community levels due to interactions between multiple
814 environmental factors (Rosbakh, Römermann & Poschlod, 2015) and
815 assembly processes that may not favour species with intermediate trait
816 values. For example, in one set of woody plant communities, over 80% of
817 traits were found to have linear or context-dependent abundance
818 distributions within communities while only one was unimodal (Cornwell &
819 Ackerly, 2010), thereby producing CWM-environment relationships that differ
820 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 (Villegger *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 Villegger *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*

867 hierarchical differences in traits (fitness differences) rather than *via* limiting
868 similarity (niche differences; Kunstler *et al.*, 2012, 2016). A consequence of
869 competitive hierarchies is a reduction in the range of trait values observed
870 within a community, where species at one end of a trait spectrum are
871 competitively excluded, and functional divergence is not observed.
872 Furthermore, high divergence could result from the success of different
873 strategies dealing with stress (as described above) rather than from
874 competition. This pattern could also be enabled by facilitation, which has
875 been shown to increase the range of trait values in a community through the
876 creation of favourable microenvironments allowing species with otherwise
877 unsuitable trait values to persist (Gross *et al.*, 2009; Butterfield & Briggs,
878 2011). In a study of alpine plant communities, Schöb, Butterfield & Pugnaire
879 (2012) found that the magnitude of the net effects of competition and
880 facilitation on the CWM, richness, and evenness of trait distributions was
881 proportional to the effects of broad environmental gradients, and that the
882 biotic effects on trait distributions often countered those of the environment.
883 In short, biotic interactions can substantially alter trait–environment
884 relationships in a variety of ways, and a better understanding of the
885 functional trait basis of interaction outcomes is essential for integrating
886 these effects into predictive models of trait–environment relationships
887 (Butterfield & Callaway, 2013).

888 In addition to single-trait indices, multi-trait indices of functional
889 composition can be used to represent the multidimensional nature of the

890 'niche' (Villegger *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

913 may in fact be necessary for elucidating response–effect patterns in complex
914 landscapes (Butterfield & Suding, 2013) and identifying multiple assembly
915 processes that act simultaneously along environmental gradients (Spasojevic
916 & Suding, 2012). On the other hand, there are examples of patterns that can
917 only be revealed through multi-trait indices, both for community assembly
918 (Villegger, Novack-Gottshall & Mouillot, 2011) and effects on ecosystem
919 processes (Mouillot *et al.*, 2011). Additionally, while most studies have linked
920 functional diversity to single ecosystem processes (e.g. productivity), there is
921 also mounting evidence that multi-trait metrics (e.g. functional divergence
922 and dispersion) may be useful in predicting multiple processes
923 simultaneously (i.e. multifunctionality; Mouillot *et al.*, 2011; Valencia *et al.*,
924 2015). At this stage in our understanding, it is important to use both single-
925 and multi-trait indices to examine individual and multifunctional responses or
926 effects in ecosystems, since no generalization is yet available as to which
927 indices may be superior for specific questions. However, useful prescriptions
928 for trait selection and aggregation exist (Villegger *et al.*, 2008) that can aid in
929 comparing and contrasting index performance as we move forward.

930

931 **(2) Applying community-level metrics at global scales**

932 For TBE to be predictive, relationships between response traits and
933 environmental conditions and disturbance regimes need to be globally
934 consistent. It is currently unknown whether statistical models that link
935 response traits to environmental conditions in one ecosystem can be easily

936 transferred and applied to another ecosystem on another continent. This lack
937 of generality is partly hindered by the lack of a global-scale database of
938 vegetation composition and associated environmental data. Efforts are
939 underway to develop such a database (sPlot, [http://www.idiv-biodiversity.de/
940 sdiv/workshops/workshops-2013/splot](http://www.idiv-biodiversity.de/sdiv/workshops/workshops-2013/splot)), which will link directly to a global-
941 scale trait database (Kattge, 2011). This research will be instrumental for
942 advancing our understanding of how traits vary along the full range of
943 environmental conditions throughout the planet. In the meantime, however,
944 there is a wealth of published trait-environment relationships that can be
945 synthesized through meta-analysis (Gurevitch & Hedges, 2001). Meta-
946 analysis can be used to determine the consistency of trait responses to
947 environmental conditions and disturbance regimes across multiple studies,
948 and can also be used to rank the importance of traits based on their effect
949 sizes and their consistency of response (e.g. Cornwell *et al.*, 2008; Díaz *et al.*,
950 2007*b*).

951 To predict the response of communities to environmental conditions in
952 new sites or times, it will be necessary to identify the critical predictor
953 variables for those new sites and times. The best-resolved trait-environment
954 relationships demonstrate the influence of temperature and precipitation
955 gradients on interspecific variation in trait values. A recent study found that
956 temperature is a stronger predictor of trait variation than is precipitation
957 across a variety of traits (Moles *et al.*, 2014), likely due to the direct effects
958 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.*, 2007a), 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.2b). Structural equation modelling (SEM) is a

982 useful tool to quantify the unique effects that are attributable to multiple
983 abiotic *versus* biotic components of the ecosystem (Mokany, Ash &
984 Roxburgh, 2008). SEM permits the specification of a network of relationships
985 that are characteristic of complex systems (Grace, 2006). The standardized
986 path coefficients that describe the statistical relationships among variables
987 are similar to partial regression coefficients, and the absolute values of these
988 coefficients can be ranked to compare their impact on an ecosystem
989 process. For example, nitrification potential was shown to be most strongly
990 driven by the direct effects of abiotic soil properties such as pH,
991 temperature, and nitrogen availability, and only weakly driven by the LES
992 traits in the understorey plant community (Laughlin, 2011). In other words,
993 altering the functional composition of leaf traits in this pine forest
994 understorey plant community would have less effect on internal nitrogen
995 cycling than if we altered the abiotic properties of the soil. In another
996 example, SEM was used to discover that ecosystem multifunctionality was
997 driven equally by both the average and the diversity of traits in a dryland
998 community (Valencia *et al.*, 2015). The ability of SEM to parse out the
999 influence of many factors and feedbacks is proving it to be an extremely
1000 useful tool for TBE as seen in several recent studies (Mokany *et al.*, 2008;
1001 Laughlin, 2011; Laliberté & Tylianakis, 2012; Lavorel *et al.*, 2013; Valencia *et*
1002 *al.*, 2015); multivariate tools such as these will have a critical role in realistic
1003 predictions of ecosystem dynamics moving forward.

1004 Finally, in addition to forecasting the future, TBE can also be used to
1005 back-cast previous palaeoecological transitions, a very useful approach to
1006 predicting changes in the future. For example, the end-Cretaceous mass
1007 extinction of plants resulted in a shift towards dominance of plants with
1008 lower LMA and higher vein density, which is consistent with a faster growth
1009 strategy in the cold and dark impact winter that followed the Chicxulub
1010 bolide impact (Blonder *et al.*, 2014). Changes in leaf vein density have also
1011 been observed over much longer timescales throughout the Cretaceous
1012 (Feild *et al.*, 2011), with the emergence of high vein densities in angiosperms
1013 likely corresponding to major shifts in climatic and hydrological processes *via*
1014 increased evapotranspiration rates and associated feedbacks (Boyce *et al.*,
1015 2009). Combining information about how traits have responded to previous
1016 climate changes with current trait–environment relationships will enhance
1017 our ability to predict how traits will respond to future environmental change.

1018

1019 **V. CONCLUSIONS**

1020 (1) Trait-based ecology can be a powerful approach to explain and predict
1021 highly complex systems. While our understanding of key components of TBE
1022 (e.g. response traits, effect traits, functional diversity) has developed
1023 continuously since Lavorel & Garnier (2002) introduced their trait-based
1024 conceptual framework, many challenges remain.

1025 (2) We have highlighted several exciting areas for future research. The
1026 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 2014a). For example, traits have been used to identify native species from

1050 regional species pools that can tolerate certain abiotic conditions or compete
1051 with invasive species (Funk & McDaniel, 2010; Kimball *et al.*, 2014), and
1052 traits that may be useful in re-establishing critical ecosystem services (e.g.
1053 pollination services: Lavorel *et al.*, 2011).

1054 (4) The potential for TBE to improve our understanding of basic and applied
1055 ecological processes makes the need for empirical tests of this framework a
1056 priority in ecology.

1057

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1065

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1919 **Figure legend**

1920

1921 **Fig. 1.** Functional traits can be used to understand a wide range of
1922 ecological processes occurring at organismal, community, and ecosystem
1923 scales. Examples are given here of how leaf, stem, and fine root traits
1924 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