

SPECIAL FEATURE

PLANT FUNCTIONAL EFFECTS ON ECOSYSTEM SERVICES

Single-trait functional indices outperform multi-trait indices in linking environmental gradients and ecosystem services in a complex landscape

Bradley J. Butterfield^{1*†} and Katharine N. Suding¹¹Department of Environmental Science, Policy and Management, University of California Berkeley, 137 Mulford Hall #3144, Berkeley, CA 94720, USA

Summary

1. Functional traits can be used to describe the composition of communities through indices that seek to explain the factors that drive community assembly, biotic effects on ecosystem processes or both. Appropriately representing functional composition is therefore essential for predicting the consequences of environmental context and management actions for the provisioning of multiple ecosystem services (ESs) in heterogeneous landscapes.

2. Functional indices can be constructed from single or multiple traits; however, it is not clear how they differ in information content or ability to predict biodiversity – ecosystem function relationships in complex landscapes. Here, we compare the utility of analogous single- and multi-trait indices in linking environmental variation and functional composition to ESs in a heterogeneous landscape, relating functional indices based on three plant traits [height, relative growth rate and root density (RD)] to variation in the physical environment and to two ESs (forage production and soil carbon) and their net ES level.

3. Two orthogonal gradients, elevation and soil bulk density (BD), explained significant variation in several dimensions of functional composition comprised of single traits. These traits in turn significantly predicted variation in ESs and their net values. Only one index measured with multiple traits (functional richness) varied with the physical environment, while none predicted variation in ES or net ES levels.

4. One ES, soil carbon, increased with the community-average value of RD, while the other, forage production, was related to the range and community-average value of height. In turn, average RD increased with soil BD while the average and range of height declined with elevation. Due to these environmental patterns, soil carbon and forage production did not covary strongly, leading to moderate net ES levels across the landscape.

5. *Synthesis*: Single-trait indices of functional composition best linked variation in environmental gradients with productivity and soil carbon. Because the environment–trait functioning relationships were independent of one another, the ESs were independently distributed across the landscape, providing little evidence of synergies or trade-offs. Single- and multi-trait indices contained unique information about functional composition of these communities, and both are likely to have a place in predicting variation in ESs under different scenarios.

Key-words: biodiversity, community assembly, ecosystem function, functional diversity, functional traits, gradient analysis, net ecosystem services

Introduction

Ecosystem services (ESs) connect ecological processes to the well-being of humans (Daily 1997). While it is clear that landscapes simultaneously produce multiple ESs and that these services interact in complex ways (Naidoo & Ricketts 2006; Egoch *et al.* 2008; Nelson *et al.* 2009), we often know

*Correspondence author. E-mail: Bradley.Butterfield@nau.edu

†Present address: Merriam-Powell Center for Environmental Research and Department of Biology, Northern Arizona University, 800 S. Beaver St, Peterson Hall #330, Flagstaff, AZ, 86011, USA.

little about the ecological processes that underpin these relationships (Kremen & Ostfeld 2005; Carpenter *et al.* 2009; Reiss *et al.* 2009). For instance, investigations of the spatial relationships among multiple ESs have yielded mixed results on whether hotspots of multiple ES delivery occur within a landscape (Pretty *et al.* 2006; Nelson *et al.* 2009), whether one service comes at the expense of another (Naidoo *et al.* 2008; Tallis *et al.* 2008; West *et al.* 2010), or whether they vary independently of one another (Chan & Daily 2008; Egoh *et al.* 2008). One reason for this inability to form a general framework is that many abiotic and biotic processes give rise to ESs, and it is their aggregation that underlies relationships among ESs (Bennett, Peterson & Gordon 2009).

Inclusion of functional traits, indicative of how organisms and ecological communities influence ESs through effects on underlying ecosystem processes, into biodiversity–ecosystem function research has provided important insights into the relationships among ESs (Kremen & Ostfeld 2005; Díaz *et al.* 2007; Hillebrand & Matthiessen 2009; Reiss *et al.* 2009; de Bello *et al.* 2010). Functional composition of ecological communities is often represented in one of two general ways, either as indices of individual traits or by combining information from multiple traits to generate one or several composite indices (Petchey & Gaston 2002, 2006; Villéger, Mason & Mouillot 2008). In recent years, the latter approach has received a great deal of methodological attention and is used increasingly in studies of community assembly (Flynn *et al.* 2009; Villéger, Novack-Gottshall & Mouillot 2011), as well as biodiversity–ecosystem function relationships in synthetic communities (Mouillot *et al.* 2011). However, studies that seek to link the processes that drive functional composition and its effects on ecosystem function and ESs tend to utilize functional metrics based on individual traits (Díaz *et al.* 2007; Gross *et al.* 2008; Klumpp & Soussana 2009; Lavorel *et al.* 2011; but see Bernhardt-Roemermann *et al.* 2011). There may be several reasons for these differing empirical approaches, yet a direct comparison of their relative utility in understanding the factors that regulate ESs in complex landscapes has yet to be conducted.

Single- and multi-trait indices of functional composition have generally been developed from similar theoretical and empirical foundations. Mason *et al.* (2005) identified three aspects of functional composition – richness, evenness and divergence – that are mathematically orthogonal whether based on one or multiple traits (Villéger, Mason & Mouillot 2008). Functional richness (FRic) may relate to the breadth of environmental conditions that are suitable for species within a community and therefore the potential for high levels of ES provisioning under a broader range of environmental conditions (i.e. part of the sampling effect of Tilman 1999). FRic can also be related to the strength of habitat filters (Cornwell, Schilke & Ackerly 2006) and may thus modulate the effects of environmental severity on ES provisioning. While FRic describes the volume of trait space within a community, functional evenness (FEve) describes how that space is filled. FEve is believed to represent the degree of complementarity or niche partitioning among co-occurring species (Mouillot *et al.* 2005), a hypothesized mechanism of biodiversity–ecosystem function

relationships (i.e. the niche differentiation hypothesis of Tilman 1999), and can vary with environmental context (Gerisch *et al.* 2012). Indices that mix richness and evenness, such as Rao's *Q* (Botta-Dukat 2005) and dendrogram-based indices (Petchey & Gaston 2002), have also been used extensively, exhibiting both effects on ecosystem processes (Díaz *et al.* 2007; Klumpp & Soussana 2009; Lavorel *et al.* 2011) as well as responses to environmental variation (Flynn *et al.* 2009; Mason *et al.* 2012). Functional divergence represents how abundance is distributed within trait space and can be thought of as functional 'specialization' (Mason *et al.* 2003). In some systems, species with extreme trait values can have particularly strong effects on ecosystem processes (e.g. legumes in grasslands (Spehn *et al.* 2005)). Finally, while FRic, evenness and divergence all have clear single- and multi-trait analogues, perhaps the simplest descriptor of functional composition, the community abundance-weighted value (Violle *et al.* 2007), is usually calculated for single traits. The use of community-weighted trait values is based on the simple premise that the most abundant species should have the strongest effects on ecosystem processes (Grime 1998), which has been borne out empirically (Garnier *et al.* 2004; Pontes *et al.* 2007; Gross *et al.* 2008; Fortunel *et al.* 2009), as has the utility of community-weighted traits in detecting shifts in environmental filters (Ackerly & Cornwell 2007). Both single- and multi-trait indices may represent similar aspects of functional composition in similar ways and be calculated from the same species, trait and abundance matrices, but the extent to which single- and multi-trait indices provide unique information, respond to environmental variation and predict variation in ESs is poorly understood.

Perhaps the most critical determinant of commonalities and differences among functional composition indices in practice, and how they influence ESs, is how different dimensions of functional composition respond to environmental gradients. The physical environment can strongly influence variation in ESs (Boyer, Kertész & Bruno 2009; Hiddink *et al.* 2009; Lavorel *et al.* 2011), which can be due to both shifts in functional composition along environmental gradients and direct effects of the physical environment (Díaz *et al.* 2007; Gross *et al.* 2008). Understanding indirect effects of environmental drivers on ESs through shifts in different aspects of plant functional composition may be central to predicting the net provisioning of multiple ESs (Lavorel & Garnier 2012). Synergies and trade-offs among multiple ESs may arise if components of functional composition that drive different ESs respond to correlated environmental gradients; even if traits that drive different ESs are not correlated across species, community-level indices of those traits may respond to similar environmental gradients (Ackerly & Cornwell 2007), resulting in a correlation between the provisioning of ESs. In contrast, aspects of functional composition that are driven by different environmental factors that are themselves uncorrelated with one another are likely to result in independent variation in different ESs and therefore idiosyncratic covariation among multiple ESs across a landscape. In such circumstances, condensing multiple traits into one or several composite indices may obscure divergent responses of individual traits to

different environmental gradients, potentially losing both the ability to predict the provisioning of multiple ESs and its underlying causes. At the same time, while single-trait indices may afford greater flexibility in detecting simple relationships, some patterns are only detectable with multi-trait indices (Villéger, Novack-Gottshall & Mouillot 2011).

In this study, we examine the relative utility of single- and multi-trait functional composition indices in predicting the variation and covariation of two ecosystem properties, green biomass and soil carbon, that represent proxies for marketable ESs across a heterogeneous rangeland ecosystem. As in most natural landscapes, our focal study system exhibits multiple, uncorrelated environmental gradients related to elevation, soil characteristics and topography. Thus, we hypothesize that single-trait indices will be most effective in linking environmental variation and ESs.

Materials and methods

SITE DESCRIPTION

Research was conducted at the University of California Sierra Foothills Research and Extension Center (39°15' N, 121°18' W). The climate is Mediterranean, with most of the average 700 mm of precipitation falling between October and April. Elevation ranges from 130 to 500 m, with rocky, igneous xeralf soils supporting open rangeland and *Quercus douglasii* savanna. Herbaceous vegetation is dominated by non-native annual grasses and forbs, along with less-abundant native forbs, bunchgrasses and geophytes. Light grazing has occurred for the past 50 years using adaptive management practices that match grazing intensity with annual and long-term productivity of different pastures. Research was conducted across 49 of these pastures, for which the twenty-year average animal units per month (AUMs; a measure of grazing intensity), elevation, slope, insolation, soil bulk density (BD) and sand content were measured and treated as environmental variables in subsequent analyses. Grazing data were provided by the research station, topographic variables were measured using digital elevation models in ArcGIS and soil variables were measured directly.

SOIL AND VEGETATION SAMPLING

Plant community composition, above- and below-ground biomass and soil characteristics were estimated in 49 sites. Sites were selected to represent the full range of environmental and herbaceous plant community variation at the research centre. Four 0.25 m² plots were located near the centre of each quadrant of the pasture, some of which were slightly relocated to be at least 10 m from the edge of any tree canopies (when present) in order to control for any possible feedback generated by woody plants. At peak biomass in mid-May 2010, per cent composition of each vascular plant species in each plot was visually estimated to determine community composition. Above-ground biomass was clipped in a 15 × 50 cm strip within each quadrat and dried for 72 h at 60 °C before weighing. Soil samples were taken in late March 2010 to 10 cm depth with a soil corer from each of the four plots per site and air-dried before further analysis. Bulk density was estimated at each site with a separate 10-cm core (Brady & Weil 2002).

Soil samples went through a multi-step process to estimate organic and physical properties of different fractions. Roots were removed

before and after dry sieving through a 2-mm mesh, dried for 72 h at 60 °C and weighed. Per cent rock content was estimated from the > 2 mm material. Particulate and mineral fractions (> and < 53 µm, respectively) were separated by wet-sieving soil suspensions with 5% sodium hexametaphosphate, dried and ground to a fine powder. Both fractions were analysed for organic carbon content via combustion gas chromatography with a Carlo Erba Elantech NC2100 elemental analyser (CE Elantech, Lakewood, NJ, USA). Soils were sampled before peak below-ground biomass to avoid impermeable, dry conditions, so root biomass estimates were adjusted by a constant value based on more intensive sampling conducted at the same research station (R. Ryals and W.E. Silver, unpub. data). Root biomass was measured due its potential contribution to soil carbon and regulation by functional composition.

ECOSYSTEM SERVICES

Green biomass and total soil organic carbon (SOC) were measured as proxies for the two ESs fodder and carbon sequestration. Green biomass was calculated as kg ha⁻¹ and log-transformed to achieve normality. Range-standardized values of POM and MAOM were averaged to calculate total SOC, which was also log-transformed for normality. Values of green biomass and SOC were averaged to calculate the net level of ESs within a pasture, after standardizing both ESs by their range in order to give them equal weights (Mouillot *et al.* 2011).

FUNCTIONAL TRAITS

An average of 10 plants per species was measured for above-ground traits, while root traits were measured on a minimum of four randomly selected plants of each species. Trait data were available for all dominant species, comprising over 85% of total cover (mean ± 1 SE of 86 ± 2.1% per pasture). Thus, only those species for which measured trait data were available were used in further analyses.

Functional traits were estimated from plants grown under controlled conditions in a greenhouse at the University of California, Berkeley campus. Conditions were set to simulate typical late winter/early spring conditions in northern California. Air temperature was maintained at or below 22 °C, with minimum night-time temperatures of c. 10 °C. Supplemental light cycled on automatically during any cloudy periods between 07:00 and 18:00 h. Plants were grown from regionally collected seed in plastic containers (21 cm depth, 3.8 cm diameter) filled with a 50/50 mixture of sand and top soil. Following germination, plants were top-watered daily with de-ionized water. After 2 weeks of growth, an aqueous 20-20-20 NPK plus micronutrients fertilizer was applied on alternate days to minimize mineral nutrient depletion from leaching. Plants were grown for 6 weeks following germination before being harvested, at which time all plants had fully developed leaves, and many were initiating flowering, which is typical for many annual species in this system.

We measured several leaf, root and whole-plant traits (Table 1a). Height, specific leaf area (SLA) and leaf dry matter content (LDMC) were measured following Cornelissen *et al.* (2003), with the exception that only two leaves per plant were measured and averaged for SLA and LDMC. Below-ground traits were measured after washing roots to remove all soil particles and storing in a 50% ethanol solution for preservation. Root density (RD) was calculated as the dry mass of the whole root system divided by the volume of water displaced in a graduated cylinder (g cm⁻³). Coarse root diameter (DiamC) was measured at the top of the primary tap root for forbs and legumes with clear architectural differentiation of the root system, whereas the average

Table 1. (a) Single- and (b) multi-trait functional composition indices used in this study. Formulae are provided in the indicated references.

(a) Single-trait	Abbrev.	(b) Multi-trait	Abbrev.
Range	Range	Richness	FRic§
Regularity	FRO*	Evenness	FEve§
Divergence	FDvar†	Divergence	FDiv§
Weighted-mean	CWM‡		

CWM, community-weighted mean; FRO, functional regularity; FEve, functional evenness; FRic, functional richness.

*Mouillot *et al.* (2005).

†Mason *et al.* (2003).

‡Violle *et al.* (2007).

§Villéger, Mason & Mouillot (2008).

diameter of several primary roots was used for grasses and other plants with weak root differentiation. Fine root-specific length (SRLF) was measured on roots below 0.2 mm in diameter (Roumet, Urcelay & Díaz 2006), which was an appropriate cut-off for absorptive versus conductive roots in the study species. SRL was also measured on coarse roots and was highly correlated with SRLF ($r = 0.56$); only the latter was used in further analyses. Total above- and below-ground biomass were used to calculate whole-plant traits. Root mass fraction (RMF, g g^{-1}) was calculated as root biomass divided by total plant biomass. Average seed mass was estimated for each species before planting and used to calculate relative growth rate (RGR, per t) as \ln (total biomass/species average seed mass).

COMMUNITY COMPOSITION INDICES

Several orthogonal traits were selected for measurement of functional composition, based on a principal components analysis of species mean trait values (see Table S1 in Supporting Information). Traits associated with plant stature and growth form loaded on the first principal component (PC), including height, SLA, RMF, -DiamC and SRLF. Traits related to regeneration (seed mass, height, -RGR) loaded on the second PC, while traits related to tissue composition (LDMC and RD) loaded on the third. Height was selected from the first PC, due its strong predicted relationship with green biomass, RGR from the second, given its potential importance in mediating coexistence in grasslands, and RD from the third as a potential driver of root biomass and soil carbon. All three traits were uncorrelated with one another (height – RGR: $r = -0.18$, $P = 0.41$; height – RD: $r = 0.27$, $P = 0.21$; RGR – RD: $r = 0.20$, $P = 0.35$).

Four single-trait indices – range, functional regularity (FRO), functional divergence and community-weighted mean (CWM) – were calculated for height, RGR and RD (Table 1a). All indices were calculated with standard scores of species mean trait values, for comparability with multi-trait indices (Villéger, Mason & Mouillot 2008). Range was calculated as the maximum trait value minus the minimum trait value of species within a community and was the only non-abundance-weighted single-trait index for comparability with its multi-trait counterpart, FRic. FRO was calculated following Mouillot *et al.* (2005) and has a maximum value of 1 when species are evenly spaced along the trait axis and abundance is evenly distributed, declining to a minimum of zero as more abundant species become clumped in trait space. Functional divergence (FDvar) was calculated following Mason *et al.* (2003), and also ranges between 0 and 1, with higher values occurring when abundance is higher towards either one or both margins of the trait distribution and lower values when the abundance

is concentrated towards the average value of that trait in a community. Lastly, the CWM was simply calculated as the abundance-weighted mean trait value for a community (Violle *et al.* 2007).

Multi-trait FRic, evenness and divergence were all calculated following Villéger, Mason & Mouillot (2008) (Table 1b), using height, RGR and RD as the traits. FRic is calculated as the convex hull volume in n -dimensional space, where n is the number of traits, and is analogous to the multidimensional range. FEve is calculated in a similar fashion to FRO, except the abundance-weighted nearest neighbour distances are calculated along the minimum spanning tree in n -dimensional trait space. Functional divergence (FDiv) is calculated as the abundance-weighted deviations from the centroid of the convex hull volume and is interpreted in a similar manner as FDvar. Standard scores of trait values were used in calculating all multi-trait indices so as to give each trait equal weight (Villéger, Mason & Mouillot 2008). Since no communities had fewer species than traits (3), dimensionality reduction was not required for the calculation of any multi-trait indices for any communities.

STATISTICAL ANALYSIS

The hypothesis that functional indices vary with environmental factors was tested with multiple regression, using the orthogonal variables elevation, BD and slope as predictors. These variables were selected based on a principal components analysis of the full set of environmental variables, where the first PC was associated with slope, insolation and rock content, the second with elevation and grazing and the third with BD and sand content (see Table S2). The three variables elevation, BD and slope were considered to be strong indicators of growing season length, water retention capacity and water acquisition, respectively, and were uncorrelated with one another (elevation – BD: $r = 0.07$, $P = 0.65$; elevation – slope: $r = 0.07$, $P = 0.62$; BD – slope: $r = 0.03$, $P = 0.86$). Multiple regression models were analysed for each of the three multi-trait indices and for each combination of individual traits and single-trait indices (total of 12). Model selection was based on AICc and adjusted R^2 , using all-subsets regression.

The second hypothesis that environmental factors, functional composition and ecosystem properties predict variation in ESs was tested with two series of nested multiple regression models, using either single- or multi-trait indices. The full model for green biomass and net ES levels included both functional indices and the three environmental variables (elevation, BD and slope), with FRic, FEve and FDiv as predictors for the multi-trait models, and range, FRO, FDvar and CWM of each trait for the single-trait models. Models with only functional indices and only environmental variables were also tested, for a total of five models (environment, single-trait, multi-trait, environment + single trait, environment + multi-trait). A third category of predictor variables, green and root biomass (collectively BM), was also included in the nested models for SOC since biomass production may represent an important intermediate step between either the physical environment or functional traits and the formation of soil carbon. Thus, a total of ten models (environment, single-trait, multi-trait, BM, environment + single trait, environment + multi-trait, environment + BM, environment + single trait + BM, environment + multi-trait + BM) was assessed for SOC. Model selection was based on AICc and adjusted R^2 , where models with $\Delta\text{AICc} < 2$ were considered to have similar support (McQuarrie & Tsai 1998). Results of these GLMs were then used to test the hypothesis that ESs regulated by independent aspects of functional composition and environmental factors would lead to moderate levels of net ES provisioning, while regulation by covarying functional indices and a single environmental

gradient would lead to either high (synergistic covariance) or low (trade-off) net ES levels. The tendency for net ES levels to be higher or lower than expected from a random relationship between ESs (i.e. a mean of 0.5) was tested with a two-tailed *t*-test.

Correlations among single- and multi-trait functional indices were explored to better understand their relative contributions to the preceding statistical models. All analyses were conducted in R ver. 2.14.1 (R Foundation for Statistical Computing, Vienna, Austria) including the *vegan*, *FD*, *psych*, *MASS* and *leaps* libraries.

Results

While derived from the same traits and theoretically representing similar aspects of functional composition, multi-trait indices contained a great deal of unique information from their single-trait analogues (Table 2). FRic shared the most communal variance with its single-trait counterparts, exhibiting strong positive correlations with range of RGR and RD, but not with range of height. FEve was positively correlated with FRO of RGR but not the other two traits, while FDiv was moderately positively correlated with FDvar of height and RGR, but not RD. FDiv was also moderately negatively correlated with CWM of RGR, but not height or RD. Among multi-trait indices, only FRic and FEve were significantly correlated (negatively) (Table 2). Thus, multi-trait indices did tend to represent different dimensions of functional composition. Within single-trait indices, range and CWM tended to be correlated across traits, and within each trait, range and CWM were positively

correlated, indicating an expansion of environmental filters in communities with higher average values for each trait. CWM was also strongly correlated with FDvar for each trait, exhibiting negative relationships for RGR and RD, while FDvar of height exhibited a strong, positive quadratic relationship with CWM of height (see Fig. S1).

With the exception of FRO, single-trait functional indices varied strongly with environmental gradients, while multi-trait indices were less responsive to environmental variation (Table 3). Both the range and CWM of height declined with elevation and BD, while FDvar of height declined with BD alone. For RGR, range and CWM increased while FDvar decreased with elevation. CWM and FDvar of RD decreased and increased, respectively, with BD. FRic was the only multi-trait index that varied with the environment, exhibiting a decrease with BD. No dimensions of functional composition varied with slope.

The best models for the ESs (i.e. green biomass, SOC and their net levels) all included single-trait functional indices, while no best statistically significant models included multi-trait indices (Table 4). The best model for green biomass included both environmental variables and single-trait indices (Fig. 1a), with green biomass declining with elevation but increasing with the range and CWM of height ($R^2_{\text{adj}} = 0.48$). Three models for SOC received equivalent support, including either a single-trait index or biomass variables, or both, while no environmental variables predicted variation in SOC

Table 2. Pearson correlation coefficients among FD indices. Bold numbers indicate $P < 0.05$, dagger symbol indicates a positive quadratic relationship. Values bounded by bold lines indicate correlations between conceptually analogous single- and multi-trait indices. Dashed lines delineate relationships among different categories of single-trait indices.

			Single-trait											
Multi-trait			Range			FRO			FD _{var}			CWM		
FRic	FEve	FDiv	Ht	RGR	RD	Ht	RGR	RD	Ht	RGR	RD	Ht	RGR	
Multi														
FEve	−0.31													
FDiv	−0.14	−0.07												
Range (single)														
Ht	0.06	−0.18	−0.06											
RGR	0.83	−0.23	−0.16	−0.24										
RD	0.81	−0.31	−0.12	−0.29	0.71									
FRO (single)														
Ht	−0.29	0.22	0.02	0.27	−0.25	−0.34								
RGR	−0.41	0.53	−0.10	0.11	−0.36	0.43	0.41							
RD	0.07	0.11	0.07	−0.02	0.12	−0.06	0.13	0.15						
FD _{var} (single)														
Ht	0.09	−0.21	0.45	0.09	0.09	0.18	−0.02	−0.25	−0.13					
RGR	−0.41	−0.19	0.44	0.36	−0.45	−0.42	0.04	0.02	−0.17	0.24				
RD	−0.37	0.11	−0.21	−0.11	−0.20	−0.24	0.16	0.27	0.12	−0.16	−0.13			
CWM (single)														
Ht	−0.23	−0.13	0.27	0.43	−0.44	−0.31	0.29	−0.05	−0.36	0.86†	0.42	−0.38		
RGR	0.41	0.23	−0.45	−0.36	0.47	0.40	−0.04	0.00	0.16	−0.26	−0.99	0.14	−0.45	
RD	0.43	−0.12	0.19	0.07	0.26	0.32	−0.17	−0.28	−0.08	0.15	0.05	−0.99	0.32 −0.07	

CWM, community-weighted mean; RD, root density; FRO, functional regularity; RGR, relative growth rate; FEve, functional evenness; FRic, functional richness.

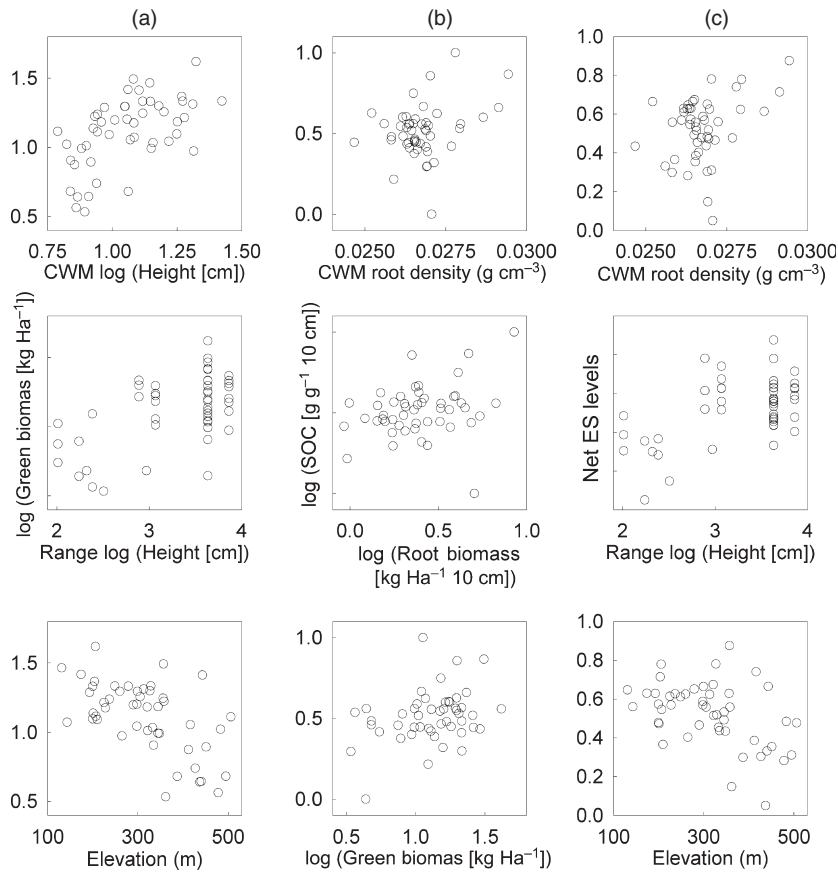


Figure 1. Relationships among ecosystem services [(a) green biomass, (b) soil organic carbon (SOC) and (c) their net level (the average of the standardized values of green biomass and SOC)] and the predictor variables retained in the best general linear models for those services.

Table 3. General linear models for multi- and single-trait functional indices. Bold numbers indicate $P < 0.05$.

Composition Index	Environmental variables				Slope
	R^2_{adj}	AICc	Elevation	BD	
Multi-trait					
FRic	0.10	54.9		(-)0.012	
FEve	—	—			
FDiv	—	—			
Single-trait					
Range					
Height	0.27	-12.0	(-) < 0.001	(-)0.054	
RGR	0.07	-1.55	0.036		
RD	—	—			
FRO					
Height	—	—			
RGR	—	—			
RD	—	—			
FDvar					
Height	0.06	-178		(-)0.046	
RGR	0.27	-389	(-) < 0.001		
RD	0.09	-993		0.020	
CWM					
Height	0.23	-9.84	(-)0.003	(-)0.023	
RGR	0.26	-12.6	< 0.001		
RD	0.10	-3.29		(-)0.014	

BD, bulk density; CWM, community-weighted mean; RD, root density; RGR, relative growth rate; FEve, functional evenness; FRic, functional richness.

(Fig. 1b). The trait-only model included a positive effect of CWM of RD, while the biomass model included positive effects of both green and root biomass. The combined trait and biomass model included only CWM of RD and green biomass ($R^2_{adj} = 0.12$). Very similar model results were found for either CWM or FDvar of RD, which were strongly negatively correlated ($r = -0.99$). Given the extra information provided by CWM in this case (i.e. directionality of the divergence; Fig. S3), only the models for CWM are presented.

The best models for net ES levels included elements of the best models for both green biomass and SOC (Fig. 1c). Two models received equivalent support for explaining variation in net ES variation, one with single-trait indices only and the other with both environment and trait effects. The traits-only model included positive effects of CWM of RD as well as the range and CWM of height. The trait plus environment model included only CWM of RD and range of height, along with a negative effect of elevation ($R^2_{adj} = 0.38$). Finally, the average level of net ES provisioning across pastures was not significantly different from that expected from a random relationship between ESs ($\mu = 0.52$; $t_{48} = 1.03$, $P = 0.31$).

Discussion

Two orthogonal environmental gradients, one related to elevation and the other to soil BD, had significant relationships with the functional composition of plant communities, resulting in

Table 4. General linear models for prediction of individual ecosystem services (ESs) and their net, combined value (the average of the standardized values of ESs). No multi-trait functional composition indices were correlated with either individual ES or net ES, nor were any measures of single-trait functional regularity (FRO), and are thus excluded from the table. FDvar was strongly correlated with CWM (see Results) and was also excluded from analyses. Bolded names indicate the models with the highest support, based on a minimum ΔAICc of 2. Numbers below predictor variables are P -values, with (–) indicating a negative relationship with the response variable. Bolded values indicate $P < 0.05$, and other values indicate $P > 0.05$ but still retained based on AICc and adjusted R^2 . Individual correlations between ESs and variables retained in their final models were all significant at $P < 0.05$; increases in P -values are due to covariances with other predictor variables. Grey bars indicate variables not considered in a given model, while grey dashes indicate no suitable model was found. Residual degrees of freedom varied from 45 (models with 3-variables retained) to 47 (single-variable retained).

Ecosystem				Environment			Single-trait range			Single-trait CWM			Biomass	
Service	Model	R^2_{adj}	AICc	Elev	BD	Slope	Height	RGR	RD	Height	RGR	RD	Green	Root
Green Biomass	Env	0.38	–155.4	(–) < 0.001 (–) 0.023										
	Traits	0.42	–158.9				0.002			0.002				
	Env + Traits	0.48	–163.4	(–) 0.015			0.032			0.01				
SOC	Env	–	–											
	Traits	0.07	–180.2									0.037		
	Biomass	0.10	–181.0										0.087	0.17
	Traits + BM	0.12	–181.8									0.11	0.070	
Net	Env	0.17	–186.1	(–) 0.002										
	Traits	0.37	–197.7				0.002			0.10		0.56		
	Env + Traits	0.38	–198.1	(–) 0.085			0.003					0.012		

BD, bulk density; CWM, community-weighted mean; RD, root density; SOC, soil organic carbon; RGR, relative growth rate.

both direct and indirect relationships with two ESs and their net levels. While several components of functional composition significantly linked the physical environment to the ESs, these were largely functional indices based on single traits: only one multi-trait index (FRic) responded to the physical environment, while none explained significant variation in individual or net ESs. This result supports our assertion that in a complex landscape with multiple environmental gradients, multi-trait functional composition indices do a poor job of linking physical environmental variation and ESs. Multi-trait indices may perform better in scenarios with simpler environmental gradients and when ESs are correlated with one another, representing either synergies or trade-offs among ESs, but are unlikely to predict net values of multiple ESs when the dimensions of functional composition related to individual ESs are themselves uncorrelated.

Despite being calculated from the same trait-by-abundance (or occurrence) matrix, single- and multi-trait indices contained mostly unique information about the functional composition of the plant communities in this study. One exception was FRic, where the range of RGR and RD were strongly positively correlated while weakly related to range of height. Consequently, the dominant axis of multi-trait richness (FRic) was associated with RGR and RD, while the trait whose range was most strongly related to environmental variation and ecosystem functioning (height) was poorly reflected in FRic. The influence of RGR and RD on FRic reflects a problem with selecting orthogonal traits from the species-by-trait matrix (Villéger, Mason & Mouillot 2008) or component axes following an orthogonal ordination (Mouillot *et al.* 2011), rather than the community-by-trait or community-by-index matrix. Bernhardt-Roemermann *et al.* (2011) provide a possible way of dealing with selection of indices through ‘RLQ’

analyses of trait–environment linkages, using both single- and multi-trait indices. Briefly, this approach finds the optimal fit between measures of functional composition and environmental variables from a set of functional indices comprised different combinations of traits. Pakeman (2011) also used RLQ to find the most parsimonious set of CWMs that linked traits to the environment, and then conducted the same procedure to link traits to ESs, finding that the same set of traits more or less linked the environment to ESs. Using the latter approach with both single- and multi-trait indices may allow us to begin to draw general relationships between environmental variation, functional traits and combinations of traits and the provisioning of ESs.

Another possible limitation of multi-trait indices is the ability to interpret contributions of individual traits to variation in a composite, multi-trait index. The relative independence of CWMs and FDiv observed in this study provides an instructive example. CWM and FDvar (single-trait divergence) were linearly correlated with two traits (RGR and RD) due to the low variation in FDvar for those traits: nearly all communities had high values of FDvar. In contrast, CWM and FDvar of height exhibited a positive, quadratic relationship, indicating substantial variation in divergence values that were associated with communities with either high or low average height. The mix of linear and quadratic relationships incorporated into calculations of multi-trait divergence (FDiv) likely contributed to the relative independence of CWMs and FDiv and also makes it difficult to interpret variation in FDiv. Mouillot *et al.* (2011) provide an interesting contrast with the present study, in which FDiv was at least as good of a predictor of net ecosystem function levels as the best component of CWMs. The study of Mouillot *et al.* was conducted in synthetic, rather than naturally occurring communi-

ties. Furthermore, in a study of community assembly through a fossil record, Villéger, Novack-Gottshall & Moullot (2011) demonstrate that only through the use of multi-trait convex hulls (FRic) could shifts in the severity of environmental filters be detected. Clearly, multi-trait indices have a place in many ecological toolboxes, and simulations of trait matrices and community abundance distributions with different covariance structures along with empirical studies in systems varying in environmental complexity and community assembly patterns may improve our ability to link biotic responses to environmental variation and ESs, the so-called holy grail of functional community ecology (Lavorel & Garnier 2002).

Environmental and floristic context appear to play an important role in linking environmental and functional variation with ESs and their net levels, even with such apparently simple ESs as green biomass production and SOC storage. For example, Lavorel *et al.* (2011) found that across a mountainous landscape green biomass was regulated by water-holding capacity along with CWMs of height and leaf N content, while soil C was regulated by CWMs of leaf dry matter and P content (root traits were not measured). In experimental mesocosms, Klumpp & Soussana (2009) found that the diversity of SLA, measured as Rao's Q , along with clipping frequency was positively correlated with ANPP, while RD alone (as in the present study) was positively correlated with SOC, resulting in independent regulation of these ESs as well. In contrast, Laliberté & Tylianakis (2012) found that CWM of SLA had a positive effect on both ANPP and soil C, resulting in high positive covariation of ESs under conditions of high soil fertility, which directly influenced ESs as well as enhanced SLA. Along with the present study, these case studies demonstrate a wide variety of environmental and functional composition effects on variants of green biomass and SOC and that their covariation can be both moderate and synergistic. These and other studies also demonstrate that the strength of linkages between functional composition indices and ESs can be highly variable. Model fits in the present study were not particularly high, which may be attributed to the lack of information on intraspecific trait variation (Albert *et al.* 2012), as well as the relatively low functional variation in the local flora. In addition to driving functional variation associated with species turnover, environmental variation can modulate trait–ES relationships (Pakeman 2011), drive intraspecific plasticity or genetic variation in traits (Jung *et al.* 2010) and interact with other environmental variables (Laliberté & Tylianakis 2012) to determine trait–ES relationships. Even for seemingly simple and interrelated ESs such as biomass production and SOC, further investigation is necessary to understand the myriad links between the environment, functional composition and ESs.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 Principal component analysis of species mean traits.

Table S2 Principal component analysis of environmental variables.

Figure S1 Relationships between CWM and FDvar.