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Quantifying species trait-functioning relationships for ecosystem management

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Keywords
Agricultural management; Ecosystem function; Functional diversity; Functional ratings; Plant functional types; Productivity.

Abbreviations
DFA = discriminant factor analysis; LAI = leaf area index; PFT = plant functional type; RGR = relative growth rate; SLA = specific leaf area.

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Abstract

Questions: Can we use plant traits to make predictions about ecosystem functioning of different species mixtures, identify inherent trade-offs of particular species, and design custom communities for desired ecosystem functions? Can we develop a methodology to address plant trait–functioning relationships in species-level units, which are missing from measures of community functional diversity but needed for management?

Location: Grazing lands northeastern USA.

Method: We measured 53 physiological, morphological and growth traits for 19 plant species from glasshouse and field experiments. We developed a two-step method to link species to ecosystem processes related to management goals of improving desirable forage production in grazing lands in northeastern USA.

Results: Species were distributed continuously, rather than clustering into discrete functional types. Grasses, legumes and forbs overlapped considerably in trait values with these common classifications failing to adequately distinguish functional differences. Factor analyses were used to assess variation in species traits, and to rate species for six plant processes through which species contribute to the production of desirable forage. Species performed well in some processes and poorly in others, illustrating complex trade-offs.

Conclusions: This methodology provides a foundation for developing tools to guide construction of communities for applied settings, and for assembling hypotheses about plant functioning in mixtures.

Introduction

Biodiversity effects on key ecosystem functions, including primary production, secondary production, and cycling of elements, have been widely studied in natural and model communities (Schlapfer & Schmid 1999; Hooper et al. 2005). Applying ecological principles of biodiversity could be used to improve agricultural management. However, to apply these principles, key questions need to be answered, including how many and which organisms are required to provide desired agricultural functions (D'Antonio & Vitousek 1992), and how much redundancy is needed for insurance against environmental fluctuations (Folke et al. 1996; McGrady-Steed et al. 1997; Naeem & Li 1997; Yachi & Loreau 1999).

With as much as 90% of terrestrial ecosystems under human management (Western & Pearl 1989), ecologists must devote attention to maintaining and improving the ecosystem services provided by these areas (Vandermeer et al. 2002; Havstad & Aamlid 2007). Recent efforts have led to the development of tools for assessing biodiversity and functional diversity for monitoring managed systems (Gondard et al. 2003; de Bello et al. 2005; Petchey & Gaston 2006). Despite these strides, we lack sufficient understanding of how to select species to create communities that provide ecosystem functions in applied settings (Sanderson et al. 2007). Such an understanding would both improve ecosystem management and enhance the mechanistic and predictive ability of ecological theory of community assembly (Weiher & Keddy 1995; Hobbs & Morton 1999; McGill et al. 2006; Ackerly & Cornwell 2007).

Although general frameworks to evaluate species growth strategies and fundamental niches exist (Westoby

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1998; Hodgson et al. 1999; Harrison et al. 2010), a framework specifically for managed systems must be structured so that it can be used to design communities that produce desired products, such as food, fiber and forage. Despite decades of research on plant functional traits and biodiversity (Grime et al. 1997; Hooper et al. 2002), we still lack a predictive model relating community composition and ecosystem function. Plant traits are the mediators between species and ecosystem functions, but traits are packaged in species-bundles, and are not independent. Species can have multiple effects on ecosystem processes through different pathways, and may possess trade-offs between positive and negative effects (Eviner & Chapin 2003). For example, plant species that increase productivity under cool temperatures but decrease productivity under warm temperatures would have both positive and negative effects on annual above-ground net primary productivity (ANPP) at different times in the season.

Temperate grazing lands provide an ideal system for exploring the pathways by which plant communities provide ecosystem functions. The dominant species of these communities are well-characterized, and the relevant ecosystem functions are clearly delineated. In grazing lands in northeastern USA, functions of interest include sustaining high annual ANPP that is distributed evenly through the season and excludes undesirable weedy species. Specifically, management objectives in these managed grazing lands are to keep ANPP high and stable across a long growing season (currently limited in early spring, peak summer and late autumn) and maintain forage quality through the exclusion of species that are unpalatable and toxic to cattle, despite periodic removal of shoot biomass (Sanderson et al. 2007). As in many managed systems, management in this system occurs at the community scale, and consists primarily of adding or removing individual species directly, or through indirect management (via grazing animals here). Understanding the functional role of individual species within the community is critical.

Our objective was to develop a method that uses species trait data to quantify the multiple mechanisms by which species could affect annual and seasonal ANPP and maintain quality forage for cattle in the temperate cool-season grasslands of the northeastern USA. We used morphological and physiological measurements from glasshouse and field studies of 19 species to arrange species along continuous axes describing six processes relating to desirable forage production. We developed species scores that can be used to make predictions about this ecosystem functioning to identify trade-offs inherent in a particular species and to aid us in development of tools to design custom communities targeting desired ecosystem functions.

Methods

Choice of species and cultivars

We examined 19 naturalized or native perennial species (eight grasses, five legumes, and six forbs) that are common and desirable components of managed grasslands in northeastern USA (Table 1). While not every species of interest for these ecosystems could be examined, the majority of key species in these ecosystems were included with effort made to incorporate a diverse range of species. Two varieties of *Schedonorus phoenix* and *Lotus corniculatus* were evaluated because these cultivars, subsequently referred to as species, differ in functional attributes (Table 1). While all species examined were adapted to grazed grasslands, they vary in tolerance to defoliation frequency, drought and nitrogen availability (USDA & NRCS 2010). All seed was purchased from companies distributing cultivars developed for this region or propagating seed collected regionally.

Plant traits

We measured 53 traits pertinent to how these species grew, acquired resources and produced forage in grazing lands (Table 2). Selected traits were related to plant use of physical space above and below ground, biomass partitioning among tissues, seasonal growth patterns, and recovery of growth following defoliation. Similar traits have been used to evaluate plant growth strategies (Hodgson et al. 1999). Fourteen traits related to plant growth, allocation and morphology were assessed under three treatments in the glasshouse: control (well-watered and well-fertilized), drought, and low nitrogen (N) (Skinner & Comas 2010). Traits were either measured in the glasshouse or in monoculture field plots, depending on where differences among species could best be determined. We followed standard measurement protocols (Hendry & Grime 1993; Weiher et al. 1999; Cornelissen et al. 2003), with modifications in both glasshouse and field to incorporate periodic defoliation found in grazed systems (Skinner & Comas 2010). Field measurements primarily assessed seasonal distribution of forage production. Ultimately, trait averages were taken by species and analysed with statistical methodologies that standardized ranges among traits.

Glasshouse measurements

For greenhouse assessment of traits, all species and cultivars were germinated on open benches during Feb and Mar 2002 in 164 ml cone-tainers (Stuewe & Sons, Corvallis, OR, USA) filled with a 1:2 by volume mixture of screened silt–loam topsoil and washed #1 silica sand. Germination was timed to synchronize the initiation of growth. Glasshouse measurements were replicated in

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Table 1. Description of the 19 species used in this study (USDA & NRCS 2010). [1]Synonymous with *Festuca arundinacea* Schreb. and *Lolium arundinaceum* (Schreb.) S.J. Darbyshire.

Species and variety	Common name	Abbreviation	Growth form
Cool-season grasses			
Bromus inermis Leyss.'Saratoga'	Smooth brome	BI	Rhizomatous
Dactylis glomerata L. 'Pennlate'	Orchard grass	DG	Bunch
Elymus virginicus L. 'Omaha'	Virginia wild rye	EV	Bunch
Lolium perenne L. 'BG-34'	Perennial ryegrass	LP	Bunch
Phalaris arundinacea L. 'Palaton'	Reed canary grass	PA	Rhizomatous
Phleum pratense L. 'Climax'	Timothy	Ph	Bunch
Poa pratensis L. 'Side Kick'	Kentucky blue grass	PP	Rhizomatous
Schedonorus phoenix (Scop.) Holub.[1] 'Barolex'	Tall fescue (endophyte-free)	S1	Rhizomatous
Schedonorus phoenix (Scop.) Holub.[1] 'Jessup Max Q'	Tall fescue (non-toxic endophyte)	S2	Rhizomatous
Legumes			
Lotus corniculatus L. 'ARS-2620'	Birdsfoot trefoil	L2	Rhizomatous
Lotus corniculatus L. 'Norcen'	Birdsfoot trefoil	L1	Single crown
Medicago sativa L. 'Amerigraze'	Alfalfa	MS	Single crown
Trifolium ambiguum M. Bieb. 'Endura'	Kura clover	TA	Rhizomatous
Trifolium pratense L. 'Plus'	Red clover	TP	Single crown
Trifolium repens L. 'Will'	White clover	TR	Stoloniferous
Non-leguminous forbs			
Achillea millifolium L.	Common yarrow	AM	Rhizomatous
Cichorium intybus L. 'Puna'	Chicory	CI	Single crown
Plantago lanceolata L. 'plan 3'	Narrow-leaf plantain	PL	Single crown
Sanguisorba minor Scop. 'Delar'	Small burnet	SM	Multiple stem
Solidago nemoralis Ait.	Grey goldenrod	SN	Rhizomatous
Taraxacum officinale G.H. Weber ex Wiggers	Dandelion	TO	Single crown

three separate glasshouse sections with germination of plants for each glasshouse section timed so all experimental steps for each glasshouse section occurred one week apart. Nine weeks after sowing each group of plants, seedlings of uniform size were transplanted into pots constructed of polyvinyl chloride (PVC) pipe 15 cm in diameter and 50 cm long filled with a 1:1 by volume mixture of the same soil and sand. The bottom of each pot was fitted with a plywood disk drilled with multiple holes 0.5 cm in diameter and lined with a fine nylon mesh. One week after transplanting, seedlings had the top 50% of their shoot removed. In each glasshouse section, four plants approximately 70 d old were harvested 1 wk after defoliation. Total shoot and root dry weights were determined from the first harvest. Four plants of each species and treatment were harvested 21 d later (4 plants × 24 species/cultivars × 3 treatments × 3 glasshouse sections for second harvest).

Detailed biomass allocation and morphological measurements taken at the second harvest included shoot height and width for each plant. Two measures of width were taken: the width of the largest extension of the shoot and the width perpendicular to that dimension on each plant. These two width measurements were averaged and used as the diameter from which to calculate projected shoot ground area for leaf area index (LAI). Shoot height and projected shoot ground area were used to calculate shoot volume. Plant shoots were dissected into leaves and stems. For all species except clovers, petioles were collected with leaves. For clovers, petioles were collected separately. In addition to standard shoot architecture measurements, shoot form was assessed through calculations of mass-weighted shoot height (wtHt), mass-weighted shoot width (wtwid), and overall index of shoot density (shDen) (Table 2). These measures accounted for the overall upright habit, spreading habit and compact shoot shape, respectively.

Soil was divided into five 10-cm layers, with roots in each layer collected separately at the second harvest. After washing through a No. 10 soil sieve, roots from each layer were dissected into fine, coarse, and tap roots. Fine roots were the two terminal branches (finest two branch orders), typically < 1 mm, serving primarily for the acquisition of soil resources rather than storage or structure. Stolon biomass was pooled with stems, and rhizome biomass with coarse and tap roots for the relevant species. Fine root measurements collected from five depth intervals (0–10, 11–20, 21–30, 31–40 and 41–50 cm) were used to calculate proportion of fine roots at deep and shallow depths (Table 2). Fine roots in the 41–50 cm pot depth were not used in assessing root distribution to avoid artifacts associated with water pooling at this depth and

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Table 2. Traits measured from glasshouse- and field-grown plants. With the exception of seed mass and initial relative growth rate, traits acquired from glasshouse-grown plants were acquired under control (well-watered, fertilized), drought, and low-nitrogen treatments, designated elsewhere with subscripts C, D and N, respectively.

Code	Test	Description
Greenhouse-derived traits		
seed$_{M}$	Seed mass	Average mass of a seed
RGR$_{init}$	Initial relative growth rate	Rate of whole plant biomass increase from emergence to 9 wks
RGR$_{regr}$	Relative regrowth rate	Innate rate of whole plant biomass increase from 7 to 28 d after removing 50% leaf area from 9 wk-old plants
re-gr$_{Abs}$	Absolute regrowth rate	Absolute rate of whole plant biomass increase from 7 to 28 d after removing 50% of leaf area from 9 wk-old plants
wtWid	Mass-weighted lateral shoot spread	Shoot width to shoot mass ratio
wtHt	Mass-weighted shoot height	Shoot height to shoot mass ratio
SLA	Specific leaf area	Leaf area to leaf mass ratio
LWR	Leaf weight ratio	Leaf mass to total plant mass ratio
LAR	Leaf area ratio	Leaf area to total plant mass ratio
LAI	Leaf area index	Ratio of total leaf area to ground area under shoot
SRL	Specific root length	Root length to root mass ratio
d4%	Allocation to deep roots	% of fine root mass in 30–40 cm pot depth from that 0–40 cm
d1%	Allocation to shallow roots	% of fine root mass in 0–10 cm pot depth from that 0–40 cm
rtL0-20%	Allocation to root length in the soil layer with high competition	% of root length in the 0–20 cm pot depth from that 0–40 cm
rt$_{L}$:lf$_{A}$	Fine root length to leaf area ratio	Proportion of fine root length to leaf area
K$_{R:S}$	Allometric coefficient of root to shoot growth	Ratio of relative growth rate of root to shoot mass from 7 to 28 d after removing 50% of leaf area
sht%$_{D/C}$	Shoot growth insensitivity to drought	Ratio of shoot mass under drought to that under control growth conditions
sht%$_{N/C}$	Shoot growth insensitivity to low N	Ratio of shoot mass under low nitrogen to that under control growth conditions
Field derived traits		
grnup$_{max}$	Maximum rate of spring growth	Maximum rate of spring ground cover development
T$_{33\%}$	Initiation date of spring growth	Time lapse from Jan 1 to 33% spring ground cover development
prod$_{earspr}$	Above-ground production, early spring	Shoot mass above 7 cm height per unit ground area in early May
prod$_{spr}$	Above-ground production, late spring	Shoot mass above 7 cm height per unit ground area in late May
prod$_{sum}$	Above-ground production, summer	Shoot mass above 7 cm height per unit ground area in driest summer growth interval
prod$_{fall}$	Above-ground production, autumn	Shoot mass above 7 cm height per unit ground area in Sep
prod$_{ltfall}$	Above-ground production, late autumn	Shoot mass above 7 cm height per unit ground area in Oct

roots that occasionally accumulated at the bottom and grew out of the pot. Thus, allocation to deep roots was assessed as a proportion of fine roots in the 30–40 cm pot depth to that in 0–40 cm (d4%). Allocation to shallow roots was assessed as a proportion of fine roots in the 0–10 cm pot depth to that in 0–40 cm (d1%). Fine root length in the 0–20 cm pot depth was assessed to evaluate the proportion of fine roots in the zone of greatest root competition (rtL0-20%).

Relative growth rate (RGR) was calculated as mean RGR over one time-interval (Cornelissen et al. 1996). The RGR of the initial growth phase was calculated for the 10 wks from seedling emergence to the first glasshouse harvest using average seed mass as the initial plant weight (Table 2). Relative growth rate during the regrowth phase was calculated over the 21-d period between the two harvests. Absolute growth during the regrowth phase was calculated as average daily absolute increase in total plant biomass during the same 21-d span. Average seed mass was determined for each species by weighing 100 seeds.

Field measurements

Field measurements were taken from plants growing in 1 m^2 plots at the Russell E. Larson Agricultural Research Center at Rock Springs (Centre County, PA, USA). Monocultural plots of each species were established from seed in four randomized complete blocks in Apr 2002, and monitored from Mar to Nov in 2003 and 2004.

Weekly digital photographs were taken in each plot for 6 wks prior to the first spring harvest in 2003 to assess cover development. The percentage of green cover was determined for a subsample of each photograph. The percentage of green pixels in each image belonging to the target species were determined using an image analysis routine implemented in R (S.C. Goslee, unpublished protocol; R Foundation for Statistical Computing, Vienna, Austria; http://www.R-project.org). A polynomial regression was fitted for each species on the average cover percent in four plots captured at each date in Sigma Plot (Systat Software Inc., San Jose, CA, USA). These curves were used to determine the date that green cover reached 33% of the ground area and the maximum rate of spring cover development.

Average vegetative height in each plot was measured weekly during the entire growing season. When the height reached an average of 25 cm among species, above-ground biomass was collected from a 0.05 m^2 section of each plot, positioned at least 15 cm from any plot edge to minimize edge effects. Plant stubble of 7 cm was left behind after sampling each section. The remainder of the plots was then mowed to a height of 7 cm. Plant heights were chosen to be consistent with cattle grazing and grassland management in this region.

Biomass samples were separated into target species and weeds. Target species biomass was divided into leaves, stem and reproductive tissues. Plots were mowed six times per growing season at 17- to 51-d intervals, depending on growth rate. Slow-release fertilizer was added to each plot following cutting to replace the nitrogen lost through removal of the vegetation. The amount of N to be added was calculated as 3.25% of the total biomass removed from each plot at the previous cutting, assuming that shoots of cool-season species contain about 20% protein (Skinner et al. 2004). Samples from summer 2004 were not used to estimate summer drought impacts because growth was atypical owing to unusually prolonged rainfall that kept soil moisture near field capacity.

Data analysis

All analyses were conducted with SAS (SAS Institute, Cary, NC, USA) on traits averaged by species. Normality of individual trait distributions was tested with the Shapiro–Wilke test with traits transformed as needed to achieve a normal distribution. Multivariate normality was checked with the Mardia test of multivariate skewness and kurtosis. It was necessary to pare down the original trait list to conduct multivariate analyses with an appropriate ratio of variables to samples (fewer traits than species, Tabachnik & Fidell 1996). Redundant traits were identified by grouping similar traits using hierarchical clustering on oblique centroid components (PROC VARCLUS; SAS Institute, Cary, NC, USA). Within each cluster of traits, one trait was selected for each cluster that was most strongly correlated with that cluster and most weakly correlated with other clusters (smallest ratio of correlation within the cluster to next closest cluster). All other traits in the cluster were dropped.

Factor analysis on the reduced trait set was used to identify combinations of traits related to the major dimensions of variation (referred to as factors). We then examined the ranking of species scores for each of these factors. Factors were extracted with principal components method to extract the maximum proportion of the total variance and varimax rotation to differentiate trait loadings among extracted factors. Eigenvalues greater than 1 were considered significant (Kaiser's rule). Fisher linear discriminant factor analysis (DFA) of the same trait set used in factor analysis with species assigned to grass, forb, and legume classifications. For DFA, the classification criterion was calculated based on a multivariate normal distribution within each class, prior probabilities were set proportional to the sample sizes and a pooled covariance matrix was used after testing homogeneity of the within-group covariance matrices with Bartlett's modified likelihood ratio test. The DFA was followed by a leave-one-out cross-validation to assess the distinctiveness of grass, forb, and legume classifications.

When unguided statistical approaches failed to find discrete clusters of species, we employed a two-step method to evaluate potential species effects on forage production in grazed pastures, first identifying plant processes that affect desirable forage production in these systems, and then rating species according to their potential performance for each process. Plant processes hypothesized to directly affect forage production were identified from analyses of species trait variation outlined above and assessment of plant growth and management aims in these pasture systems. An individual factor analysis, conducted with the same methodology given above, was then used to evaluate species rankings in multivariate trait space for each plant process. As these methods standardize variation among trait variables, similar relative differences among traits are assumed to contribute equally to each factor.

Results

Reduced trait set

The first round of cluster analysis was used to pare the set of traits to 25 by eliminating the most redundant. Morphological traits (e.g. specific leaf area, SLA) measured in all three glasshouse treatments represented similar variation among species and, thus, were retained in only one treatment. Eliminated traits also included allocation traits (e.g. root length in the competitive soil zone, rtL0-20%) redundant with other measures of allocation (in this case, the ratio of fine roots to leaves, rtL/lfA).

A second cluster analysis of traits revealed clustering of more dissimilar traits that described similar variation

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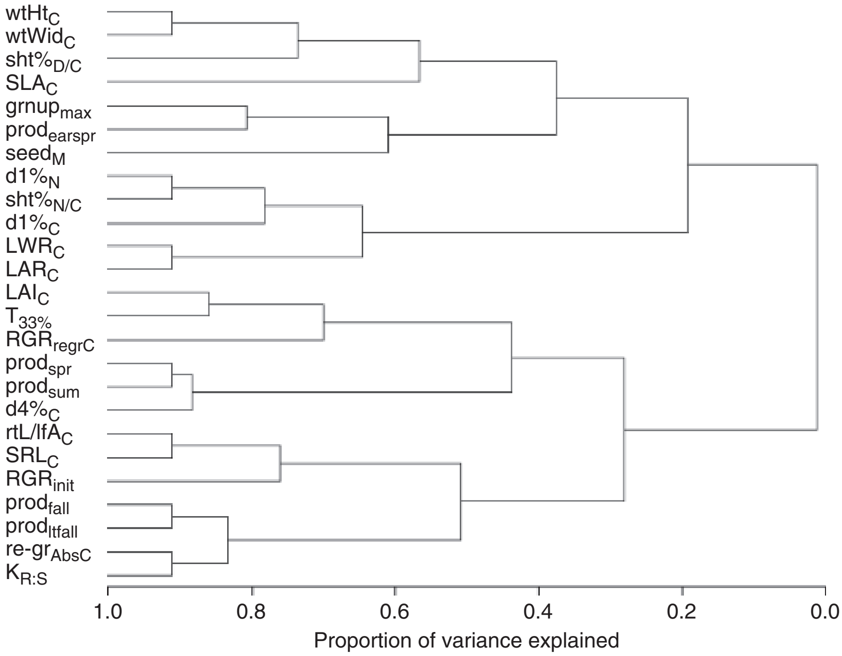

Fig. 1. Dendrogram of 25 glasshouse- and field-measured traits grouped by the variation among species expressed by each trait. Traits are described in Table 2. Species included in the analysis are listed in Table 1.

(Fig. 1). One cluster grouped summer above-ground biomass production in the field, occurring when water at the soil surface was most limited, with proportional allocation to deep roots (d4%) assessed in the glasshouse and late spring above-ground biomass production in the field. Shoot growth insensitivity to limited N supply (sht%$_{N/C}$) was associated with fine root allocation to shallow depths (d1%$_N$), which is where nodulation of legumes might be most active. The amount of root length per leaf area (rtL/lfA$_C$) was associated with specific root length (SRL$_C$), suggesting that morphological differences were a component of allocation partitioned below and above ground among these species. Similar traits such as leaf area ratio (LAR$_C$) and leaf weight ratio (LWR$_C$) also clustered together, as did above-ground biomass production in early and late autumn, and mass-weighted shoot height and width. Thus, this second cluster analysis allowed for further reduction of the 25 traits to 17 that accounted for the greatest variation among species (Table 3; Fig. 1).

Factor analysis with 17 traits

Factor analysis yielded six significant factors, which explained 83% of the variation among all species (Table 3). These six factors were linked to potential trait-mediated processes affecting forage production as follows. Factor 1 related to regrowth following defoliation, which was associated with autumn above-ground biomass production in the field. Factor 2 related to pasture establishment, being strongly influenced by seed mass and initial RGR. Factor 3 was less-interpretable, with strong loadings on plant growth insensitivity to drought, upright shoot form and slow RGR following defoliation. Factor 4 described early spring production, and factor 5 summer biomass production and drought resistance. Factor 6 was associated with high leaf area index (LAI$_C$) and slow rate of early spring green cover development (grnup$_{max}$), and appeared to identify species that colonize gaps.

Factor scores showed continuous distribution of all species, demonstrating the absence of discrete functional types in this data set (Fig. 2). Furthermore, there was continuous overlap among grass, legume and forb species across all six factors. Discriminant factor analysis and cross-validation using the same set of 17 traits indicated 62% overlap among grass, forb, and legume classifications.

Two-step guided approach

As the unguided statistical approach failed to find discrete clusters of species, we sought a more complex approach to evaluate plant processes governing the production of desirable forage and assess the potential ability of different species to play a role in these processes. Six plant processes were identified related to a priori goals of maintaining desirable forage production with uniform productivity across seasons. These processes were related to maintaining forage production at four major portions

Table 3. Factor analysis loading coefficients for traits on each significant factor after orthogonal (varimax) rotation. Bold type indicates loading coefficients accounting for the largest variation (greater than ±60) explained by each significant factor (with eigenvalue > 1, Kaiser's rule).

Trait code	Trait	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6
seed_M	Seed mass	23	**−95**	10	11	−2	−8
RGR_{init}	Initial relative growth rate	20	**93**	−20	−4	12	4
RGR_{regrC}	Relative regrowth rate, control trt	−17	17	**−69**	−30	−15	−27
re-gr_{AbsC}	Absolute regrowth rate, control trt	**74**	10	−53	−5	0	−15
wtHt_C	Massweighted shoot height, control trt	−17	−10	**75**	20	5	−21
SLA_C	Specific leaf area, control trt	3	−4	8	13	**88**	5
LAR_C	Leaf area ratio, control trt	**−83**	23	−25	−10	−6	7
LAI_C	Leaf area index, control trt	−24	34	−31	−7	−31	**74**
rtL:lfA_C	Fine root length to leaf area ratio, control trt	52	37	23	−34	33	46
$\text{d1\%}_C$	Allocation to shallow roots, control trt	−41	35	−2	5	**68**	7
$\text{d1\%}_N$	Allocation to shallow roots, low N trt	**−66**	37	2	20	36	−6
$\text{sht\%}_{D/C}$	Shoot growth insensitivity to drought	−1	−8	**82**	−42	7	−3
grnup_{max}	Maximum rate of spring growth	4	8	−13	37	−25	**−79**
$\text{T}_{33\%}$	Initiation date of spring growth	−14	−6	−15	**−82**	−14	28
$\text{prod}_{earspr03}$	Above-ground production, early spring	−24	−19	5	**84**	2	−13
prod_{sum03}	Above-ground production, summer	19	−7	−29	55	**−64**	7
prod_{fall03}	Above-ground production, autumn	**79**	30	−20	5	−25	−6

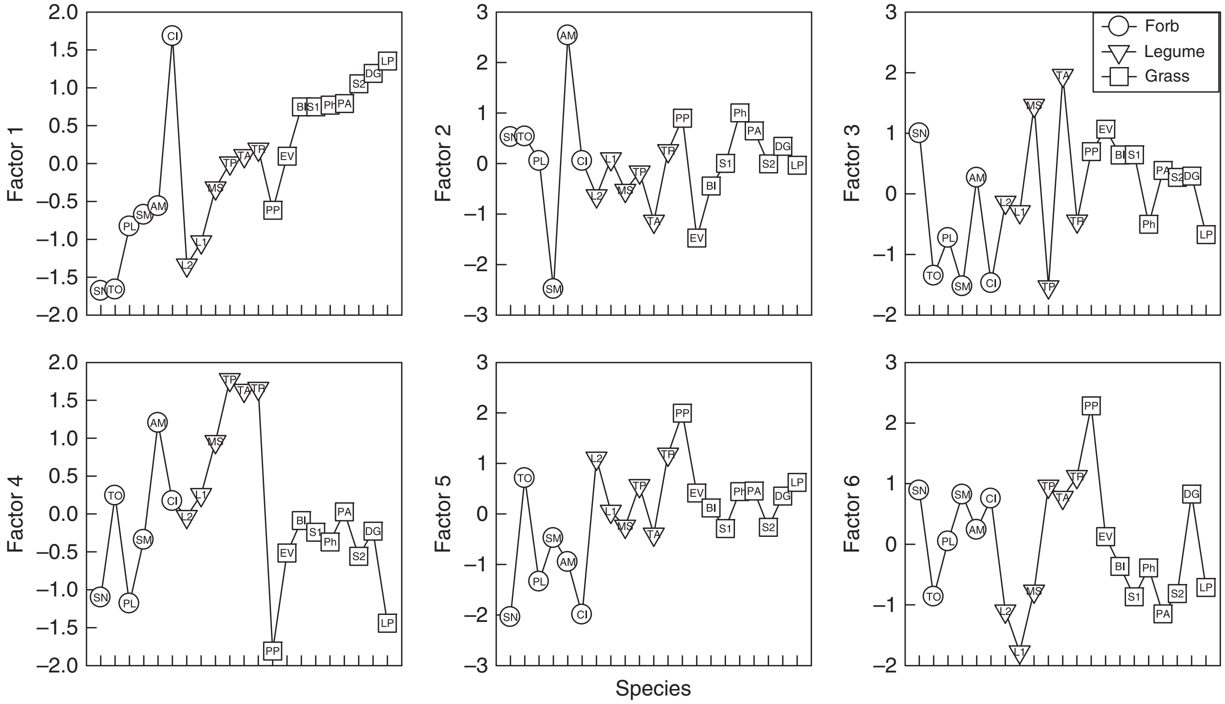

Fig. 2. Ordination of species by their scores on significant factors extracted by factor analysis of 17 plant functional traits. Trait loading coefficients for each factor are given in Table 3. Eigen values for each factor are given in the Supporting Information, Appendix S1. Species are displayed in order of forb/legume/grass classification and then their score on factor 1 within each classification with lines highlighting the magnitude of difference among species. Species abbreviations are given in Table 1.

of the growing season (1) early spring (green-up through early May); (2) late spring (early May to the end of May); (3) summer (Jun–Aug); and (4) autumn (Sep–early Nov). Other important processes included (5) growth under low N, which is important for maintaining productivity when N is limiting, and (6) vegetative colonization of open gaps, important for increasing the extent of desirable species and excluding undesirable species from invading

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Table 4. Plant processes with potential effects on quality forage productivity of northeastern US grazing lands, traits associated with each process, and the scores from individual factor analyses for each process using those traits. The six plant processes relate to management aims of maximizing quality forage productivity (through high and even productivity across the season, limited invasions from undesirable plant species) and minimizing inputs (through encouraging hydraulic redistribution in soil profile during summer months, growth under low nitrogen).

Management implication	Plant process	Trait	Trait code	Factor score
Seasonality	P1: Early spring productivity	Early spring field production 2003	$\mathrm{prod}_{\mathrm{earspr03}}$	0.83
		Early spring field production 2004	$\mathrm{prod}_{\mathrm{earspr04}}$	0.61
		Initiation date of spring growth	$\mathrm{T}_{33\%}$	– 0.95
Seasonality	P2: Late spring productivity	Late spring field production 2003	$\mathrm{prod}_{\mathrm{spr03}}$	0.36
		Late spring field production 2004	$\mathrm{prod}_{\mathrm{spr04}}$	0.81
		Absolute regrowth rate	$\mathrm{re\text{-}gr}_{\mathrm{AbsC}}$	0.82
Seasonality, soil hydraulic redistribution	P3: Summer drought resistance	Summer field production 2003	$\mathrm{prod}_{\mathrm{sum03}}$	0.84
		% Root allocation at 30–40 cm depth	$\mathrm{d4\%}_{\mathrm{C}}$	0.74
		% Root allocation at 0–10 cm depth	$\mathrm{d1\%}_{\mathrm{C}}$	– 0.80
		SLA	$\mathrm{SLA}_{\mathrm{C}}$	– 0.65
Seasonality	P4: Autumn productivity	Autumn field production 2003	$\mathrm{prod}_{\mathrm{fall03}}$	0.94
		Late autumn field production 2003	$\mathrm{prod}_{\mathrm{ltfall03}}$	0.91
		Absolute regrowth rate	$\mathrm{re\text{-}gr}_{\mathrm{AbsC}}$	0.79
Invasibility	P5: Gap colonization	LAI	$\mathrm{LAI}_{\mathrm{C}}$	0.87
		SRL	$\mathrm{SRL}_{\mathrm{C}}$	0.87
		% root allocation at 0–10 cm depth	$\mathrm{d1\%}_{\mathrm{D}}$	0.69
N fixation	P6: Growth under low N	Shoot growth insensitivity to low nitrogen (N)	$\mathrm{sht\%}_{\mathrm{N/C}}$	0.94
		% root allocation at 0–10 cm depth	$\mathrm{d1\%}_{\mathrm{N}}$	0.77
		Fine root length to leaf area ratio	$\mathrm{rtL{:}lfA}_{\mathrm{N}}$	– 0.76

the community. Plant traits related to these six processes were identified using latent factors from factor analysis (Table 3), trait cluster patterns from cluster analysis and expert knowledge of plant performance in these grasslands (Table 4).

Including only traits related to a particular process in individual factor analyses produced one significant factor for each process (Table 4). Species placement along a factor axis can be used as a quantitative trait-based measure of performance for that process (Fig. 3). In the two cases where two varieties of a species were studied (*Schedonorus phoenix* and *Lotus corniculatus*), both genotypes generally fell near each other along the functional axes.

Several species were highly rated for more than one plant process (Fig. 3; Table 5). One such species was *Trifolium pratense*, which was ranked highly for four plant processes (P1, P2, P3, & P6) and above the median for the other two functions (P4 & P5). Several species that were highly rated for some paths were poorly rated for other paths, suggesting trade-offs in functions for these species.

Discussion

This methodology was developed to provide a framework for evaluating functional roles of plant species in grazing lands in northeastern USA to guide field experiments testing specific hypotheses related to the production of desirable forage by different plant mixtures. Employing a two-step guided methodology emerged as a necessary approach for assessing species effects on ecosystem functioning for two reasons. First, independent analysis of each plant process allowed us to identify species that could perform well, or poorly, for each process, offering an examination of individual species effects and their potential trade-offs. Second, breaking down the effects of species into multiple pathways allowed us to break down the potentially complex effects of species in a mixture, and reveal the possibilities of intricate positive and negative effects of combining species, which may be at the core of species interactions in community functions (Table 5). Species redundancies could be identified with this approach by finding species with similar potentials across different plant processes, although we did not find redundancies. This approach could also be used to explain measurements of species complementarity in field experiments.

The general method developed here can be applied to any ecosystem where management of individual species in a community is required to meet a complex goal that is dependent on the interactions of species and their attributes in a community. In our case, the theoretical framework presented here, together with results from on-going field trials, is being used to develop a decision support tool that can be used in formulating species mixtures for the management of grazing lands in northeastern USA. This

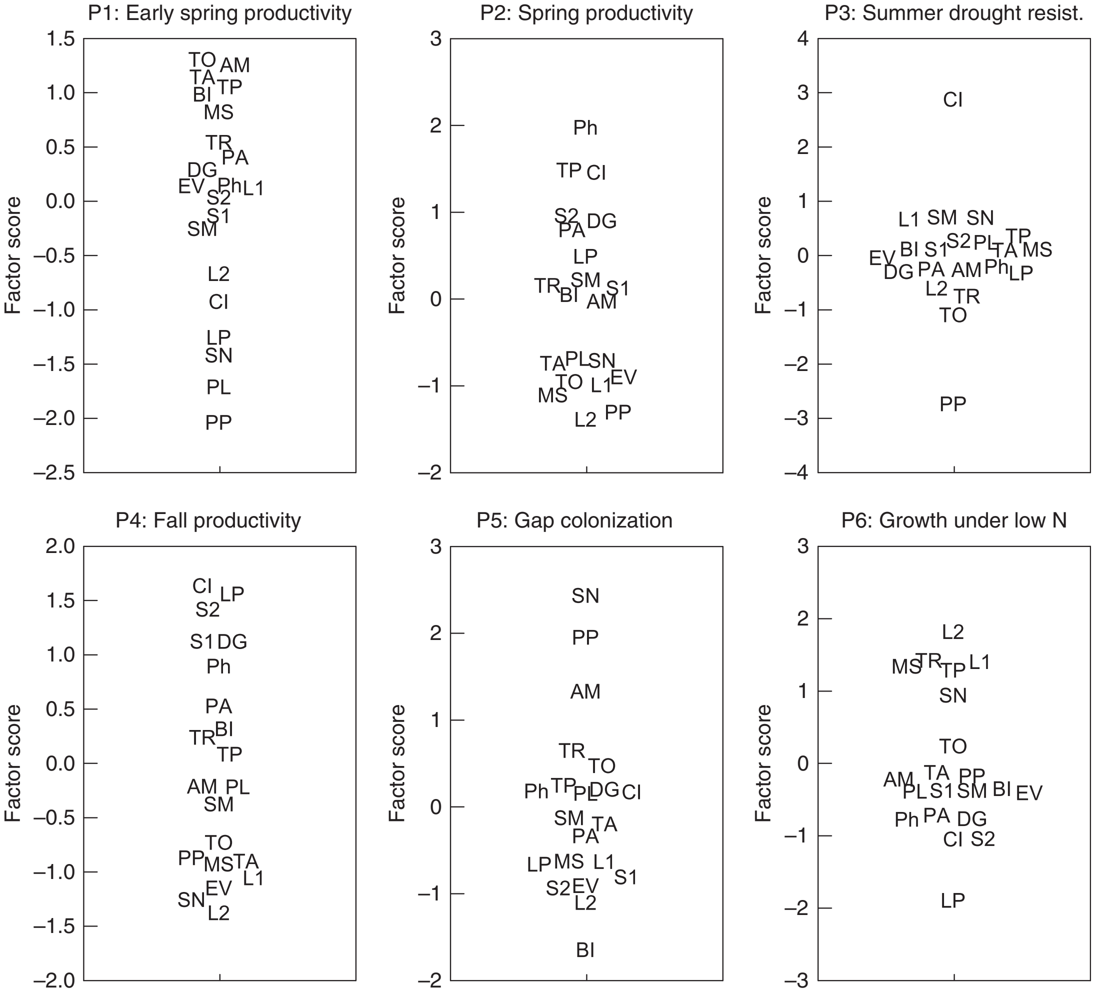

Fig. 3. Species scores for each plant process derived from independent factor analysis of each plant process. The variables and their loading scores used in each individual factor analysis are listed in Table 4. Species abbreviations are given in Table 1. Horizontal spread of species is for visual clarity only.

support tool will guide managers in field-scale planning by suggesting additional plant species that can be added to an existing pasture. This tool will also guide seed companies in developing species mixtures for northeastern grazing lands by providing a theoretical framework to guide the composition of species mixtures, which are currently designed through limited trial and error. With time, as new species become of interest for northeastern grazing lands, re-evaluation of individual plant processes and reanalysis to rank species will be required, which is inevitable with any method as the system under consideration changes.

Two main approaches relating species and traits to ecosystem functions have been used in the past: measures of overall functional diversity and classification of species into plant functional types (PFTs) (Gitay & Nobel 1997; Petchey & Gaston 2006; Harrison et al. 2010). Although diversity indices and PFTs have been used successfully as indirect indicators of ecosystem functioning in monitoring applications, such as rangeland monitoring of grazing (Gondard et al. 2003; de Bello et al. 2010), neither approach was suitable here. Although PFTs seemed suitable, our initial results identified continuous trait variation among species, suggesting that clustering species into discrete groupings was not appropriate. Accumulating evidence indicates that measured traits are more likely to be continuously than discretely distributed (Diaz et al. 2001; Lavorel & Garnier 2002; Petchey & Gaston 2006). More importantly, diversity indices and PFTs do not allow for the consideration of trade-offs among species or the evaluation of complex multiple effects of individual species (Pakeman & Marriott 2010). In many applications, not just agricultural, taxonomic or functional identity of individual species within a community is more important than the general diversity of a community (Johnson et al. 2008; Mokany et al. 2008). Clustering species, while

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Table 5. Summary of species' rankings illustrating potential trade-offs in their effects on the six plant processes. Species were marked as high or low on each process if they fell roughly within the highest or lowest third in the ordination from individual factor analysis conducted for each (Fig. 3). Species are ordered by the net number of processes that they may affect in positive directions. *Caused primarily by allocation towards reproduction.

Plant process	Species																		
	TP	CI	S1 or S2	AM	DG	Ph	SM	SN	PA	BI	TR	MS	TA	PL	L1 or L2	LP	TO	PP	EV
P1: Early spring productivity	↑	↓		↑				↓		↑		↑	↑	↓		↓	↑*	↓	
P2: Late spring productivity	↑	↑	↑		↑	↑		↓	↑			↓	↓	↓	↓		↓	↓	↓
P3: Summer drought resistance	↑	↑	↑				↑	↑			↓			↑			↓	↓	
P4: Autumn productivity		↑	↑		↑	↑		↓				↓	↓		↓	↑	↓	↓	↓
P5: Gap colonization			↓	↑				↑		↓		↓			↓	↓		↑	↓
P6: Growth under low N	↑	↓	↓		↓	↓		↑	↓		↑	↑			↑	↓			

providing more information about species than general diversity indices, still evades the identification of multiple effects of species (e.g. *Trifolium pratense*, a nitrogen-fixing plant highly productive under low N that grows quickly in the spring, is drought resistant and productive during the summer, but has low productivity in the autumn). Functional complexity and trait trade-offs are important components of species effects in a community, although perhaps more essential for applications such as ours seeking to construct species mixtures to serve ecosystem functions rather than identify changes in ecosystem functioning, as these approaches have been used previously. While functional diversity indices and PFT approaches have merit, we needed to take a different approach to evaluating species traits that could lead to direct mechanistic hypotheses of individual species effects on ecosystem functioning (Suding et al. 2003; Hooper et al. 2005; McGill et al. 2006; Lavorel et al. 2008).

A sophisticated evaluation framework of species effects on ecosystem processes served our management aim (e.g. to maximize annual desirable forage productivity and reduce seasonal variation) by addressing the complexity involved with meeting this aim. Although other studies have addressed complex effects of organisms on ecosystem functions (Solan 2000; Eviner & Chapin 2003; Jones et al. 2006; Lavelle et al. 2006), the potential complexity of species effects here was exposed by independently evaluating species effects on different plant processes. This represents a fundamental methodological departure in the evaluation of species effects on ecosystem functioning because it allowed us to more clearly consider the complexity of individual species and their effects on ecosystem functioning. In addition, managed ecosystems are often managed for more than one goal. Directly incorporating the complexity of this goal may be fundamental for producing a conceptualization of species to assist with the management of complex aims.

Because species traits come bundled in individual species rather than occurring as individual entities, it is inevitable that desirable species traits will also be bundled with less desirable traits. Furthermore, just as species may have multiple desirable traits, they may also have multiple undesirable traits. In the data presented here, most species rated high on some processes and low on others, suggesting that there were trade-offs in traits for these species (Table 5). For example, *Cichorium intybus* was poorly rated for early spring productivity and N tolerance but highly rated for spring, summer and autumn productivity. This species starts growing late in the season but is highly productive thereafter, provided that N is not limiting. Most species were rated low on at least one process with the exception of three species that had high ratings (positive) without low ratings (*T. pratense, Achillea millifolium* and *Sanguisorba minor*), although one of these species (*S. minor*) rated high for only one process. Many species were rated low for more processes than they rated high (e.g. *Lotus corniculatus*, *Lolium perenne*, *Poa pratensis*, *Taraxacum officinale*, *Elymus virginicus*), suggesting that the negative impacts of species on the functioning of a community may be just as, or more important to consider than their positive impacts (Table 5).

Mechanistic research investigating interactions between species and ecosystem functioning is beginning to occur (Eviner 2004; Eviner et al. 2006; Jones et al. 2006; Ansquer et al. 2009). A shift to more mechanistic studies in community ecology will move forward more quickly if guided by an appropriate framework that can assist in directing hypothesis-driven research. In the work presented here, a multistep approach was needed to guide modeling of traits and functional aspects of plants. This was likely because of the complex nature of species effects, which can occur through many direct and indirect processes that may be unequal in strength (McGill et al. 2006; Petchey & Gaston 2006). Field experiments will be needed to assess the contribution of each of the processes identified here in maximizing annual forage productivity and reducing seasonal variation of communities differing in composition. However, equipped with this framework, we are now in a position to develop specific hypotheses of how to construct communities to meet our management

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objectives for northeastern grazing lands. We need field experiments to test hypotheses addressing the cumulative result of positive and negative species effects in constructed pasture communities, and to test specific effects of combining species, before we can use this framework to develop species mixtures for our system. Specifically, we need to experimentally determine, when a community is composed of species that are productive at different times in the season, if annual productivity will be determined by the proportion of each species and their productivity at different times in the season or if species productive at different times in the season compensate for the lack of productivity of others, leading to greater annual productivity despite the proportion of ground area taken up by each throughout the year.

A method linking species composition of communities to ecosystem processes is essential for sustainable management of ecosystems (West 1993). The method presented here reflects the complexity of species' effects on ecosystem functioning and the occurrence of species effects through multiple pathways. Management in many areas proceeds through the addition or removal of individual species. A trait- and process-based framework that incorporates species roles is crucial for understanding the ecosystem-scale effects of these manipulations. Ultimately, the value of this framework is that it could be used to construct communities to fulfill specific functions in managed systems, and to design hypothesis-driven research leading to improved adaptive management of complex agricultural and natural systems.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Eigenvectors of the correlation matrix, and proportional and cumulative variation explained by each eigenvalue from factor analysis of the 17 traits listed in Table 3. Eigenvalues greater than 1 were considered significant. Factor scores for traits loading on each significant factor are given in Table 3.

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