Propagule pools mediate community assembly and diversity-ecosystem regulation along a grassland productivity gradient

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Summary

1 The relative importance of regional species pools and local ecological processes in governing landscape variation in plant species diversity and productivity was evaluated in a Kansas grassland.

2 We examined the impact of multispecies sowing treatments and experimental canopy disturbances on plant species diversity and ecosystem processes along a complex natural gradient of plant standing crop.

3 Data collected 4 years after sowing showed that plant invasion and diversity were seed limited in unproductive sites, but microsite limited in productive sites. Effects of sowing on plant diversity along the natural landscape gradient were paralleled by significant effects of sowing on measures of local plant production and community resilience to disturbance.

4 These results support the shifting limitations hypothesis (SLH) that landscape gradients in local plant diversity should reflect shifts in the major regulating factor, from species pools to local ecological processes, as one moves from sites of inherently low to inherently high productivity.

5 Our findings also indicate that diversity at the level of the available propagule pool acts to constrain ecosystem productivity and stability by mediating local community assembly, by determining the availability of key species, and by governing opportunities for functional compensation within the community.

6 In total, our results support an emerging view that community processes and ecosystem functions are dynamically linked and act reciprocally to constrain each other.

Key-words: community assembly, diversity, ecosystem regulation, grassland, invasion, microsite limitation, productivity gradient, propagule pools, seed limitation

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Introduction

Patterns of plant composition and diversity along gradients of productivity, and the mechanisms that produce these patterns, continue to motivate research and fuel debate. Research into this topic has taken on increased meaning in recent decades as habitat modification and species loss have accelerated, and as the consequences of these changes for ecosystem functioning have become more apparent (Schulze & Mooney 1993; Naeem *et al*. 1994; Chapin *et al*. 1997; Vitousek *et al*. 1997; Grime 1998; Symstad *et al*. 1998). Conventionally, community ecologists have viewed plant species composition and diversity at the local scale as being strongly dependent on local factors, such as underlying ecosystem properties (resource availability, productivity), biotic interactions and disturbances (Huston 1979; Tilman 1988; Huston 1994; Grace 1999). However, recent work has re-focused attention on the role of regional phenomena, species pools and dispersal limitations as important mediators of local community assembly and diversity (Ricklefs 1987; Taylor *et al*. 1990; Gough *et al*. 1994; Zobel 1997; Huston 1999; Loreau & Mouquet 1999; Kupferschmid *et al*. 2000; Zobel *et al*. 2000; Xiong *et al*. 2003). The recognition that many communities may be unsaturated, such that their diversity is constrained by species pools and limits to immigration, has caused some to question the importance of competition and niche relations in regulating community structure

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(Cornell & Lawton 1992; Pärtel *et al.* 1996; Zobel 2001). However, recent theoretical work on competitive meta-communities has highlighted the importance of regional source pools, interpatch dispersal and local biotic interactions in regulating local diversity and ecosystem functioning (Loreau *et al.* 2003). Although there is little doubt that local ecological processes and regional factors combine to regulate community assembly (Schluter & Ricklefs 1993), it is unclear how the relative contributions of these differently scaled processes might vary with environmental circumstance.

There are numerous hypotheses to explain plant diversity along productivity gradients (see review by Grace 1999). Here, we evaluate three classes of hypotheses, which are useful in distinguishing the possible roles of species availability in regulating local diversity. These hypotheses are termed here the niche limitation hypothesis (NLH), the species pool hypothesis (SPH) and the shifting limitations hypothesis (SLH). Together, these general hypotheses encompass most of the more specific models that have been discussed.

The NLH assumes that richness at all locations along a productivity gradient will be limited by local processes such as species interactions, the availability of establishment microsites, or more generally, niche availability. The NLH is represented by equilibrium models of coexistence such as the resource-ratio hypothesis (Tilman 1982) and variations of the resource-ratio hypothesis that incorporate resource heterogeneity (Tilman & Pacala 1993). These models do not consider the possibility of limitation by species availability. The SPH, in the form we present it, stems from Taylor *et al.* (1990), Eriksson (1993) and Zobel (1997) and provides an extreme alternative to the NLH. The SPH explains patterns of local diversity along entire gradients of productivity as a consequence of constraints imposed by regional species pools. In our strict interpretation of the SPH, local ecological processes and niche availability do not limit diversity at any position along a gradient. Of particular relevance to our study, the SPH interprets the decline in richness associated with habitat eutrophication as a simple consequence of species pool exhaustion resulting from a shortage of species in the regional pool adapted to nutrient-enriched conditions. The SLH contains elements of the NLH and the SPH and incorporates equilibrium and non-equilibrium perspectives. Models of community organization developed by Grime (1979) and Huston (1994, 1999) suggest that the role of regional species pools in limiting local colonization and richness should be greatest in sites of moderate productivity, but should decline in importance as one moves from moderate to high productivity due to the increasing relevance of competitive exclusion. We refer to this model as the shifting limitations hypothesis (SLH) because it predicts shifts in the relative importance of local vs. regional control of diversity along a gradient of productivity. The assumptions and predictions of the SLH are inherent to the dynamic equilibrium model (DEM; Huston 1979, 1994). The DEM predicts that diversity will be maximum at low-to-moderate productivity due to slow population dynamics and slow rates of exclusion (non-equilibrium conditions that favour invasion), but that diversity should be lowest in productive habitats because of rapid population growth and exclusion, except under conditions of suitably intense or frequent disturbance that might prevent competitive equilibrium from being reached.

In 1999 we established a propagule addition experiment in Kansas grassland to test the applicability of the NLH, SPH or SLH to plant diversity patterns along a natural gradient of standing crop (Foster 2001). In this experiment, seeds of 34 plant species were sown into field plots across this natural gradient to experimentally enhance the pool of potential colonists available to local plant neighbourhoods. In our system, local-scale species richness (1 m^2 scale) declines monotonically with increasing standing crop biomass (Foster 2001), rather than showing a unimodal pattern. Our predictions regarding how species pool enhancements (sowing) would affect diversity in undisturbed communities under assumptions of the NLH, SPH and SLH (Fig. 1) were tailored to reflect the monotonic richness-productivity relationship of our site, and are thus relevant to the declining phase of a unimodal relationship. In the context of our study, NLH predicts no change in richness in response to sowing at any undisturbed location along the standing crop gradient (Fig. 1a). The SPH predicts a measurable increase in richness in response to sowing across the entire gradient, including in sites of high standing crop (Fig. 1b). The SLH predicts that richness will increase to the greatest extent in habitats of relatively low standing crop, but that the magnitude of this enhancement effect will decline to insignificant levels as standing crop increases due to the increasing importance of local competitive exclusion (Fig. 1c). However, like the DEM, the SLH predicts that disturbance would serve to counteract competitive exclusion within sites of high potential productivity, leaving such sites open to colonization from the broader species pool. Thus, under conditions of disturbance, the SLH predicts that sowing would increase richness across the entire standing crop gradient producing an effect of sowing similar to Fig. 1(b) (SPH under non-disturbed conditions).

Results from the first 2 years of the study were consistent with the SLH (Foster 2001): in non-disturbed plots, sowing significantly enhanced richness only in unproductive sites; in disturbed plots, sowing significantly enhanced richness in both unproductive and productive sites. Our preliminary findings, however, covered a period when most of the established sown species were present as juvenile plants, and we could not rule out the possibility that our results would prove transient. A lack of persistent impacts on the community would be more consistent with the NLH.

The first aim of this study was to examine community-level responses to multispecies sowing treatments observed in the fourth year of this experiment. Because any process that alters the composition and/or diversity

Predicted effects of sowing on richness (*S*) under
non-disturbed conditions
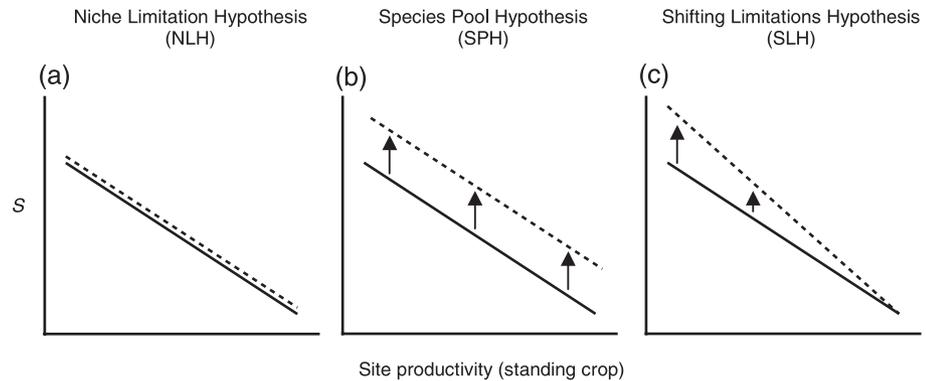
Fig. 1 Alternative predictions of the (a) NLH, (b) SPH and (c) SLH for the effects of sowing on species richness (S) in non-disturbed plots and in the context of a monotonically declining richness-productivity relationship. Solid lines represent non-disturbed, non-sown plots; dashed lines represent non-disturbed, sown plots. In plots that were experimentally disturbed, we expected sowing to increase richness significantly in all cases (NLH, SPH and the SLH), but to some unknown extent, across the entire gradient of productivity.

of a community might also feed back to alter ecosystem rates and processes (Schulze & Mooney 1993; Loreau *et al*. 2003), the second aim of the study was to evaluate the extent to which propagule limitations constrain primary production and resilience in the face of disturbance at different positions along our natural standing crop gradient. Although community ecologists often view measures of community structure as dependent variables, it has been argued that species identity and species diversity can have important feedback effects on the functional attributes of communities such as primary production, nutrient retention or ecosystem stability (Vitousek *et al*. 1987; Hobbie 1992; Schulze & Mooney 1993; Naeem *et al*. 1994; Tilman 1999; Suding *et al*. 2004). Feedback effects of key species or functional groups on ecosystem function have been well documented in a number of systems (Pastor & Post 1986; Vitousek *et al*. 1987; Wedin & Tilman 1990; Hobbie 1996; Hooper & Vitousek 1997), strengthening our appreciation of how community and ecosystem-level processes are dynamically linked. However, although supported by a number of theoretical, empirical and experimental studies (Naeem *et al*. 1994; Loreau 1998; Hector *et al*. 1999; Tilman 1999; Reich *et al*. 2001; Fridley 2003) the importance of diversity *per se* to the regulation of ecosystem function remains controversial. Regardless of these controversies, there is a need to assess whether measures of community structure are to be most profitably viewed as simple dependent variables under unidirectional control by underlying ecosystem processes and environmental conditions (Huston 1997), or whether community structure and function should be viewed as being mutually regulated by reciprocal cause and effect feedbacks (Tilman *et al*. 1996; Loreau *et al*. 2002a; Loreau *et al*. 2003).

Here we address three questions. (i) To what extent are local invasion, species composition and diversity limited by the availability of colonists (propagule pools) vs. the

availability of suitable microsites and local competitive constraints (niche availability)? (ii) Does the relative importance of propagule limitation and microsite limitation vary with habitat productivity (measured as standing crop biomass), as predicted by the SLH, or is diversity regulated in this grassland by processes more consistent with the SPH or the NLH? (iii) What are the consequences of species pool limitations for plant productivity and resilience in the face of disturbance?

Methods

STUDY SITE

This experiment was conducted at the Nelson Environmental Studies Area (NESA) of the University of Kansas. NESA is located in the prairie-forest ecotone of north-eastern Kansas, 12 km north of the city of Lawrence (39°03′ N, 95°12′ W). The experiment was established in a 20-ha field dominated by perennial grasses: *Bromus inermis* Leyss. (introduced C3 grass); *Festuca arundinaceae* Schreb. (introduced C3 grass); *Poa pratensis* L. (introduced C3 grass); and *Andropogon virginicus* L. (native C4 grass). The field is undergoing succession following abandonment in 1984 from use as a hay field and is being colonized by native plants from nearby prairie (Foster *et al*. 2002). Species richness of the site is moderate with most of the diversity determined by native and introduced perennial dicots. Topography within the site is undulating, forming the typical ridge-to-swale geomorphology of the region. Uplands include convex ridges and hill-slopes. Lowlands are gently concave, forming swales along ephemeral drainages (Kettle & Whittemore 1991). Soils are clay loam (montmorillonitic, mesic Aquic Argiudolls). Vegetation standing crop varies considerably across the site, ranging from as low as 78 g m^{-2} on upland ridges to as high as 866 g m^{-2} in low swales. The climate of the region is humid continental,

Table 1 Characteristics of sown species and their occurrence in non-sown and sown plots in 2003. Occurrence refers to the number of non-sown or sown plots (*n* = 80 for each category) where a given species was recorded in 2003. Habitat refers to the habitat type(s) in the surrounding landscape in which a given species has been recorded. Habitat classifications follow Kettle & Whittemore (1991). Taxonomy follows Great Plains Flora Association (1986)

Species	Life form**	Family	Origin†	Habitat	Seed mass (mg seed⁻¹)	Number of plots occupied	
						Non-sown	Sown
Achillea millefolium	PF	Asteraceae	N	G-O-P	0.16	1	5
Amorpha canescens	PL	Fabaceae	N	P	4.22	0	47
*Andropogon gerardi**	C4-PG	Poaceae	N	G-P	3.26	5	40
Asclepias tuberosa	PF	Asclepiadaceae	N	G-P	5.34	0	45
*Aster novae-angliae**	PF	Asteraceae	N	P	0.34	0	2
Bouteloua curtipendula	C4-PG	Poaceae	N	P	4.72	0	5
Chrysanthemum leucanthemum	PF	Asteraceae	I	P	0.62	0	0
*Dactylis glomerata**	C3-PG	Poaceae	I	G-O-F	1.12	0	1
Desmanthus illinoensis	PL	Fabaceae	N	G-P	6.30	4	57
Echinacea pallida	PF	Asteraceae	N	P	5.42	0	41
*Elymus canadensis**	C3-PG	Poaceae	N	G-P-F	4.02	0	0
Eragrostis trichodes	C3-PG	Poaceae	N	P	0.28	0	0
*Festuca arundinacea**	C3-PG	Poaceae	I	G-O	2.08	29	36
Festuca ovina	C3-PG	Poaceae	N	O	0.81	0	0
Lespedeza capitata	PL	Fabaceae	N	P	3.68	0	69
*Liatris pycnostachya**	PF	Asteraceae	N	G-P	3.24	0	0
Medicago sativa	PL	Fabaceae	I	G-O	1.92	0	0
*Melilotus officinalis**	BL	Fabaceae	I	G-O	1.94	0	1
*Monarda fistulosa**	PF	Lamiaceae	N	G-P-F	0.36	6	47
*Panicum virgatum**	C4-PG	Poaceae	N	G-P	1.46	0	25
Petalostemum candidum	PL	Fabaceae	N	P	1.15	0	8
Petalostemum purpurea	PL	Fabaceae	N	P	1.82	0	10
*Phleum pratense**	C3-PG	Poaceae	I	G-O	0.48	0	4
*Poa pratensis**	C3-PG	Poaceae	I	G-O	0.36	63	71
*Ratibida columnifera**	PF	Asteraceae	N	P	0.64	0	20
Ratibida pinnata	PF	Asteraceae	N	G-P	1.06	0	34
Rudbeckia hirta	PF	Asteraceae	N	G-O-P	0.33	0	33
Salvia azurea	PF	Lamiaceae	N	P	3.56	0	66
Schizachyrium scoparium	C4-PG	Poaceae	N	G-P	1.82	2	18
*Sorghastrum nutans**	C4-PG	Poaceae	N	P	2.24	0	50
Sporobolus cryptandrus	C4-PG	Poaceae	N	G	0.08	0	0
Trifolium pratense	PL	Fabaceae	I	G-O	1.82	0	12
Trifolium repens	PL	Fabaceae	I	G-O	0.68	5	6
*Tripsacum dactyloides**	C4-PG	Poaceae	N	O-P	86.88	4	40

*Species common to either productive lowland prairies or fertile old-fields of the region.

**P = perennial, B = biennial, L = legume, F = non-legume forb, G = grass.

†N = native, I = introduced.

G = cool-season grassland, O = successional and disturbed areas, P = Prairie, F = Forest.

with a mean annual temperature of 12.9 °C and mean annual precipitation of 930 mm. Seasonal temperature extremes are wide, with minimum temperatures in winter as low as –29 °C and maximum summer temperatures as high as 43 °C. The seasonal distribution of precipitation is unimodal, peaking in June.

EXPERIMENTAL PROCEDURE AND MEASUREMENTS

In September 1999, forty 2.5 × 2.5 m blocks, each comprised of four 1 × 1 m plots, were established throughout the 20-ha field. Block locations were selected using a stratified random approach that assured adequate representation of ridge, mid-slope and swale microsites and sampled across several microwatersheds. In each

block, 1 m² plots were separated by 0.5-m walkways. A 2 × 2 factorial set of treatments was randomly assigned to the plots in each block: two levels of seed addition of 34 grassland species (seeds sown, seeds not sown; Table 1) were employed, crossed with two levels of annual disturbance designed to remove biomass and alter microsite availability (disturbance, no disturbance). In 2000 and 2001, disturbances were applied by: (i) removing litter and scarifying the soil with a rake in January; and (ii) clipping the canopy to 15 cm height in April and June. In 2002 and 2003 the plots were clipped in April only and were not raked. Seeds were sown by hand into the appropriate plots in January 2000 (400 seeds per species). Each of the sown species is a member of the regional pool. Sown species were chosen to represent a range of life histories, functional groups, historical

origins and habitat affinities (Table 1). In the fall of 1999, prior to the addition of the seeds, 16 of the 34 sown species were found to occur naturally within the 20-ha study site, and the remaining 18 species were found in nearby old-field and prairie habitats within 2 km of the study site. Of the 16 species present within the immediate study area, nine were found to be present in at least one plot prior to sowing, but all were present at trivial levels of abundance except the C3 grasses, *Festuca arundinaceae* and *Poa pratensis*.

The plant abundance and diversity data reported here were collected during a percentage cover survey conducted in late June 2003. Calibrations of ocular cover estimates were facilitated by comparing species abundances within plots with variously sized cardboard cut-outs of known cover (ranging from 0.01 to 5% cover). Cover was evaluated for each species independently in each plot such that the sum of species cover values could exceed 100% and thus reflect multi-layering of the vegetation. Canopy interception of photosynthetically active radiation (% PAR interception) was measured in each plot in early June and late July 2003 using a 0.8-m PAR ceptometer probe (Decagon devices, Pullman, WA, USA). On each date five measurements were taken below and above the canopy within each plot so that PAR interception could be expressed as a percentage of full sun [(1–(PAR below canopy/PAR above canopy)) × 100]. Below-canopy measurements were taken just above the litter layer in order to measure light interception by the living green canopy. In mid-July, when the vegetation was at or near its peak standing crop, canopy height was measured in all plots at each of nine points in a 3 × 3 grid and then averaged to obtain a single height value for each plot.

To obtain an index of potential productivity that could be associated with each block, and used as a predictor variable, we measured above-ground standing crop in mid-July (2000–03) by clipping a 0.8 m × 1 m strip of vegetation in unmanipulated locations adjacent to each block (within 0.5 m). Each year biomass was separated into living and litter components, dried at 70 °C to constant mass and weighed. To obtain soil samples for nitrogen analysis, two 2.54 cm × 10 cm deep soil cores were taken within 0.5 m of each block in mid-June 2002. The two soil cores from each block were mixed together, air dried, and sent to the Kansas State University Soil Testing Laboratory for analysis of total soil nitrogen. Soil moisture (% volumetric) was measured within 0.5 m of each block in early June 2002 using a TRIME-FM, Time Domain Reflectometry (TDR) System (Mesa Systems Co., Medfield, MA, USA). Measurements integrated over the top 11 cm of soil were taken 3 days after a substantial rainfall event, providing measures of soil moisture near field capacity.

DATA ANALYSES

Using 2003 cover data, we calculated four measures of diversity: species richness (S), Shannon diversity (H′

Magurran 1988), community evenness (E calculated as H′/ln S), and functional group diversity (H'_{FG}). H'_{FG} was calculated as Shannon diversity using cover data aggregated by functional category (non-legume forbs, legumes, C3 grasses, C4 grasses, woody plants).

Vegetation standing crop, harvested from undisturbed locations adjacent to each block (as described above), was used as an integrative index of potential productivity for each block location along the landscape gradient, and served as an independent variable and covariate in the analyses described below. We used mean values of standing crop calculated for a given block (mean block standing crop) by averaging across the 4 years in which standing crop was harvested. This produced a stable index of relative productivity potential across the complex landscape gradient that integrated interannual variability in standing crop.

To examine the potential effects of the experimental manipulations on plant productivity within a given treatment plot, we evaluated several non-destructive measures of canopy structure and productivity taken in a plot: (i) total vegetative cover; (ii) canopy PAR interception (average of June and July measurements); (iii) mean vegetation height; and (iv) a productivity index (*PI*) derived from a principal component analysis (PCA) that included the non-destructive productivity measurements i–iii above as component variables. We used these non-destructive indicators of productivity for each individual treatment plot, rather than destructive biomass harvests, so that the study could remain ongoing.

To evaluate the effects of disturbance and sowing on measures of diversity and on the non-destructive indices of productivity, we first employed a two-factor, within-subjects analysis of variance (ANOVA) to examine effects on treatment means. We then conducted within-subjects analysis of covariance (ANCOVA) using block standing crop as a covariate to further evaluate variation in diversity and *PI* and to test the null hypothesis that the magnitude of the observed treatment effects on diversity and *PI* were constant across the natural standing crop gradient.

We applied the log transformation to block standing crop data to linearize relationships between diversity and standing crop for ANCOVA. Log transformations were also applied to the percentage cover of individual species and functional groups to reduce heteroscedasticity. All statistical analyses were performed using SPSS statistical software (version 11.5). Taxonomy follows the Great Plains Flora Association (1986).

Results

CHARACTERIZING THE COMPLEX STANDING CROP GRADIENT

To characterize the complex environmental gradient spanned by our experimental blocks, we used correlation analysis (Spearman rank correlation coefficients, r_s) to evaluate covariation in block standing crop, vegetation height (measured in control plots), total plant

Table 2 Correlation matrix (Spearman coefficients) illustrating relationships among the environmental variables. All coefficients in bold are statistically significant ($P < 0.05$)

	Standing crop	Vegetation height	Total cover	Total N	PAR interception	Soil moisture
Standing crop	1	0.17	**0.52**	**0.71**	**0.73**	**0.55**
Vegetation height		1	**0.30**	0.19	**0.33**	0.02
Total cover			1	**0.47**	**0.67**	0.25
Total N				1	**0.61**	**0.73**
PAR interception					1	**0.45**
Soil moisture						1

Table 3 Percentage cover (means ± 1 SE) of the 12 most abundant sown species, percentage cover (means ± 1 SE) of sown species in aggregate, and sown species richness (means ± 1 SE). Significant effects of disturbance or sowing ($P < 0.05$) are indicated by the letters D (disturbance) and S (sowing)

Species	–D –S	–D +S	+D –S	+D +S	Effects ($P < 0.05$)
Amorpha canscens	–	0.30 ± 0.15	–	0.53 ± 0.13	
Andropogon gerardi	–	0.67 ± 0.33	0.38 ± 0.37	3.22 ± 0.72	D
Asclepias tuberosa	–	0.18 ± 0.06	–	0.20 ± 0.05	
Desmanthus illinoensis		1.18 ± 0.45	0.35 ± 0.35	3.70 ± 1.18	D
Festuca arundinacea	3.09 ± 0.92	2.95 ± 0.72	5.75 ± 1.34	3.50 ± 1.91	
Lespedeza capitata	–	2.65 ± 0.68		9.98 ± 1.56	D
Monarda fistulosa	–	1.28 ± 1.54	0.10 ± 0.01	1.72 ± 0.42	
Poa pratensis	7.06 ± 1.39	6.60 ± 1.04	6.05 ± 1.01	4.55 ± 0.86	D
Ratibida columnifera	–	0.10 ± 0.01	–	0.85 ± 0.25	D
Salvia azurea	–	1.80 ± 0.32	–	4.10 ± 0.66	D
Sorghastrum nutans	–	0.78 ± 0.22	0.23 ± 0.23	3.66 ± 0.67	D
Tripsacum dactyloides	–	4.06 ± 1.03	0.57 ± 0.38	4.84 ± 1.29	–
Sown species cover (in aggregate)	10.36 ± 1.47	23.47 ± 2.85	13.66 ± 2.32	47.67 ± 3.45	D, S, D × S
Sown species richness	0.76 ± 0.42	6.17 ± 0.61	0.30 ± 0.11	10.67 ± 0.44	D, S

cover (measured in control plots), total soil nitrogen, PAR interception (measured in control plots), and soil moisture (Table 2). Among these variables, the only non-significant correlations were the relationships of vegetation height to soil nitrogen, soil moisture and block standing crop, and the relationship between soil moisture and total cover (Table 2). All other variables were significantly positively correlated. The positive association of standing crop to all but one variable indicates that standing crop is a suitable integrative index of site conditions and potential productivity along the natural landscape gradient.

RESPONSES OF SOWN SPECIES

In 2003, 27 of the 34 sown species were recorded in at least one of the 160 plots (Table 1). Of these 27, all occurred more frequently in sown than non-sown plots, and 18 were exclusive to sown plots. The total number of sown species occurrences in the 80 sown plots (793) was 6.7 times greater than in the 80 non-sown plots (119). Of the 119 occurrences in non-sown plots, 92 are attributed to the abundant C3 grasses, *F. arundinaceae* and *P. pratensis*, which were present in many of these plots prior to the start of the study.

Of the 12 most abundant sown species, the percentage cover of six showed significant positive responses to

disturbance (Table 3), while a seventh, *Poa pratensis*, showed a significant negative response. Only two sown species, *F. arundinaceae* and *P. pratensis*, were abundant enough in non-sown plots to test for a mean effect of sowing on cover, and neither showed such an effect.

The mean aggregate cover and mean richness of sown species was increased significantly by both disturbance and by sowing (Table 3). A significant disturbance by sowing interaction indicated that sowing had increased mean sown species cover to a greater extent in disturbed plots (effect of sowing in disturbed plots, $F_{1,39} = 101.11$, $P < 0.001$; effect of sowing in non-disturbed plots, $F_{1,39} = 52.80$, $P < 0.001$). In sown plots, the richness of sown species declined significantly with increasing block standing crop in both the non-disturbed and disturbed plots (Fig. 2). However, a significant disturbance–standing crop interaction indicated that the slope of this relationship was made significantly less negative by disturbance, reflecting an increase in sown species richness in response to disturbance that increased in magnitude as block standing crop increased.

SPECIES DIVERSITY: MEAN EFFECTS

As evaluated by simple two-factor ANOVA, mean species richness (S), evenness (E) and Shannon diversity (H') were all increased significantly by disturbance and
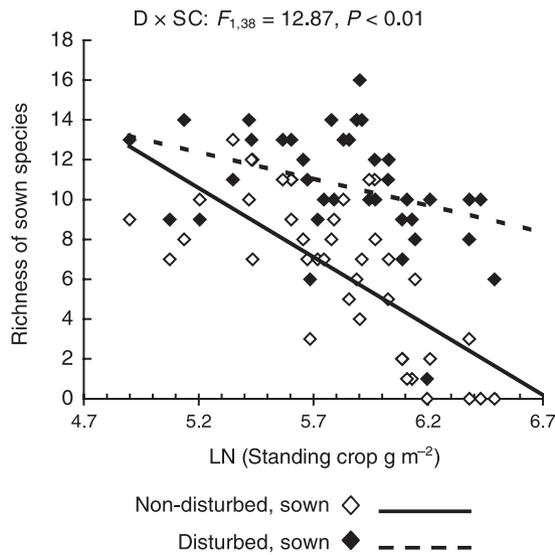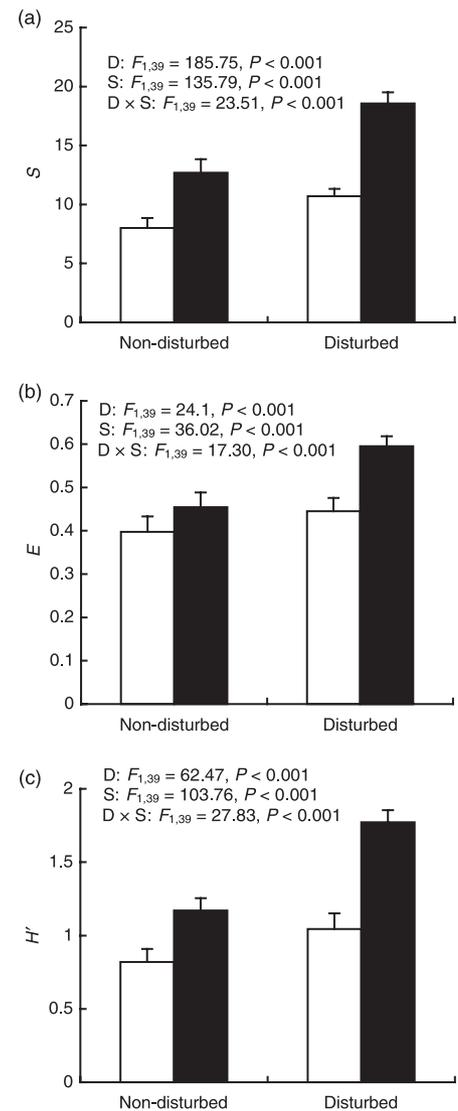
Fig. 2 Sown species richness as a function of block standing crop in non-disturbed plots ($r^2 = 0.52$, $P < 0.001$) and disturbed plots ($r^2 = 0.15$, $P < 0.05$).

Fig. 3 Mean (+ 1 SE) response of (a) species richness (S), (b) evenness (E) and (c) Shannon diversity (H') to disturbance and sowing. Open bars represent non-sown plots, filled bars represent sown plots.

sowing (Fig. 3). Significant interactions between disturbance and sowing indicated that sowing had increased mean S, E and H' more in disturbed than non-disturbed plots (effect of sowing on S in disturbed plots, $F_{1,39} = 207.87$, $P < 0.001$; effect of sowing on S in non-disturbed plots, $F_{1,39} = 66.44$, $P < 0.001$; effect of sowing on E in disturbed plots, $F_{1,39} = 42.4$, $P < 0.001$; effect of sowing on E in non-disturbed plots, $F_{1,39} = 5.99$, $P < 0.05$; effect of sowing on H' in disturbed plots, $F_{1,39} = 108.36$, $P < 0.001$; effect of sowing on H' in non-disturbed plots, $F_{1,39} = 37.71$, $P < 0.001$). These interactions also indicate that disturbance had increased diversity more in sown than non-sown plots (effect of disturbance on S in sown plots, $F_{1,39} = 101.11$, $P < 0.001$; effect of disturbance on S in non-sown plots, $F_{1,39} = 52.80$, $P < 0.001$; effect of disturbance on E in sown plots, $F_{1,39} = 37.62$, $P < 0.001$; effect of disturbance on E in non-sown plots, $F_{1,39} = 4.76$, $P < 0.05$; effect of disturbance on H' in sown plots, $F_{1,39} = 63.49$, $P < 0.001$; effect of disturbance on H' in non-sown plots, $F_{1,39} = 21.94$, $P < 0.001$).

SPECIES DIVERSITY: EFFECTS ALONG THE STANDING CROP GRADIENT

In general, sowing enhanced diversity (S, E, H') in undisturbed plots to a greater extent in blocks of low standing crop than in blocks of high standing crop. In disturbed plots, however, sowing tended to increase diversity to a similar extent across the entire standing crop gradient (Fig. 4).

Species richness (S) declined significantly with increasing block standing crop, but with a slope that varied significantly among treatments (three-way interaction; Fig. 4a). In the absence of disturbance, this slope was made significantly more negative by sowing, reflecting

an increase in richness in response to sowing that decreased in magnitude as block standing crop increased (sowing by standing crop interaction, $F_{1,38} = 12.89$, $P < 0.01$). In the presence of disturbance, sowing had no effect on the slope of the relationship, reflecting an increase in richness in response to sowing that did not vary in magnitude with standing crop (sowing by standing crop interaction, $F_{1,38} = 2.17$, $P > 0.05$). In both non-sown and sown plots the slope of the richness–standing crop relationship was made significantly less negative by disturbance, reflecting an increase in richness in response to disturbance that increased in magnitude with block standing crop (disturbance by standing crop interaction for non-sown plots, $F_{1,38} = 7.18$, $P < 0.05$; disturbance by standing crop interaction for sown plots, $F_{1,38} = 8.86$, $P < 0.01$).

Evenness (E) varied significantly with block standing crop in all four treatments (Fig. 4b); however, these
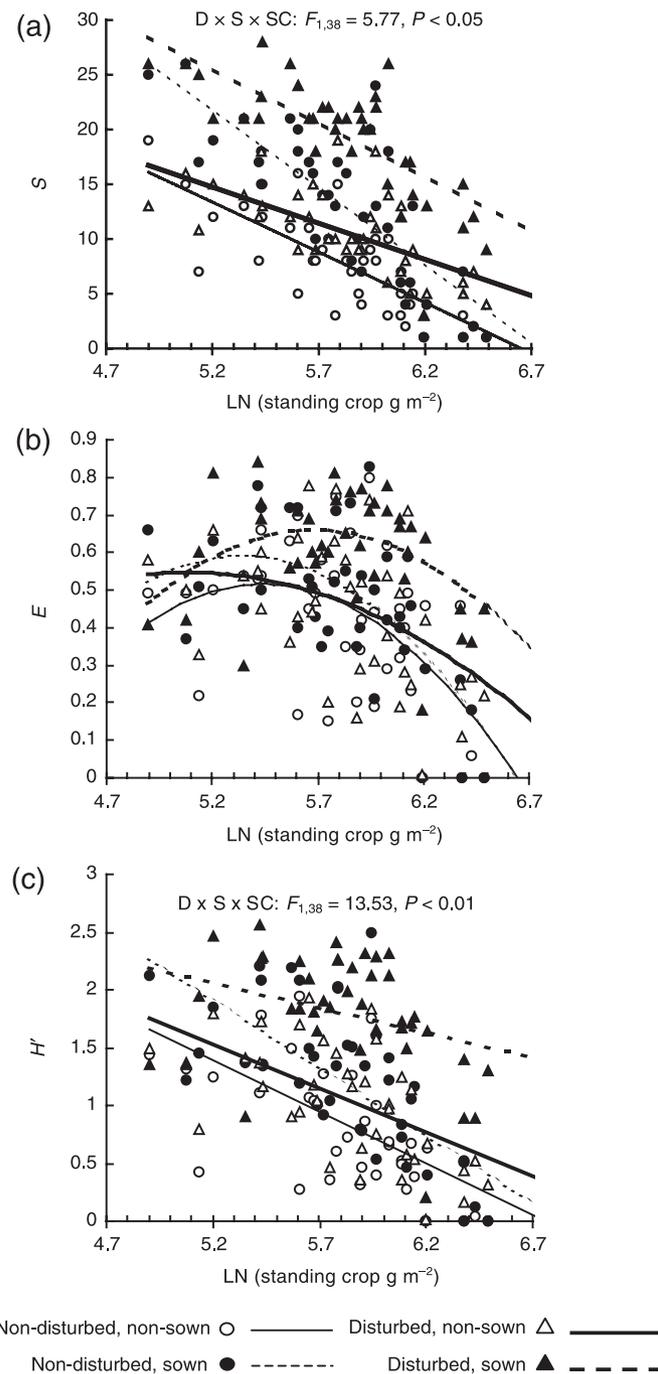
Fig. 4 Species richness (a), evenness (b) and Shannon Diversity (c) as a function of block standing crop at all levels of disturbance and sowing (*S* in non-disturbed, non-sown plots, $r^2 = 0.62$, $P < 0.001$; *S* in non-disturbed, sown plots, $r^2 = 0.66$, $P < 0.001$; *S* in disturbed, non-sown plots, $r^2 = 0.44$, $P < 0.001$; *S* in disturbed, sown plots, $r^2 = 0.54$, $P < 0.001$; *E* in non-disturbed, non-sown plots, $r^2 = 0.37$, $P < 0.001$; *E* in non-disturbed, sown plots, $r^2 = 0.54$, $P < 0.001$; *E* in disturbed, non-sown plots, $r^2 = 0.24$, $P < 0.01$; *E* in disturbed, sown plots, $r^2 = 0.25$, $P < 0.01$; *H'* in non-disturbed, non-sown plots, $r^2 = 0.40$, $P < 0.001$; *H'* in non-disturbed, sown plots, $r^2 = 0.50$, $P < 0.001$; *H'* in disturbed, non-sown plots, $r^2 = 0.32$, $P < 0.01$; *H'* in disturbed, sown plots, $r^2 = 0.12$, $P < 0.05$).

relationships were strongly non-linear. Polynomial regression showed that evenness peaked either at low-intermediate or intermediate standing crop depending on the treatment. Because of these strong non-linearities, ANCOVA could not be used to evaluate interactions of sowing and disturbance with standing crop. Instead, we used an alternative approach to test the null hypothesis that the effect of sowing on evenness did not differ

between low and high standing crop. We divided blocks into low and high standing crop categories, with the dividing point determined by the median level of standing crop (365 g m^{-2}). This division resulted in fairly equal sample sizes for each category (low standing crop, *n* = 19; high standing crop, *n* = 21). Using this approach, we found that in the absence of disturbance, sowing significantly increased evenness at low standing crop ($F_{1,18}$ =

4.86, $P < 0.05$), but had no significant effect at high standing crop ($F_{1,20} = 1.89$, $P > 0.05$). In the presence of disturbance, sowing significantly increased evenness at low and high standing crop (low standing crop, $F_{1,18} = 8.20$, $P < 0.05$; high standing crop, $F_{1,20} = 55.48$, $P < 0.001$).

Shannon diversity (H') declined significantly and linearly with block standing crop, but with a slope that varied significantly among treatments (three-way interaction; Fig. 3c). In the absence of disturbance, this slope was made significantly more negative, reflecting an increase in H' in response to sowing that declined in magnitude as standing crop increased (sowing by standing crop interaction: $F_{1,38} = 4.49$, $P < 0.05$). In the presence of disturbance, sowing had no effect on the relationship, reflecting an increase in H' in response to sowing that did not vary in magnitude with standing crop (sowing by standing crop interaction, $F_{1,38} = 2.69$, $P > 0.05$). In the absence of sowing, the slope of the H'– standing crop relationship did not differ significantly between disturbed and non-disturbed plots (disturbance by standing crop interaction, $F_{1,38} = 1.11$, $P > 0.05$), reflecting an increase in H' in response to disturbance that did not vary in magnitude with block standing crop. In the presence of sowing, this slope was made significantly less negative by disturbance (sowing by standing crop interaction, $F_{1,38} = 21.42$, $P < 0.001$), reflecting an

increase in H' in response to disturbance that increased in magnitude as block standing crop increased.

FUNCTIONAL GROUPS: ABUNDANCE

Using simple two-factor ANOVA, we found that the mean, aggregate cover of the four dominant functional groups, was significantly affected by sowing or by both sowing and disturbance (Fig. 5a). Mean cover of forbs was significantly increased by sowing, whereas C3 grasses were significantly reduced by both disturbance and sowing. The mean cover of C4 grasses was increased significantly by disturbance and sowing; however, sowing had a greater effect in disturbed plots (disturbance– sowing interaction; effect of sowing in disturbed plots, $F_{1,39} = 20.72$, $P < 0.001$; effect of sowing in non-disturbed plots, $F_{1,39} = 10.22$, $P < 0.001$). The mean cover of legumes showed the same pattern as C3 grasses (disturbance–sowing interaction; effect of sowing in disturbed plots, $F_{1,39} = 48.63$, $P < 0.001$; effect of sowing in non-disturbed plots, $F_{1,39} = 19.10$, $P < 0.001$).

FUNCTIONAL GROUPS: DIVERSITY

Mean functional group diversity (H'_{FG}) was increased significantly by both disturbance and sowing (Fig. 5b),
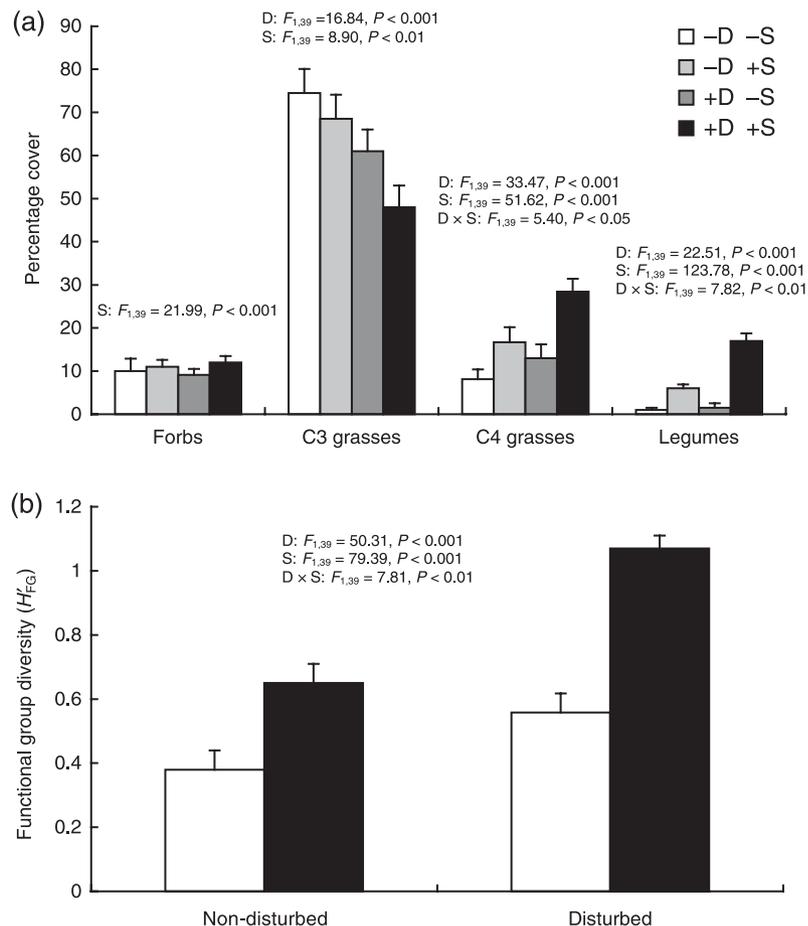
Fig. 5 Mean (+ 1 SE) response of the four dominant functional groups (a) and functional group diversity (b) to disturbance and sowing. In panel (b) open bars represent non-sown plots, filled bars represent sown plots.
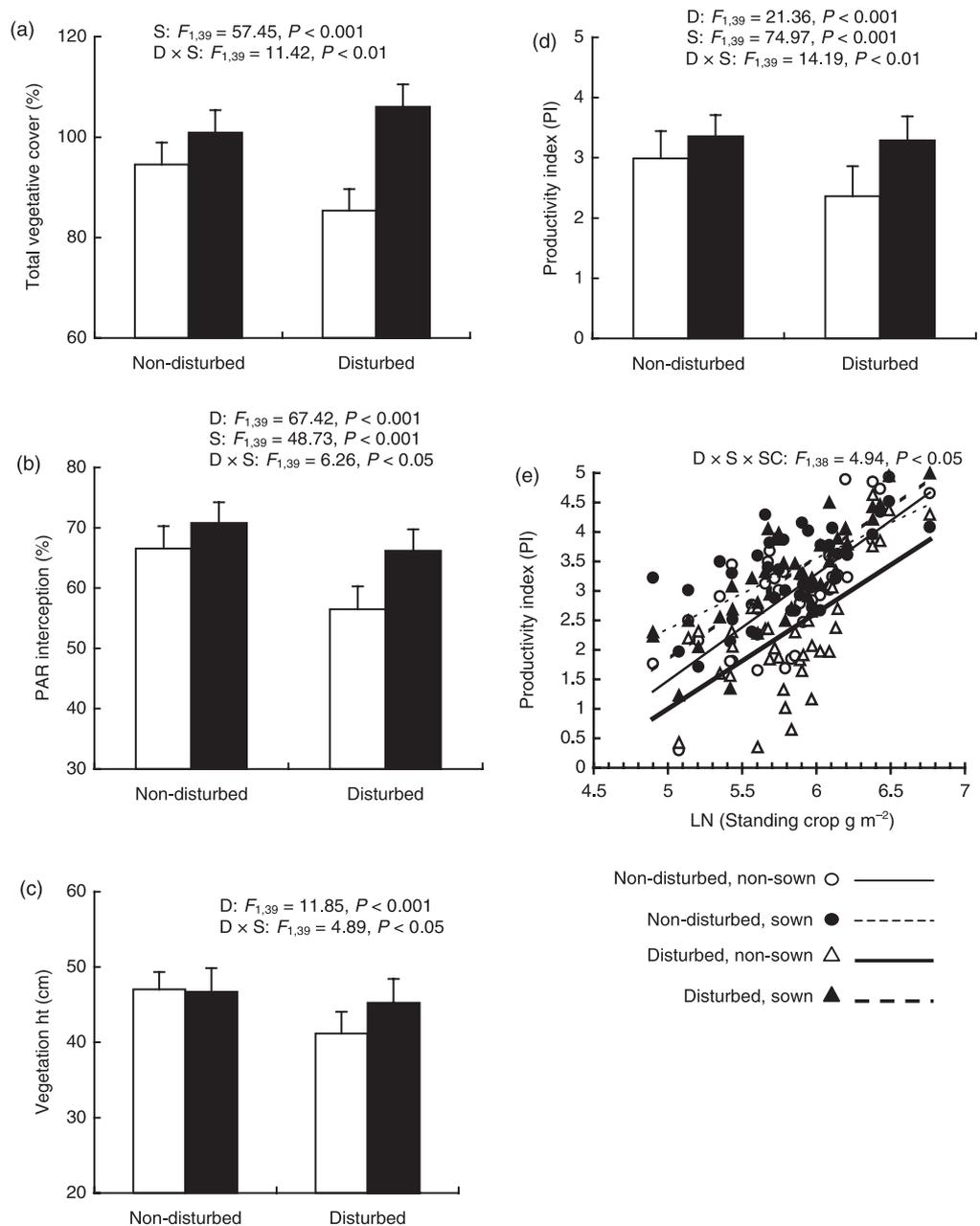
Fig. 6 (a–d) Mean (+ 1 SE) response of four productivity measures to disturbance and sowing: (a) total vegetative cover, (b) canopy PAR interception, (c) vegetation height, and (d) productivity index (*PI*) derived from PCA. Open bars represent non-sown plots, filled bars represent sown plots. (e) *PI* as a function of block standing crop at all levels of disturbance and sowing (non-disturbed, non-sown plots, $r^2 = 0.54$, $P < 0.001$; non-disturbed, sown plots, $r^2 = 0.38$, $P < 0.001$; disturbed, non-sown plots, $r^2 = 0.40$, $P < 0.001$; disturbed, sown plots, $r^2 = 0.67$, $P < 0.001$).

with a greater effect of sowing in the disturbed plots (disturbance–sowing interaction; effect of sowing in disturbed plots, $F_{1,39} = 54.89$, $P < 0.001$; effect of sowing in non-disturbed plots, $F_{1,39} = 21.23$, $P < 0.001$).

PRODUCTIVITY RESPONSES: MEAN EFFECTS

Mean, total vegetative cover was increased significantly by sowing (Fig. 6a). An interaction between disturbance and sowing indicated that sowing increased total cover to a greater extent in disturbed than non-disturbed plots (effect of sowing in disturbed plots, $F_{1,39} = 49.37$, $P <$

0.001; effect of sowing in non-disturbed plots, $F_{1,39} = 6.07$, $P < 0.05$) and that disturbance reduced total cover only in the absence of sowing (effect of disturbance in non-sown plots, $F_{1,39} = 49.37$, $P < 0.001$; effect of disturbance in sown plots, $F_{1,39} = 1.92$, $P > 0.05$).

Mean PAR interception was increased significantly by sowing, but decreased significantly by disturbance (Fig. 6b). An interaction between disturbance and sowing indicated that sowing increased mean PAR interception to a greater extent in disturbed than non-disturbed plots (effect of sowing in disturbed plots, $F_{1,39} = 32.12$, $P < 0.001$; effect of sowing in non-disturbed

plots, $F_{1,39} = 12.20$, $P < 0.01$) and that disturbance reduced mean PAR interception to a greater extent in non-sown than sown plots (effect of disturbance in non-sown plots, $F_{1,39} = 48.80$, $P < 0.001$; effect of disturbance in sown plots, $F_{1,39} = 11.18$, $P < 0.01$).

A significant interaction between disturbance and sowing for mean vegetation height reflected a positive effect of sowing on mean vegetation height (Fig. 6c) that was manifested only in the disturbed plots (effect of sowing in disturbed plots, $F_{1,39} = 6.32$, $P < 0.05$; effect of sowing in non-disturbed plots, $F_{1,39} = 0.42$, $P > 0.05$) and a negative effect of disturbance that was manifested only in non-sown plots (effect of disturbance in non-sown plots, $F_{1,39} = 22.36$, $P < 0.001$; effect of disturbance in sown plots, $F_{1,39} = 0.77$, $P > 0.05$).

The first principal component (PC1), derived from a PCA of the three non-destructive productivity measures explained 58.5% of the variance in the data. Each productivity variable was positively loaded and significantly correlated with PC1 (vegetative cover, $r = 0.91$, $P < 0.001$; PAR interception, $r = 0.92$, $P < 0.001$; vegetation height, $r = 0.26$, $P < 0.001$). PC1 represents a contrast between sites of low cover, low PAR interception and low vegetation height vs. sites of high cover, high PAR interception and high vegetation height. Because of this contrast, and because of a strong correlation between this PCA axis and block standing crop (see below) we used PC1 as an integrative productivity index (*PI*) and response variable in the analyses that follow.

Mean *PI* was increased significantly by sowing (Fig. 6d). An interaction between disturbance and sowing indicated that sowing increased mean *PI* to a greater extent in disturbed than non-disturbed plots (effect of sowing in disturbed plots, $F_{1,39} = 60.33$, $P < 0.001$; effect of sowing in non-disturbed plots, $F_{1,39} = 16.92$, $P < 0.01$) and that disturbance decreased mean *PI* significantly only in non-sown plots (effect of disturbance in non-sown plots, $F_{1,39} = 35.72$, $P < 0.001$; effect of disturbance in sown plots, $F_{1,39} = 0.41$, $P > 0.05$).

PRODUCTIVITY RESPONSES: EFFECTS ALONG THE STANDING CROP GRADIENT

In general, sowing enhanced *PI* in undisturbed plots to a greater extent in blocks of low standing crop than in blocks of high standing crop. In disturbed plots, however, sowing tended to increase *PI* to a similar extent across the entire standing crop gradient (Fig. 6e).

PI increased significantly and linearly with block standing crop, but with a slope that varied among treatments (Fig. 6e; three-way interaction). In the absence of disturbance, the slope of the *PI*-standing crop relationship was made significantly less positive by sowing, reflecting an increase in *PI* in response to sowing that declined in magnitude as standing crop increased (sowing by standing crop interaction, $F_{1,38} = 8.61$, $P < 0.01$). In the presence of disturbance, sowing had no effect on the slope, reflecting an increase in *PI* in response to sowing that did not vary across the gradient (sowing by

standing crop interaction, $F_{1,38} = 0.14$, $P > 0.05$). In the absence of sowing, disturbance had no effect on the slope, reflecting a decrease in *PI* in response to disturbance that did not vary in magnitude across the gradient (disturbance by standing crop interaction, $F_{1,38} = 0.46$, $P > 0.05$). In the presence of sowing, the slope of the *PI*-standing crop relationship was made significantly more positive by disturbance (disturbance by standing crop interaction, $F_{1,38} = 4.49$, $P < 0.05$).

Discussion

Results reported here support the initial findings of Foster (2001) that richness was seed limited in unproductive sites, but microsite limited in productive sites, thus supporting the SLH. Results after four growing seasons demonstrate that the initially observed effects of sowing on richness have been retained. Unlike the first two growing seasons, when only a few of the sown species exceeded trivial levels of abundance, many of these species had become quite abundant by year four, particularly at low-to-moderate standing crop and under conditions of disturbance. The invasion and subsequent growth of sown species led to substantial changes in the community beyond confirmation of initial changes in richness, including increases in equitability among species (community evenness), Shannon diversity, functional diversity and ecosystem productivity, the magnitude of which varied across our complex gradient of standing crop and in response to disturbance. In total, our results are consistent with the view that community processes and ecosystem functions are dynamically linked and act reciprocally to constrain each other (Loreau *et al*. 2003).

CONTROLS ON SPECIES DIVERSITY

Initial evidence in support of the SLH was correlative and came from an evaluation by Huston (1999) of data obtained from a descriptive study conducted in Estonia (Pärtel *et al*. 1996). These analyses showed that local richness increased as a linear function of regional richness across a range of unproductive communities, but showed an asymptotic relationship across a range of highly productive communities. These patterns suggested that regional controls over local diversity predominate in unproductive communities, but that local processes, presumably competition, predominate in productive communities. A more thorough analysis of these same data (Pärtel *et al*. 2000) produced the same general conclusions.

Such descriptive approaches that evaluate empirical relationships between small- and large-scale richness patterns are fraught with statistical problems and have confounding interpretations (Leps 2001; Wilson & Anderson 2001), and are thus of limited value in examining the influence of species pools. Although sowing experiments are not without their own set of shortcomings, they have been used as an alternative approach to

examine the importance of species pool limitation by providing an opportunity to manipulate the availability of species to local plant neighbourhoods.

Sowing experiments by Tilman (1997), Zobel *et al.* (2000) and Foster & Tilman (2003) all showed significant propagule limitations of richness in unproductive grasslands, consistent with the prediction of SLH that relatively low productivity systems should be unsaturated. Lord & Lee (2001) conducted a sowing experiment in highly productive sedge tussock communities of New Hampshire and also produced results consistent with the SLH. However, our sowing experiment is the first to experimentally test the role of propagule availability in limiting diversity across a wide range of productivity levels as is required to test the SLH. As predicted by the SLH, we found that under non-disturbed conditions both components of species diversity (*S* and *E*) were increased by the experimental enhancement of colonists across much of the standing crop gradient, with the exception of the most productive sites. Evidence that control of diversity in undisturbed sites shifted from propagule limitation to competitive exclusion or microsite limitation as standing crop increased is provided by our finding that *S*, *E* and *H'* were increased by sowing within sites of high inherent productivity only under conditions of canopy disturbance and enhanced light availability.

CONTROLS ON ECOSYSTEM FUNCTION

Plant productivity, measured as above-ground standing crop, varies over an order of magnitude at our study site, reflecting the dominant impact of the underlying soil resource-topographic gradient in regulating spatial variation in primary production. However, we found that alterations in species composition and diversity produced by sowing were accompanied by increases in local plant production across much of the natural gradient. These findings suggest that although underlying abiotic conditions and resource levels may determine the maximum potential productivity of a given patch, the productivity level actually realized in a patch may also depend upon propagule availability, local diversity or the particular species present to exploit available resources.

Through what mechanism did sowing lead to increased production in this experiment? Can we explain this result in terms of the diversity-productivity hypothesis (Johnson *et al.* 1996; Tilman *et al.* 1996; Loreau *et al.* 2002b) and attribute enhanced production directly to the greater diversity achieved in our plots? Our findings are certainly consistent with this hypothesis and with the findings of experimental studies that have shown a positive effect of local plant diversity on ecosystem processes under conditions where diversity was experimentally manipulated (Tilman *et al.* 1996; Hector *et al.* 1999; Tilman 1999; Reich *et al.* 2001). In this light, we might interpret our results in terms of the sampling probability effect (Huston 1997; Wardle 1999;

Ruijven & Berendse 2003; Smith & Knapp 2003) and argue that by exposing our plots to a more diverse array of potential colonists than is typically found in the propagule rain to local plant neighbourhoods we increased the probability that highly productive species or functional traits would be represented. Of the 34 species sown into our plots, 14 were found in at least one sown plot at covers exceeding 5%, and thus all may have contributed to increases in community productivity to some extent. However, we can identify key species that were particularly abundant and whose contributions to productivity might be interpreted in the context of a sampling effect. For example, the most frequent and locally abundant sown species was a legume, *Lespedeza capitata*. This species was present in all but 11 sown plots, with a mean cover of 5.9% and a maximum value of 38%. Beyond the contribution of its own biomass, it is possible that *L. capitata*, a nitrogen-fixer, could have contributed indirectly to enhanced productivity by providing extra nitrogen to neighbouring plants. Legumes have been singled out as contributing disproportionately to increased productivity through a sampling probability effect in biodiversity-ecosystem function studies (Ruijven & Berendse 2003).

The sampling probability effect, inherent to a number of biodiversity-ecosystem function experiments, has been criticized as a sampling artifact because unlike in natural communities, gradients of diversity in these experiments were synthesized through the random selection of species from defined species pools (Aarssen 1997; Huston 1997; Wardle 1999). However, community assembly as it occurs in nature is a distinctly non-random phenomenon that selects community members from a broader propagule pool in a manner biased by natural ecological sorting processes (Grime 1998; Huston *et al.* 2000; Smith & Knapp 2003). Our results differ from previous biodiversity-ecosystem function experiments because they show that both local biodiversity and productivity can be enhanced by the biased sampling of a defined propagule pool occurring via local biotic sorting, rather than by randomized selection of species carried out by the experimenter. We suggest that this effect, emerging through natural community assembly, constitutes a legitimate ecological sampling effect, and as such, illuminates an important role of biodiversity at the scale of the broader regional propagule pool in mediating ecosystem processes at the local scale. This interpretation is consistent with the argument of Grime (1998) that filter and founder effects, which depend upon the regional reservoir of potential colonists, can be important in governing ecosystem function instead of, or in addition to, the more immediate and local effects of extant diversity that might occur via local niche complementarity.

With this in mind, our results do provide some evidence that functional complementarity among extant sown and non-sown species contributed to the enhancement of productivity in our sown plots. Although moderately diverse and inhabited by a range of life-forms,

this grassland is largely dominated by C3 grasses. Sowing increased the abundance of forbs, legumes and C4 grasses (Fig. 5a), and increased functional diversity (Fig. 5b), potentially complementing the dominant C3 grasses. The increase in functional diversity in response to sowing, which was particularly strong under conditions of disturbance, can be partially explained by the increased abundance of forbs, legumes and C4 grasses, but also by a reduction in dominance by the resident C3 grasses, which most likely occurred as a result of competitive suppression. It is instructive to note that none of the five non-resident C3 grasses sown into this experiment invaded effectively (Table 1), perhaps due to the close functional similarity of these species to the dominant residents.

Our results also suggest that enhanced propagule availability, and the greater species and functional diversity associated with it, can impart enhanced resilience to the community in response to disturbance. As shown in Fig. 6, canopy disturbance, applied early in the growing season, led to a significant decline in each of the four indices of plant production in non-sown plots. However, in the more diverse sown plots, disturbance either had no effect on productivity or it reduced productivity to a significantly lesser extent than observed in the non-sown plots. Apparently then, the more diverse communities in sown plots possessed on average a greater capacity to compensate for the loss of canopy biomass. We believe that this increased resilience stems from the greater presence of species in sown plots that possess a capacity for active growth during the warmer months (particularly C4 grasses) when the dominant C3 grasses are inactive and are least able to contribute to canopy recovery. This result is consistent with the diversity-stability hypothesis (Elton 1958; Goodman 1975; McNaughton 1977; Tilman & Downing 1994; Lehman & Tilman 2000), but additionally echoes Loreau *et al.* (2003), who argued that increases in local diversity linked to enhanced immigration among patches within meta-communities provides enhanced opportunities for functional compensation in the face of perturbation.

THE SUCCESSIONAL CONTEXT

Because our experiment was conducted in a successional grassland, in the process of recovery from past agricultural use (18 years post-abandonment), we may ask whether our results are unique to degraded systems or whether they may also apply to less disturbed, more diverse native grasslands. Because colonization from distant source pools is fundamental to succession (Cooper 1923; McDonnell & Stiles 1983; Pickett *et al.* 1987; Wood & del Moral 1987; Tilman 1993), it is in recovering successional systems such as ours that we might expect diversity and ecosystem function to be most strongly limited by species availability. Several studies of succession have illustrated the steady accumulation of species and vegetative cover and/or biomass with time (Keever 1983; Inouye *et al.* 1987) consistent with

propagule limitation of diversity and ecosystem function. For example, across a chronosequence of old-fields at Cedar Creek, Minnesota, richness, vegetative cover and total soil nitrogen increase with field age (Inouye *et al.* 1987; Knops & Tilman 2000). At Cedar Creek, key functional groups associated with changes in ecosystem function include the C4 prairie grasses and legumes, which are poorly dispersed and slow to colonize abandoned fields (Tilman 1993; Knops & Tilman 2000). As a result, dispersal limitations translate into constraints on the rate of recovery of community and ecosystem processes, a scenario that may apply to our system as it recovers from its previous agricultural use.

The management history of our study site may also partly explain its invasibility and susceptibility to community change once constraints to propagule availability have been relaxed. The history of haying at our site resulted in dominance by a single functional group (planted C3 grasses). As a result, resources may be under-utilized in many locations in this grassland, leaving them open to exploitation by complementary invaders. This possibility is supported by our findings that many locations were open to invasion by species from initially under-represented functional groups (particularly C4 grasses and legumes), but not by the non-resident C3 grasses that were sown into the plots. This scenario apparently does not apply to the more productive locations in our grassland that are resistant to invasion unless disturbed (Foster *et al.* 2002).

Although successional status and management history could partly explain our findings, we note that the sowing experiments of Tilman (1997), Zobel *et al.* (2000) and Foster & Tilman (2003) all found positive effects of sowing on richness in native, non-successional, grasslands, suggesting that propagule limitations of diversity may be general to a wide range of unproductive grasslands and not unique to successional systems. In addition to our study, Tilman (1997) provides evidence that propagule limitation of productivity may not be unique to successional systems either, by showing effects of sowing on vegetative cover in nutrient-poor savanna. The study of Wilsey & Polley (2003), which was specifically designed to examine effects of propagule limitation on diversity and community biomass in native Texas grasslands, found no such effect on productivity. It is thus unclear under what set of conditions we would expect local productivity to be constrained by seed availability in unproductive grasslands.

Overall, our results support the shifting limitations hypothesis and suggest that landscape gradients in local plant diversity should reflect shifts in the regulatory significance of local ecological processes and species pools as one moves from habitats of inherently low to inherently high productivity. Our findings also support the view that propagule pools can feed back to influence ecosystem processes by mediating community assembly, by determining the availability of key species, and by governing opportunities for functional compensation within the community.

Acknowledgements

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