



Plant traits – a tool for restoration?

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Introduction

Restoration of native habitats is a crucial strategy for biological conservation. Progress in the successful restoration of native habitats is slowed, however, by our limited ability to generalize and predict species responses to restoration management treatments. The scientific literature contains numerous studies describing the effects of restoration

Abstract

Question: Most results of restoration efforts are species-specific and/or site-specific and therefore are not general enough to be easily applied to other species and other sites. Our research addresses the issue of species-specific results by investigating the feasibility of using plant traits instead of taxonomic identity to characterize species responses to restoration treatments.

Location: Ten bunchgrass prairie sites in the Pacific Northwest of North America (Oregon and Washington, USA; British Columbia, Canada).

Methods: We developed two types of quantitative models for each of ten prairie restoration sites: (1) plant trait models, which related plant traits to species field responses following restoration management treatments; and (2) species identity models, which related species taxonomic identity to species field responses following restoration management treatments. Species identity models determined the maximum amount of variability of field responses that can be explained by differences in individual species' responses to management treatments. Plant trait models determined what proportion of this explanatory power can be attributed to plant traits. The two model types addressed the following specific questions: (1) how much of the variability in field responses (changes in cover) of plants to restoration management treatments is explained by plant traits; and (2) how well do plant traits explain the variability of field responses (changes in cover) following restoration management treatments compared to models relating field responses to species identity?

Results: (1) The plant trait models explained much of the variability within each of the ten restoration sites, with R^2 values ranging between 31% and 69%. (2) The species identity models explained between 47% and 74% of variability of change in cover (R^2). Thus, the plant trait models explained nearly as much variability as the species identity models. In seven out of nine sites, the plant trait models were superior to the species identity models, as measured by AIC, i.e. the trait models did well at explaining variability with less model complexity.

Conclusion: Strong explanatory power of plant trait models supports the feasibility of using plant traits instead of species taxonomic identity as a common language to characterize plant field responses (changes in cover) to restoration treatments.

management treatments on vegetation, but the studies are often species-specific and site-specific. General patterns, which are necessary to develop predictions of the effects of management, are therefore difficult to identify.

One promising approach to address the issue of species-specific results is using plant traits as a common language to characterize plant responses rather than using taxonomic identity (McIntyre et al. 1999; Lavorel & Garnier

2002; Kahmen & Poschold 2004). Functional plant traits are well-defined characteristics (McGill et al. 2006) that relate to plant species' patterns of establishment, growth and resource allocation, and that evolved in response to abiotic environmental conditions and interactions with other species (Reich et al. 2003). Thus, functional plant traits are those that strongly influence a plant's performance (McGill et al. 2006).

Traits are universal (i.e. all plants have traits), whereas plant species differ according to geographic location. As a result, focusing on species taxonomic identity hinders our ability to make ecological generalizations beyond sites with similar species composition. For example, restoration studies generally describe the responses of particular species to management treatments. It is difficult to generalize or compare these results to other results with different species. Overcoming this limitation requires simplification of species taxonomic identities to a more general measure, such as plant traits (Diaz et al. 1998, 2001; Pakeman 2004; de Bello et al. 2005; Bernhardt-Römermann et al. 2011).

Relatively few studies have investigated the use of plant traits for predicting the effects of management and restoration of native habitats (Goodridge 2002; Gondard et al. 2003; Pywell et al. 2003; Roberts et al. 2010; Sandel et al. 2011). A plant trait approach would allow us to develop models that show relationships between plant traits and plant species responses to restoration treatments, thus allowing the results of vegetation responses to management treatments to be reported or modelled as plant traits rather than by species names. Moreover, these trait-response relationships could also provide insight into the actual causes of vegetation change to restoration treatments.

Research goal and objectives

Our research addressed the issue of species-specific results by investigating the feasibility of using plant traits as a common language, instead of taxonomic species, to evaluate species responses, thus allowing results to be applied more generally. Our approach was to develop two types of quantitative models for each of ten bunchgrass prairie restoration sites: (1) plant trait models, which related plant traits to species field responses following restoration management treatments; and (2) species identity models, which related species taxonomic identity to species field responses following restoration management treatments. Plant trait models were designed to determine the amount of variability of the change in abundance that is explained by plant traits. Species identity models were designed to determine the *maximum* amount of variability in the change in abundance that is explained due to differences in species.

Species identity models would be expected to fit observed data well, but could not be used to compare results between sites that do not share similar species. Plant trait models could potentially be used to compare results between sites that do not share similar species. If the plant trait models and the species identity models have similar explanatory power and the plant trait model is more parsimonious (i.e. fewer explanatory variables), then plant trait models would be preferred, i.e. an entire species list can be reduced to a subset of key functional plant traits.

Specifically, we used the two model types to answer the following questions: (1) how much of the variability of field responses of plants following treatments is explained by plant traits, and (2) how well do plant traits explain the variability of field responses of plants following treatments compared to models relating field responses to species identity? We defined field responses as the change in abundance before and after treatments.

Methods

Study sites, restoration treatments and measurement of plant field responses

In 2005, we began a 5-yr study to develop and evaluate strategies for restoring bunchgrass prairies invaded by non-native weeds (Stanley et al. 2008, 2011). Identical experimental blocks were established within prairie habitats at ten sites in the Pacific Northwest, extending from central Oregon to southern British Columbia. The management treatments, which were developed collaboratively by scientists and land managers from The Nature Conservancy, Institute for Applied Ecology and several partner organizations, included combinations of application of sethoxydim, a grass-specific herbicide (2% solution with surfactant) to reduce dominant exotic grasses; spring or autumn mowing to reduce thatch, weed seed production and stored reserves of exotic grasses; prescribed burning, to reduce thatch and moss and prepare seedbeds for germination; and post-burn application of glyphosate, a broad-spectrum herbicide (1.5% solution, 2–4 wk post-burn) to reduce broad-leaved non-native weeds that typically resprout quickly after fire compared to native species. These treatments were applied in various combinations over 4 yr, along with a no-treatment control, to 5 m × 5 m plots, which were replicated four times at each site. The treatment combinations for the first 2 yr were *Treatment A*: spring 2005 and 2006 application of sethoxydim, autumn 2006 prescribed burn followed by application of glyphosate; *Treatment B*: spring 2005 mow, autumn 2006 prescribed burn followed by application of glyphosate; *Treatment C*: spring 2005 and 2006 mow, autumn 2005 and 2006 mow; *Treatment D*: spring 2005 and 2006 application of sethoxydim, autumn 2005 and 2006 mow.

To determine plant responses to the management treatments, cover of each plant species was measured in spring 2005 (before any restoration treatments) in four 1 m × 1 m sampling quadrats in each of the 5 m × 5 m plots. Cover measurements were repeated in spring of 2007 after 2 yr of annual management treatments. Cover was assessed visually, using calibrated templates, to the nearest 1% in each sampling quadrat.

Plant trait measurements and database

Plant traits were measured on target species in the vegetation plots from the restoration project sites described above. Criteria for final inclusion as a target species for plant trait measurements included abundance at project sites, seed availability and whether the species could be grown from seed in the growth chamber. Of the 142 species encountered in the plots at the ten research sites, the 42 species included in the analysis accounted for an average of about two-thirds of the total cover.

Using plant traits lists in Weiher et al. (1999) and Cornelissen et al. (2003) as guidelines, we selected 27 plant traits that in our judgment best reflected the mechanisms of the changes in plant cover to our restoration treatments (Table 1). Plant trait data came from several sources. We made the following plant measurements under controlled conditions (growth chamber) using the protocols of the Integrated Screening Programme (Hendry & Grime 1993), which consist of a range of standardized laboratory-based procedures: specific leaf area, leaf area ratio, leaf mass ratio, above-ground biomass, below-ground biomass, relative growth rate and unit leaf rate (Table 1). In addition to these growth chamber measurements, average seed mass for each species was calculated from measurements made on ten replicates per species (each replicate consisted of ten seeds). For the other plant traits and attributes, we used values readily available in the published literature, including local floras, reference books and databases. Missing data were infrequent, about 2% of the data. These plant trait data were included in our database, The Willamette Valley Prairie Plant Trait Database, which includes species from the entire Pacific Northwest region (Wilson 2006).

For a trait to be useful in explaining plant performance, the trait must vary widely between different species. Among the quantitative traits, phenological traits tended to have some of the lowest variation [coefficients of variation (CV) of 0.12–0.50]. Traits of size under standardized growing conditions tended to show some of the highest variation: above-ground biomass (CV = 1.2), root biomass (CV = 1.1) and leaf area (CV = 2.9). Growth rates and ratios, such as relative growth rate and specific leaf area, tended to have intermediate levels of variation. A measure of the useful variation within categorical traits is Hill's

index ($I_1 = e^{H'}$), where e is the base of natural logarithm and H' is the Shannon-Weiner diversity index (Hill 1973). Variation among species was high within many categorical traits, such as growth form ($I_1 = 3.6$), clonality ($I_1 = 4.3$) and dormancy breaking mechanism ($I_1 = 4.8$). Overall, for both quantitative and categorical traits, the study species showed more than ample variation in traits.

Methods of analysis

Variable selection, variable reduction

Several of the plant trait variables contained overlapping information. The inclusion of such redundant (collinear) variables causes statistical problems, such as inflated standard errors, reduced power and arbitrary model structure (Harrell 2001). To avoid such problems, we performed a hierarchical cluster analysis (*varclus* procedure of S-Plus; Harrell 2001) based on the nonparametric similarity of the trait variables. Similarity was measured as Spearman's rank correlation (r_s). Clusters were defined as having a joint correlation of $r_s > 0.6$. Hierarchical cluster analysis identified six clusters of variables and ten individual variables, each showing no strong correlation with all other traits. A single trait was chosen to represent each cluster based on two criteria: the trait had to (1) have data for all species in the database, and (2) have previously demonstrated usefulness in the literature. In addition, flowering peak month was augmented with its square to allow for non-linear effects in this phenological variable. Thus, the final list of variables for statistical analysis consisted of 17 plant trait variables (Table 2). Note that the response variable (change in plant cover) played no role in variable selection.

Transformations

Analysis of Box-Cox transformations (Venables & Ripley 1999; Kutner et al. 2005) showed that the square-root transformation was the best transformation at fitting the assumptions of the statistical models. Therefore we used as our measure of field performance

$$(\text{Cover in 2007})^{1/2} - (\text{Cover in 2005})^{1/2}$$

We calculated this measure individually for every species within each quadrat. Only one explanatory variable (seed mass) was transformed to meet standard statistical assumptions. Residuals were acceptably homoscedastic and approximately normally distributed in all cases.

Statistical analyses

We tested the power of a series of linear models to explain field performance (change in plant cover) of

Table 1. Description of plant traits and attributes used in the final analysis.

Trait	Data type	Choices for categorical data	Notes for quantitative data
Clonality	C	Clonal above-ground, clonal below-ground short, clonal other, clonal bulbs or corms, clonal rhizomes, clonal above-ground short, clonal below-ground long, clonal abovegr. long, clonal tubers, non-clonal, unknown	
Diaspore feature	C	Mucilage, minute, pappus or hair, balloon, wing, elaiosome, hook or barb, fleshy, fruit, none, awn	
Dispersal peak month	Q		Month (Jan = 1) that has the most dispersal
Dormancy breaking mechanism	C	Not fire, light, after-ripening, fire, not dormant, not stratification, stratification, not light, scarification, not scarification, not after-ripening	
Flowering peak month	Q		Month (Jan = 1) that has the most flowering
Germination peak month	Q		Month (Jan = 1) that has the most germination
Germination rate	Q		Percentage
Growth form (C)	C	Climber or scrambler, cushion, erect leafy, long basal, other, palmoid, prostrate, semi-basal, short basal, short succulent, tall succulent, tussock (Cornelissen et al. 1996)	
Growth form (standard)	C	Dicot forb, fern, graminoid, monocot forb, shrub, suffrutescent, tree, vine	
Habitat	C	Riparian, upland prairie, wetland prairie, wetland, woodland	
Maximum height	Q		Meter
Leaf area of 21-d seedling	Q		L_A [measured under standardized conditions (Hendry & Grime 1993)]
Leaf area ratio	Q		L_A/T_M [measured under standardized conditions (Hendry & Grime 1993)]
Leaf mass ratio	Q		L_M/T_M [measured under standardized conditions (Hendry & Grime 1993)]
Leaf shape	C	Linear, lanceolate, cuneate, orbicular, ovate, oblong obovate, oblanceolate	
Life form	C	Phanerophyte, chamaephyte, hemicryptophyte, geophyte, therophyte	
Shoot mass of 21-d seedling	Q		S_M [measured under standardized conditions (Hendry & Grime 1993)]
Root + shoot mass of 21-d-old seedling	Q		$R_M + S_M$ [measured under standardized conditions (Hendry & Grime 1993)]
Perenniality	C	Annual, annual/biennial, biennial, facultative perennial, perennial	
Reproductive schedule	C	Monocarpy, polycarpy	
Relative growth rate	Q		$(\log_e T_{M2} - \log_e T_{M1}) / (t_2 - t_1)$ [measured under standardized conditions (Hendry & Grime 1993)]
Root system	C	Fibrous, tap	
Seed mass	Q		Grams
Specific leaf area	Q		L_A/L_M [measured under standardized conditions (Hendry & Grime 1993)]
Stem arrangement	C	Single upright, multiple upright, creeping	
Unit leaf rate	Q		$(T_{M2} - T_{M1}/t_2 - t_1) \times (\log_e L_{A2} - \log_e L_{A1}/L_{A2} - L_{A1})$ [measured under standardized conditions (Hendry & Grime 1993)]
Where native	C	Willamette Valley other North America, South America, Europe, Asia, Eurasia, Africa, cosmopolitan	

A = area; M = dry mass; L = leaf; R = root; S = shoot (leaf + stem); T = total plant; subscripts 1 and 2 indicate initial time (7 d) and time two (21 d) of measurement, respectively. Data type: C = categorical, Q = quantitative.

Table 2. Results of hierarchical cluster analysis, which was conducted to identify clusters of closely related trait variables, and to select the trait variable that best represents the underlying biological trait associated with the cluster. Each of the six clusters was represented by a single trait variable; in addition, flowering peak month was supplemented with its two-degree polynomial. The final list of variables for statistical analysis consists of 17 plant trait variables (See Table 1 for complete description of the traits).

Cluster name	Representative variable	Other variables in cluster
Size	Root + shoot mass of 21-d-old seedling	Shoot mass of 21-d seedling, leaf area of 21-d seedling
RGR	Relative growth rate	Leaf mass ratio
SLA	Specific leaf area	Leaf area ratio
Phenology	Flowering peak month, flowering peak month ²	Dispersal peak month, germination peak month
Growth form	Growth form (C)	Diaspore feature, growth form (standard), root system
Perenniality	Perenniality	Reproductive schedule (i.e. monocarpy or polycarpy), life form
Height	Maximum height	
Germination	Germination rate	
Seed mass	Seed mass	
Dormancy	Dormancy breaking mechanism	
ULR	Unit leaf rate	
Habitat	Habitat	
Stems	Stem arrangement	
Clonality	Clonality	
Nativity	Where native	
Leaf shape	Leaf shape	

species identity and plant traits. Our models testing the explanatory power of species identity were in the form of analyses of variance:

$$(\text{Cover in } 2007_i)^{1/2} - (\text{Cover in } 2005_i)^{1/2} = b_0 + b_1 \text{ Identity}_i + b_2 \text{ Treatment} + b_3 \text{ Identity}_i \times \text{Treatment},$$

where i refers to each species. Thus, the identity and response of each species in each quadrat within a site constituted a data point in the analysis data set. Our models testing the power of plant traits followed a similar approach but required a step-wise approach. For each site analysis, all 17 plant trait variables and their interaction with the treatment variable were examined, using the forward step-wise procedure in S-Plus, which includes variables based on their ability to decrease the AIC value. AIC measures the fit of a model, penalized by model complexity. AIC value could not be calculated for one of the sites (Scatter Creek) because of an unbalanced analysis matrix. Incomplete distribution of categories of traits across the ten sites prevented a single analysis using site as a categorical variable. We analysed instead each site individually.

Results

Variation explained by plant traits

The plant trait models (relating plant traits with change in cover) for each of the ten restoration sites explained a relatively large amount of variability, with R^2 values ranging between 31% and 69% (Table 3). The proportion of variability explained by only the treatments for the models is very small (Table 3); in contrast, traits contributed three-quarters to nearly all the variability explained by these models. Therefore, the trait models captured most of the changes in the plant cover.

Variation explained by plant traits vs species identity

We measured two aspects of explanatory power: R^2 and AIC. Because the species identity models let each taxonomic species vary independently, for this experimental design they explain the maximum amount of variability due to differences in species responses to the management treatments. The R^2 values of these species identity models were high, ranging between 47% and 74% (Table 3). Yet,

Table 3. Comparison of species identity models and plant trait models for each of ten remnant native bunchgrass prairie sites in the Pacific Northwest. Species identity models relate species taxonomic identity to species cover change following restoration management treatments. Plant trait models relate plant traits to species cover change following restoration management treatments. Treatment R^2 is the proportion of variability in cover change explained by treatments for each site's species identity model and for each site's plant traits model. R^2 is the overall proportion of variability explained by the model. The difference between treatment R^2 and overall R^2 is the amount of variability in cover change explained by species in the species identity models and explained by traits in the plant trait model. AIC is a statistical test that balances explanatory power and model complexity. Smaller values of AIC indicate greater explanatory power after accounting for parsimony (i.e. number of explanatory variables).

Site	Treatment R^2	Species identity models		Plant traits models	
		R^2	AIC	R^2	AIC
Bellfountain	0.02	0.51	1495.1	0.34	1494.5
Cowichan	0.03	0.74	744.0	0.69	734.3
Glacial	0.03	0.72	775.2	0.64	768.1
Hoskins	0.02	0.51	1092.6	0.41	1104.2
Mima	0.09	0.48	975.4	0.37	954.3
Morgan	0.07	0.49	585.0	0.38	565.0
Pigeon	0.05	0.52	1337.3	0.37	1285.1
Scatter	0.02	0.55	1001.9	0.45	*
Triangle	0.05	0.51	1122.8	0.31	1124.0
Weir	0.04	0.47	669.1	0.39	631.1

Bold type highlights the AIC of the superior model (i.e. the model with greater explanatory power and parsimony).

*AIC value could not be calculated for the Scatter site because of an unbalanced analysis matrix.

the plant trait models explained nearly as much variability as a *proportion* (between 0.60 and 0.93) of the amount of variation explained by the species identity models. Using AIC, a value that balances explanatory power and model complexity, the plant trait models were superior to the species identity models in seven out of nine sites (Table 3). A total of 17 different plant traits were included among the ten site models (Table 4), with seven traits showing significant interactions with the restoration treatments (Table 5).

Discussion

Our results demonstrate that plant traits explain variation in species responses under different management treatments almost as well as taxonomic identity, allowing the results of restoration experiments to be reported or modelled as plant traits rather than by species names, with the potential for more successful generalization. The relatively high R^2 values demonstrate that the traits selected for the models were highly relevant to field performance (change in plant cover). Plant trait studies frequently focus on the role of single traits; however, it is unrealistic to expect that a single trait would reflect a complex field response to restoration management treatments. Multiple trait analyses, such as done in this study, are likely to have greater explanatory power and generality (Kuster et al. 2008; Roberts et al. 2010).

Even though these plant trait models showed relatively high explanatory power, they are correlative models, and thus no causation between plant traits and field responses can be inferred. However, these models provide a clear description of the relationship between plant traits and the changes in plant cover, which can provide a starting point for testing hypotheses about mechanisms. Different traits were included in each of the ten site models, resulting in a total of 17 different plant traits (Table 4). As a result, any given trait variable was used in one to six of the site models, and site models included between two and six trait variables (Table 4).

Comparisons of plant traits found in plant trait models among sites need to be undertaken with care. The absence of a particular trait in a model is not necessarily due to its lack of biological importance, but from statistical procedures that reward parsimony. Thus, the presence of a trait in multiple models indicates the general importance of that trait, but absence of a trait does not necessarily indicate lack of a relationship. The most common trait, found in all ten models, was *clonality* (six of ten sites) (Table 4). Clonality is related to both vegetative regeneration and persistence after disturbances, particularly fire and mowing, treatments used in this study that directly affect cover. The next most common traits (in four of ten site models) were *dormancy breaking mechanism*, *seed germination rate* and *seed mass*, all

associated with seed regeneration, which directly affects cover of annuals in particular. All of these traits common to multiple sites are most likely to be associated with the direct cause of the changes in cover (Weiher et al. 1999).

From a restoration perspective, significant treatment–trait interactions are a priority concern, as land managers are interested in knowing which treatments are related to enhanced or decreased abundance of species with particular traits. Seven of the 17 traits included in the models showed significant interaction with the restoration treatments (Table 5). *Clonality* was the most common, interacting with treatments in four out of six sites. Among these four sites, patterns of relationships between attributes of *clonality* and restoration treatments were inconsistent, except for the attributes *non-clonal* and *other*. At all four sites, *non-clonal* plants were consistently promoted more by treatments A and B compared with the other treatments. Both treatments A and B included autumn prescribed burning, which can promote species regenerating from seed through seedbed preparation.

For the *dormancy-breaking* trait, patterns of relationships between attributes and change in cover were also inconsistent, with two exceptions. Species with the attribute *fire requirement* tended to be promoted by all treatments (even those that included no prescribed fire) with the exception of treatment D (spring application of grass-specific herbicide and autumn mowing) at Bellfountain. Species with the *light requirement* also tended to be promoted by all treatments, with the exception of treatment A (spring application of grass-specific herbicide and autumn prescribed burn followed by the herbicide glyphosate) at Bellfountain. The increase in cover in the control treatment for species with a light requirement is unexpected, given the relative lack of vegetation removal as applied in the other restoration treatments.

Somewhat clearer patterns emerged with the quantitative variables. As the trait *mass of 21-d-old seedlings* increased, cover increased with all treatments (Table 5). This pattern is consistent with the hypothesis that bigger seedlings are better able to survive unfavourable growing conditions. The trait *seed mass* also showed a positive relationship with cover following all treatments, with the exception of treatment D (Table 5). This pattern is also consistent with the hypothesis that species with larger seeds establish larger seedlings better able to survive unfavourable growing conditions. The negative relationship with treatment D is surprising given that the other three restoration treatments included either the grass-specific herbicide application or mowing.

In contrast to *seed mass* and *seedling mass* traits, *seed germination* showed a negative relationship with all treatments (Table 5). This pattern does not match considerable research showing that species with higher germination

Table 4. Plant traits included in the final models that relate plant traits to changes in plant cover following restoration management treatments for each of ten remnant native bunchgrass prairie sites in the Pacific Northwest. The variable 'treatment' is forced into the model at all sites, i.e. the variable 'treatment' is required to be in the model. 'Main' indicates that the trait was an explanatory variable in the model. 'Interaction' indicates treatment-trait interaction.

Site	Clonality	Dormancy breaking mechanism	Growth form	Habitat	Leaf shape	Perenniality	Stem arrangement	Where native	Flowering peak month
Belfountain		Main and interaction							
Cowichan	Main							Main and interaction	
Glacial	Main and interaction		Main	Main		Main			
Hoskins		Main and interaction			Main				
Mima	Main and interaction								
Morgan	Main and interaction					Main	Main		
Pigeon		Main and interaction	Main						
Scatter	Main	Main and interaction				Main			Main
Triangle		Main							
Weir	Main and interaction	Main	Main						
Number (of sites)	6	4	3	1	1	3	1	1	1
Site	(Flowering peak month) ²	Germination rate	Maximum height	Seed mass*	Relative growth rate	Specific leaf area	Unit leaf ratio	Shoot + root mass of 21-d seedling	Number (of 17 traits)
Belfountain		Main		Main and interaction	Main				4
Cowichan		Main							3
Glacial				Main		Main			5
Hoskins		Main		Main					4
Mima									3
Morgan			Main				Main		2
Pigeon				Main				Main and interaction	5
Scatter		Main and interaction							3
Triangle	Main				Main and interaction			Main	6
Weir									2
Number (of sites)	1	4	1	4	2	1	1	2	2

*The variable seed mass received a square-root transformation.

Table 5. Trait–treatment interaction coefficients. Coefficients indicate the expected mean change in cover $[(\text{Cover in 2007})^{1/2} - (\text{Cover in 2005})^{1/2}]$ for each combination of treatment and trait (for quantitative traits) or treatment and attribute (for categorical traits).

Site	Trait	Attribute	Treatments						
			A	B	C	D	R		
Bellfountain	(sqrt) seed mass		0.19	0.77	0.57	−0.37	0.51		
Pigeon	Seedling mass		0.70	0.74	0.75	0.76	0.78		
Scatter	Seed germination		−1.00	−0.99	−0.97	−1.01	−0.99		
Triangle	Relative growth rate		−4.18	−7.26	0.32	−0.28	0.46		
Glacial	Clonality	Above-ground	1.10	1.47	0.92	0.49	0.84		
		Bulbs or corms	1.61	1.60	0.49	0.76	0.36		
		Other	−0.51	−0.48	1.65	1.84	2.32		
		Rhizomes	1.49	1.02	0.71	1.03	0.57		
		Non-clonal	1.13	1.20	1.04	0.71	0.73		
Mima		Above-ground	0.01	−0.31	0.44	−0.51	−0.07		
		Bulbs or corms	0.15	0.28	0.12	−0.25	−0.75		
		Other	−1.42	−0.83	1.41	0.28	0.12		
		Rhizomes	−0.04	−0.30	0.11	−0.56	0.35		
		Non-clonal	0.86	0.72	−2.53	0.60	NA		
Morgan		Above-ground	−0.14	0.51	0.24	−0.32	0.21		
		Bulbs or corms	0.37	0.32	0.11	0.04	−0.34		
		Other	−0.39	−1.05	0.31	0.80	0.82		
		Rhizomes	0.16	0.21	0.22	−0.01	−0.08		
		Non-clonal	0.50	0.50	−0.39	0.00	−0.12		
Weir		Above-ground	0.20	0.41	−0.48	−0.72	0.31		
		Bulbs or corms	−0.39	0.61	0.09	−0.43	−0.15		
		Other	−0.59	−1.14	0.79	1.11	−0.45		
		Rhizomes	0.27	−0.31	−0.55	0.02	0.30		
		Non-clonal	0.24	0.15	−0.12	−0.26	−0.29		
Bellfountain	Dormancy-breaking mechanism	Fire	1.42	0.48	0.19	−0.57	0.15		
		Light	−3.92	1.43	1.29	1.03	1.84		
		Not after-ripening	NA	NA	NA	NA	NA		
		Not dormant	0.34	−0.22	0.31	1.01	0.22		
		Not stratification	1.31	−0.07	0.16	0.20	0.06		
		Scarification	1.29	0.46	0.15	−0.07	−0.17		
		Stratification	1.55	−0.08	−0.10	0.39	−0.10		
		Hoskins		Fire	2.52	2.21	2.06	2.66	2.05
				Light	2.67	2.96	2.19	1.52	2.16
Not after-ripening	NA			NA	NA	NA	NA		
Not dormant	2.30			2.40	2.28	1.27	3.25		
Not stratification	2.10			2.33	2.47	2.79	1.81		
Scatter		Scarification	2.40	3.06	2.08	2.22	1.74		
		Stratification	1.81	0.84	2.72	3.34	2.80		
		Fire	NA	NA	NA	NA	NA		
		Light	NA	NA	NA	NA	NA		
		Not after-ripening	−1.28	−0.89	−1.45	−0.31	−1.02		
		Not dormant	−1.73	−1.29	−0.20	−1.95	0.20		
		Not stratification	−0.90	−0.43	−1.33	−0.82	−1.47		
Cowichan	Where native	Scarification	−0.18	−1.54	−1.36	−0.66	−1.22		
		Stratification	−0.87	−0.81	−0.63	−1.21	−1.45		
		Eurasia	NA	NA	NA	NA	NA		
		Europe	−6.93	−7.07	−9.07	−7.07	−9.11		
		Cosmopolitan	−8.68	−9.00	−5.90	−7.81	NA		
		Willamette Valley	−7.94	−7.47	−8.58	−8.67	−6.59		

Treatment A: spring 2005 and 2006 application of sethoxydim (herbicide that targets Poaceae), autumn 2006 prescribed burn followed by application of glyphosate (broad spectrum herbicide); *Treatment B:* spring 2005 mow, autumn 2006 prescribed burn followed by application of glyphosate; *Treatment C:* spring 2005 and 2006 mow, autumn 2005 and 2006 mow; *Treatment D:* spring 2005 and 2006 application of sethoxydim, autumn 2005 and 2006 mow; *Treatment R:* no treatment control. NA: insufficient data to estimate that coefficient.

rates produce more cover, thus suggesting that the actual mechanism for the decrease in cover is not due directly to seed germination. *Relative growth rate* showed a positive relationship with cover with no management treatment (R) and with the mowing only treatment C, suggesting that species with higher growth rates may be more sensitive to fire and herbicides.

Although statistical constraints prevented a direct test of the consistency of trait models across sites, our results show that the models differed at each site, even though all sites were upland bunchgrass prairies. These inconsistencies among sites illustrate the complexity of ecological relationships. Statements such as restoration treatment 'X' will promote growth of species with attribute 'A' and inhibit growth of species with attribute 'B' are too simplistic and do not take into account the complexity of environmental factors that influence the outcome of a restoration treatment (Richardson et al. 2012). One approach to address this issue is to incorporate 'core environmental traits' (e.g. climatic data, soil carbon and nitrogen concentrations; Garnier et al. 2007) into the model, thus potentially allowing application of the plant trait model to more than one site. Moreover, much of the remaining unexplained variability is likely caused by within-site variation in abiotic conditions and biotic interactions. Thus, incorporating environmental factors explicitly within a plant trait model could significantly increase its explanatory power.

Conclusion

Development of general and predictive plant trait models is a multi-step process. Using plant traits allows application of results to species not included in the study. Our results demonstrate that plant traits are strongly related to vegetation responses following management treatments, explaining the variability almost as well as do species taxonomic identities. As a result, vegetation responses can be reported or modelled using plant traits rather than species names. Thus, even with the limitation of models that are inconsistent among sites, we have made a first step in the development of general and predictive trait-based models.

Site-to-site variation in plant traits included in the models suggests that differences in initial environmental factors affected the vegetation response to management treatments. Thus, more general models to predict vegetation responses to restoration treatments will need to incorporate environmental factors, allowing application of the plant trait model to changing environmental conditions. If such models have high explanatory value, then the power to predict vegetation responses at new sites or with different species composition can be tested (Webb et al. 2010).

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References

- de Bello, F., Leps, J. & Sebastia, M. 2005. Predictive value of plant traits to grazing along a climatic gradient in the Mediterranean. *Journal of Applied Ecology* 42: 824–833.
- Bernhardt-Römermann, M., Gray, A., Vanbergen, A.J., Bergès, L., Bohner, A., Brooker, R.W., De Bruyn, L., De Cinti, B., Dirnböck, T., Grandin, U., Hester, A.J., Kanka, R., Klotz, S., Loucougaray, G., Lundin, L., Matteucci, G., Mészáros, I., Oláh, V., Preda, E., Prévosto, B., Pykälä, J., Schmidt, W., Taylor, M.E., Vadineanu, A., Waldmann, T. & Stadler, J. 2011. Functional traits and local environment predict vegetation responses to disturbance: a pan-European multi-site experiment. *Journal of Ecology* 99: 777–787.
- Cornelissen, J.H.C., Castro Diez, P. & Hunt, R. 1996. Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. *Journal of Ecology* 84: 755–765.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D., Reich, P., ter Steege, H., Morgan, H., van der Heijden, M., Pausas, J. & Poorter, H. 2003. A handbook of protocols for standardized and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335–380.
- Diaz, S., Cabido, M. & Casanoves, F. 1998. Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science* 9: 113–122.
- Diaz, S., Noy-Meir, I. & Cabido, M. 2001. Can grazing response of herbaceous plants be predicted from simple vegetative traits? *Journal of Applied Ecology* 38: 497–508.
- Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Fortunel, C., Freitas, H., Golodets, C., Grigulis, K., Jouany, C., Kazakou, E., Kigel, J., Kleyer, M., Lehsten, V., Lepš, J., Meier, T., Pakeman, R., Papadimitriou, M., Papanastasis, V.P., Quested, H., Quéfier, F., Robson, M., Romet, C., Rusch, G., Skarpe, C., Sternberg, M., Theau, J., Thébault, A., Vile, D. & Zarovali, M. 2007. Assessing the effects of land-use change on plant traits, communities and

- ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. *Annals of Botany* 99: 967–985.
- Gondard, H., Sandrine, J., Aronson, J. & Lavorel, S. 2003. Plant functional types: a promising tool for management and restoration of degraded lands. *Applied Vegetation Science* 6: 223–234.
- Goodridge, J. 2002. The effects of native plants on non-native plant abundance in a restoration setting: differences among native species and the predictive ability of species traits. MS Thesis, Oregon State University, Corvallis, OR, US.
- Harrell, F.E. Jr 2001. *Regression modeling strategies*. Springer, New York, NY, US.
- Hendry, G.A.F. & Grime, J.P. (eds.). 1993. *Methods in comparative plant ecology: a laboratory manual*. Chapman and Hall, London, UK.
- Hill, M.O. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54: 427–432.
- Kahmen, S. & Poschlod, P. 2004. Plant functional trait responses to grassland succession over 25 years. *Journal of Vegetation Science* 15: 21–32.
- Kuster, E.C., Kuhn, I., Bruelheide, H. & Klotz, S. 2008. Trait interactions help explain plant invasion success in the German flora. *Journal of Ecology* 96: 860–868.
- Kutner, M.H., Nachtsheim, C.J., Neter, J. & Li, W. 2005. *Applied linear statistical models*, 5th ed. McGraw-Hill Irwin, Boston, MA, US.
- Lavorel, S. & Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16: 545–556.
- McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*. 21: 178–185.
- McIntyre, S., Lavorel, S., Landsberg, J. & Forbes, T.D.A. 1999. Disturbance response in vegetation – towards a global perspective on functional traits. *Journal of Vegetation Science* 10: 621–630.
- Pakeman, R.J. 2004. Consistency of plant species and trait responses to grazing along a productivity gradient: a multi-site analysis. *Journal of Ecology* 92: 893–905.
- Pywell, R.F., Bullock, J.M., Roy, D.B., Warman, L., Walker, K.J. & Rothery, P. 2003. Plant traits as predictors of performance in ecological restoration. *Journal of Applied Ecology* 40: 65–77.
- Reich, P.B., Wright, I.J., Cavender-Bares, J., Craine, J.M., Oleksyn, J., Westoby, M. & Walters, M.B. 2003. The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Science* 164: S143–S164.
- Richardson, P.J., MacDougall, A.S., Stanley, A.G., Kaye, T.N. & Dunwiddie, P.W. 2012. Inversion of dominance–diversity relationships along a latitudinal stress gradient. *Ecology*. In press.
- Roberts, R.E., Clark, D.L. & Wilson, M.V. 2010. Traits, neighbours, and species performance in prairie restoration. *Applied Vegetation Science* 13: 270–279.
- Sandel, B., Corbin, J.D. & Krupa, M. 2011. Using plant functional traits to guide restoration: a case study in California grassland. *Ecosphere* 2: 1–6.
- Stanley, A.G., Kaye, T.N. & Dunwiddie, P.W. 2008. Observations from a multisite, collaborative research project. *Native Plant Journal* 9: 247–254.
- Stanley, A.G., Dunwiddie, P.W. & Kaye, T.N. 2011. Restoring invaded Pacific Northwest Prairies: management recommendations from a region-wide experiment. *Northwest Science* 85: 233–246.
- Venables, W.N. & Ripley, B.D. 1999. *Modern applied statistics with S-PLUS*, 3rd ed. Springer, New York, NY, US.
- Webb, C.T., Hoeting, J.A., Ames, G.M., Pyne, M. & Poff, N.L. 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology Letters* 13: 267–283.
- Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E. & Eriksson, O. 1999. Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science* 10: 609–620.
- Wilson, M.V., compiler. 2006. *Willamette valley prairie plant trait database*. Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR, US.