

## Patterns of species density and productivity at different spatial scales in herbaceous plant communities

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A major challenge in evaluating patterns of species richness and productivity involves acquiring data to examine these relationships empirically across a range of ecologically significant spatial scales. In this paper, we use data from herb-dominated plant communities at six Long-Term Ecological Research (LTER) sites to examine how the relationship between plant species density and above-ground net primary productivity (ANPP) differs when the spatial scale of analysis is changed. We quantified this relationship at different spatial scales in which we varied the focus and extent of analysis: (1) among fields within communities, (2) among fields within biomes or biogeographic regions, and (3) among communities within biomes or biogeographic regions. We used species density ( $D$  = number of species per  $m^2$ ) as our measure of diversity to have a comparable index across all sites and scales. Although we expected unimodal relationships at all spatial scales, we found that spatial scale influenced the form of the relationship. At the scale of fields within different grassland communities, we detected a significant relationship at only one site (Minnesota old-fields), and it was negative linear. When we expanded the extent of analyses to biogeographic regions (grasslands or North America), we found significant unimodal relationships in both cases. However, when we combined data to examine patterns among community types within different biogeographic regions (grassland, alpine tundra, arctic tundra, or North America), we did not detect significant relationships between species density and ANPP for any region. The results of our analyses demonstrate that the spatial scale of analysis – how data are aggregated and patterns examined – can influence the form of the relationship between species density and productivity. It also demonstrates the need for data sets from a broad spectrum of sites sampled over a range of scales for examining challenging and controversial ecological hypotheses.

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The resurgence of interest in the processes determining the relationship between species richness and productivity has highlighted the importance of considering the effect of spatial scale on these patterns (Rosenzweig 1995, Waide et al. 1999, Mittelbach et al. unpubl.). The relationship is generally expected to be “hump-shaped” or unimodal, particularly in plant communities (Grime

1973, Tilman and Pacala 1993, Huston 1994, 1999), except across broad geographic gradients when positive linear relationships generally are observed most commonly (Currie 1991, Rosenzweig 1995).

Huston (1999) recently has argued that a unimodal relationship is a “ubiquitous multiscale pattern” and is expected “... at scales ranging from over a few meters,

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over which lawn fertility and species richness vary consistently, to the entire globe ...". Although unimodal patterns have been detected at a variety of scales, a recent literature review by Mittelbach et al. (unpubl.) has shown that the predominant form of the relationship between species richness and productivity depends on the ecological and spatial scale examined. For terrestrial plants, they found that hump-shaped relationships were the predominant pattern in studies that made comparisons among community types sampled at regional or smaller scales (<4000 km) or across community types. In studies that focused on a single community type, unimodal, monotonically increasing and decreasing patterns were equally prevalent in the literature (Mittelbach et al. unpubl.).

It is extremely difficult to evaluate how different aspects of spatial scale influence the relationship between productivity and species richness from a literature survey. Discerning these patterns from the literature is hampered because methods differ among studies and often the necessary original data are not provided. Moreover, combining data from studies using different methodologies can confound patterns if these relationships are scale-dependent (cf. Pastor et al. 1996, Scheiner et al. 2000). Relatively few studies have explicitly examined how combining data at different scales of spatial aggregation can influence the relationship between species richness and productivity (see Moore and Keddy 1989, Ter Heerdt et al. 1991), and these have found that the pattern varies with scale.

To determine how spatial scale of analysis affects the relationship between productivity and species richness, data are needed from studies that both encompassed a wide geographic area and that included detailed sampling at the local scale. Because of the accessibility of data, comparability of measurements, and distribution of sites, the Long-Term Ecological Research (LTER) network in the USA provided an excellent source of data for such an analysis (Franklin et al. 1990, Ingersoll et al. 1997). We obtained data on plant species composition and productivity for herb-dominated plant communities from six LTER sites (Table 1) across which annual primary productivity and the climatic controls on primary productivity differ (Leith 1975, Foley 1994). Having original data from these sites allowed us to examine the relationship between plant species richness and productivity at different spatial scales by varying the focus (spatial scale at which the data are aggregated) or extent (scale over which the pattern is evaluated) of analysis.

Our goals were to quantify the form of the relationship between species density and productivity in a variety of herb-dominated plant communities and to determine whether this pattern was consistent across a range of spatial and ecological scales. Documenting the form of this relationship along natural productivity gradients at these different sites also provided impor-

tant information necessary for the interpretation of fertilization studies conducted at these same sites. A meta-analysis of the effect of experimental fertilization on species density and productivity in different fields at these same sites is presented in a companion paper (Gough et al. 2000).

## Methods

### The sites

Our analyses are based on data from herbaceous plant communities at six LTER sites: Cedar Creek (CDR), Kellogg Biological Station (KBS), Short Grass Steppe (SGS), Konza Prairie (KNZ), Arctic Tundra (ARC), and Niwot Ridge (NWT). Detailed descriptions of these sites can be found at the LTER Network web site (<http://lternet.edu>). We selected these sites because they had data and metadata on plant species composition and productivity of communities dominated by herbaceous, perennial vascular plants at several spatial scales. Consequently our analyses focus on comparisons within and among communities dominated by a similar life form. Although the disturbance regimes at these sites differed (e.g. burning, light to moderate grazing), we did not include disturbance type as a factor in our analyses because replication of each disturbance regime was insufficient across sites for a meaningful analysis.

For each site, we obtained data either for replicate fields of one community type or for different community types that were representative of the natural gradient of productivity at that site (see Table 1). The number of community types for which we obtained data and the number of replicate fields of a community type that had been sampled differed among LTER sites (Table 1, Fig. 1). In total, we had data for 59 fields (= areas sampled), representing 17 different types of herbaceous vascular plant communities.

We used the designation of community type made by investigators at each site. These distinctions were based on differences in dominant plant species composition or past land-use practices that were expected to influence community composition. Our analyses included communities from arctic tundra (meadows and heathlands), alpine tundra (meadows) and temperate grasslands (prairies and old-fields). At the arctic and alpine sites, data were provided from several different plant community types, but with only one replicate (= field) of each type (Table 1). In contrast, at each of the four grassland sites, data were available for replicate fields of a single community type from each site: short-grass prairie (SGS), tall-grass prairie (KNZ), old-fields in Minnesota (CDR) and old-fields in Michigan (KBS). We designated old-fields in Minnesota and Michigan as two distinct community types based on differences in species composition and above-ground net productivity

Table 1. LTER sites and community types used for comparisons of productivity and species density. ANPP was estimated at each LTER site based on annual above-ground production from clipped plots. The range in mean ANPP among fields is given for the four grassland community types and is based on 3–5 plots in the grassland sites, 6–32 plots in the tundra sites. Species density ( $D$ ) = measured or estimated number of species per  $m^2$  was estimated from harvested plots used to estimate ANPP or from surveys of adjacent plots (see text for details). For ARC and NWT, the first value given for ANPP ( $g\ m^{-2}\ yr^{-1}$ ) and  $D$  (number of species  $m^{-2}$ ) is the mean over all community types from that site. No range is reported for the community types in ARC and NWT because only a single field was sampled for each. Methods used to estimate ANPP and  $D$  are summarized separately for each parameter. The biome designation for each LTER site is given in bold.

Biome, LTER site and Community Type	ANPP	Range (fields)	Methods for ANPP	$D$	Methods for $D$	Citations for methods
<b>Grasslands</b>						
CDR, Cedar Creek, MN Minnesota old-fields (13 fields)	114.2	63.0–163.5	4 evenly spaced plots (0.3 $m^2$ ) per field per year; averaged for 1993–1996	11.2	Percent cover from 100 plots (0.50 $m^2$ ) within a field combined to estimate $D$	Inouye et al. 1987, Inouye 1998
KBS, Kellogg Biological Station, MI Michigan old-fields (9 fields)	354.6	209.7–602.6	Randomly scattered 1.0 $m^2$ plots; $n = 3–5$ per field	13.2	ANPP harvested plots used for $D$	Huberty et al. 1998
SGS, Short Grass Steppe, Colorado Short-grass prairie (6 fields)	72.4	44.7–107.2	5 random 0.25 $m^2$ plots from 3 transects per field; $n = 15$ per field	8.7	ANPP harvested plots used for $D$ ; combined for a transect estimate of $D$ ( $n = 3$ per field)	Milchunas et al. 1990, Inouye 1998
KNZ, Konza Prairie, Kansas Tall-grass prairie (18 fields = watersheds)	375.7	215.1–611.0	4 random 0.1 $m^2$ plots from 5 transects per site; $n = 20$ per field	11.2	Percent cover in 4 10- $m^2$ plots adjacent to ANPP plots; interpolated for a per $m^2$ transect estimate of $D$ ( $n = 4$ per site)	Briggs and Knapp 1995
<b>Arctic tundra, ARC</b>						
Tooth Lake, Alaska <i>Carex</i> meadow	118.3		Plots (0.04 $m^2$ ) harvested at intervals along a 400–600 m transect; woody production estimated from regressions. $n = 6–15$ per community	15.5	Censused in $m^2$ plots containing smaller quadrats used for ANPP estimates	Shaver 1986, Chapin et al. 1995
Dry heath slope <i>Equisetum</i> slope	111.6			8.1		
Hilltop heath	102.1			14.4		
Lower non-tussock	84.4			11.9		
Moist tussock	119.4			11.1		
Upper non-tussock	128.3			10.6		
Wet graminoid	119.9			13.6		
	181.6			9.0		
<b>Alpine tundra, NWT</b>						
Niwot Ridge, Colorado Fellfield	174.4		Randomly selected 1.0- $m^2$ plots from a 350 m $\times$ 500 m grid; $n = 7–32$ per community	12.1	Species presence censused at 200 points in each $m^2$ plot sampled for ANPP	Walker et al. 1994
Dry meadow	198.2			16.3		
Moist meadow	170.8			10.6		
Wet meadow	179.2			10.9		
Snow bed	207.6			13.0		
	116.2			9.6		

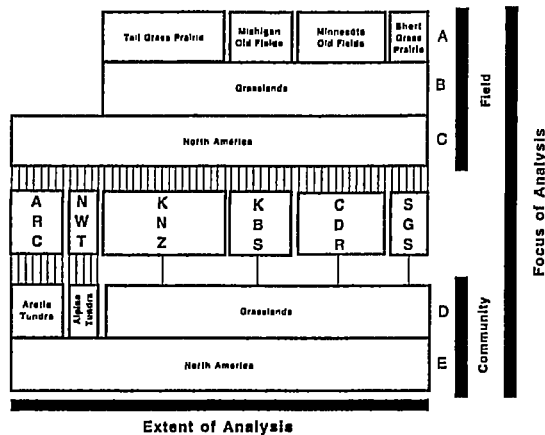


Fig. 1. Diagrammatic representation of the hierarchical design used in this analysis evaluating the relationship between species density and ANPP at different spatial scales defined by different combinations of focus (scale at which the data are aggregated) and extent (scale over which the pattern is examined). Each of the central white rectangles represents a different LTER site, with vertical lines above the rectangle representing fields and vertical lines below the rectangle representing communities. When focus was set as the field, patterns were quantified for three extents of interest (shaded rectangles): (A) within community types, separate analyses within each of the four grassland LTER sites (6 fields at SGS, 13 fields at CDR, 9 fields at KBS, 18 fields at KNZ), (B) within grasslands (46 fields), and (C) within North America (59 fields). When the focus was established as the community type, patterns were quantified for two extents of interest (shaded rectangles): (D) within biomes, separate analyses for the four grassland community types, the five alpine tundra community types, and eight arctic tundra community types, and (E) within North America for 17 unique community types.

(ANPP) paralleling the distinction between tall- and short-grass prairie.

### Estimates of ANPP

At all sites, ANPP was estimated from a single harvest of live and standing dead herbaceous vegetation at peak biomass. In three of the arctic communities (dry heath, hilltop heath, moist tussock) dwarf shrubs constituted 20–40% of the cover, so annual woody production was estimated by regression (see Shaver 1986, Chapin et al. 1995). The plot sizes, spatial distribution of plots, and number of replicates that were used to estimate ANPP differed among sites (Table 1). However, because ANPP scales linearly with area sampled, we could express ANPP at each site in common units ( $\text{g m}^{-2} \text{yr}^{-1}$ ) despite these methodological differences. Although ANPP data are collected every year at most of these sites, species composition data were only available for certain years. To make comparisons among all sites over the same time frame, we requested data from all sites for 1993–1996 and used only the subset of these data for years in which floral surveys were conducted. When we had data from a site for more than one year,

we used the year that had the most replicates of a community type or that was considered to be a representative year by the site investigators.

### Estimates of species density and richness

We used species density ( $D$ ), the mean number of species per plot, as our measure of species diversity. Although species richness is often used to refer to the number of species in a plot of fixed area (see Zobel 1997), we follow Magurran (1988) and use  $D$  to refer to the number of species in a plot of fixed area. We define species richness ( $S$ ) as the total number of species at a site, equivalent to actual or local pool of Zobel (1997). We also examined the relationship between productivity and  $S$ , and obtained estimates of  $S$  by combining data from all plots within a field or community type at a site. However, we do not present those analyses here (but see Discussion) because the sample sizes and dispersion of plots differed across sites resulting in biased estimates of  $S$  (see Palmer 1990).

Species density was measured either from the plots harvested for ANPP (Michigan old-fields, short-grass prairie, alpine tundra) or from surveys of species composition in plots adjacent to the ANPP plots (Minnesota old-fields, tall-grass prairie, arctic tundra). The plot size used to sample species composition differed among sites (Table 1) and unlike ANPP, species density does not scale linearly with plot area (Palmer 1990). Thus to derive estimates of species density at an equivalent scale across sites, we used methods developed by Inouye (1998) and Scheiner et al. (2000) to extrapolate estimates of species density to a common grain (= plot area) for all fields and communities. We used a plot size of  $1 \text{ m}^2$  because this was the most common plot size used at these sites (Table 1).

In the short-grass prairie (SGS) and Minnesota old-fields (CDR), species composition was measured using  $0.25\text{-m}^2$  and  $0.5\text{-m}^2$  plots, respectively. To estimate species density per  $1 \text{ m}^2$ , we conducted simulation analyses in which all possible combinations of quadruples (SGS) or pairs (CDR) of plots were used to determine an estimated number of species per  $\text{m}^2$  (see Inouye 1998). For the Minnesota old-fields, these combinations were done for an entire field ( $n = 100$  plots per field), yielding a single estimate of species density for each field. For the short-grass prairie, the combinations were done separately for each of three transects ( $n = 5$  plots per transect) in each field. The mean from these combinations over each transect was used to estimate species density (per  $\text{m}^2$ ) for each field. Sample sizes for these estimates were 4950 for the Minnesota old-fields and 1365 for the short-grass prairie.

At the tall-grass prairie, species composition is measured in replicate  $10\text{-m}^2$  plots in each watershed (= field), so we used downward extrapolation to esti-

mate the number of species per 1 m<sup>2</sup>. Although it is possible to estimate the number of species in a desired area by dividing the larger unit into plots of the desired grain, it is necessary to know the spatial location of plants within the plot to determine the number of species in the smaller quadrat. In the absence of such data, we used a linear model to extrapolate to 1 m<sup>2</sup> based on a least-squares line determined from mean species density at 20 m<sup>2</sup> (estimated by upward extrapolation between proximate quadrats along a transect) and mean species density at 10 m<sup>2</sup> (the actual data). Separate analyses were made for each of the four transects in each field (= watershed). As a check on the accuracy of these estimates of species density, we compared them to a direct measure of the number of species per 1 m<sup>2</sup> for a nearby, comparable field at this site (in a frequently burned watershed, S. Collins unpubl.). Our estimates of species density were similar to the species density measured in this field at 1 m<sup>2</sup>, which suggested that the extrapolation was reasonable.

### Statistical analyses

We examined the relationship between species density and ANPP at several spatial scales defined by different combinations of the focus and extent of the data (see Palmer and White 1994, Scheiner et al. 2000). We varied the focus (= spatial scale at which the data are aggregated) from the scale of plots to community types and the extent (= spatial scale over which the pattern is examined) from fields to biogeographic units (Fig. 1). The smallest scale we report here is for fields within community types (focus = field, extent = community type). Our sample sizes for the scale of plots within fields were generally small (particularly in the grassland sites where replicate fields are sampled) and we found few significant relationships at this scale. The limited sample size at this scale likely affected our ability to detect significant relationships, so we did not include that analysis here. The largest scale we analyzed was for community types within biogeographic units. Our data set for some analyses at this extent also had a limited sample size, but we report it here for consistency and comparison. At this scale, our ability to detect significant relationships did not appear to be affected by sample size.

At all spatial scales we calculated the relationship between species density and ANPP, and focus here on patterns observed: (1) among fields within communities (focus = field; extent = community; Fig. 1A), (2) among fields within biomes or regions (focus = field; extent = biome or region; Fig. 1B, C), and (3) among communities within biomes or regions (focus = community; extent = biome or region; Fig. 1D, E). We used both first- (linear) and second-order (quadratic) polynomial regressions to evaluate the form of the relationship

between species density and ANPP at each of these spatial scales. For all analyses we used a probability level of  $p \leq 0.05$  for significance.

#### *Patterns among fields within community types*

We assessed the relationship between species density and ANPP among fields within each of the four grassland sites because replicate fields had been sampled in each community type (Fig. 1A, Table 1). In the alpine and arctic tundra sites, data were collected from only a single sampling location (= field) for each community type, so we could not conduct the within-community type scale of analysis for these two sites.

#### *Patterns among fields within biogeographic regions*

At this scale, we assessed the relationship between species density and ANPP by combining the data in two ways. First, we used data for all 46 fields sampled in grassland sites (6 from short-grass prairie, 18 from tall-grass prairie, 9 from Michigan old-fields, and 13 from Minnesota old-fields) to assess the pattern across a wide geographic gradient of grasslands (Figs 1B, 3a). Second, we used data for all fields in our sample ( $n = 59$ ), regardless of site, to examine the pattern in herb-dominated communities from all six LTER sites at the continental scale of North America (Figs 1C, 3b).

#### *Patterns among community types within biogeographic regions*

We assessed this relationship using community types as the focus for three biome types (Fig. 1D): grassland, alpine tundra, and arctic tundra. For the grassland biome, we estimated species density and ANPP for each community type as the mean over the replicate fields sampled at each of the four grassland LTER sites (SGS, CDR, KBS, and KNZ; Fig. 1D). For alpine tundra, we used data from the five community types sampled at the Niwot Ridge site in Colorado (NWT; Table 1, Fig. 4b). For arctic tundra, we based the analyses on the eight different community types sampled at Toolik Lake, Alaska (ARC; Table 1, Fig. 4c). The final analysis (Fig. 1E) was conducted at a continental scale (North America) and was based on all 17 community types in our data set (Table 1, Fig. 4d).

## Results

### Variation in species density and ANPP

There was considerable variation in species density and ANPP within and among these six sites. In the four grassland communities, there was a two- to three-fold range in ANPP among fields at a single site (Table 1). Across all 46 grassland fields, ANPP ranged from a low of 45 (at the short-grass prairie) to over 600 g m<sup>-2</sup> yr<sup>-1</sup> (Michigan old-fields and tall-grass prairie). There

Table 2. Summary of regression analyses examining the relationship between species density ( $D$ ) and ANPP in herb-dominated communities at six LTER sites in the USA. Quadratic relationships were considered significant only if the  $p$ -value for the squared term ( $X^2 p$ ) was  $< 0.05$ . Analyses are listed separately for within- and among-community types.  $n$  = sample size,  $b_0$  =  $y$ -intercept,  $b_1$  = regression coefficient for  $X$  (slope of linear analysis),  $b_2$  = regression coefficient for  $X^2$  term,  $comm.$  = community. The overall significance of the quadratic relationship ( $p$ ) and for the  $X^2$  term ( $X^2 p$ ) is given for the polynomial analysis. Significant relationships are highlighted in bold.

Extent	Focus	Linear		Quadratic			$R^2$	$p$	$b_2$	$b_1$	$b_0$	$R^2$	$X^2 p$
		$n$	$b_0$	$b_1$	$p$	$R^2$							
Within communities	Field	6	9.444	-0.010	0.729	0.03	0.03	1.628	0.220	-0.002	0.621	0.27	0.395
	Field	13	17.489	-0.055	0.025	0.38	0.38	18.384	-0.071	0.000	0.091	0.38	0.919
	Field	9	17.916	-0.015	0.256	0.18	0.18	30.266	-0.084	0.000	0.357	0.29	0.370
	Field	18	18.422	-0.007	0.161	0.12	0.12	16.278	0.004	0.000	0.365	0.13	0.732
Among communities	Field	46	10.668	0.009	0.007	0.16	0.16	7.415	0.041	0.000	0.001	0.29	0.006
	Field	59	10.671	0.009	0.002	0.15	0.15	7.764	0.037	0.000	<0.001	0.26	0.007
	Commun.	4	8.260	0.017	0.113	0.79	0.79	7.422	0.028	0.000	0.459	0.79	0.940
	Commun.	5	2.662	0.054	0.167	0.52	0.52	22.366	-0.205	0.001	0.394	0.61	0.584
	Commun.	8	17.330	-0.047	0.180	0.28	0.28	18.386	-0.064	0.000	0.443	0.28	0.956
	Commun.	17	10.097	0.012	0.119	0.15	0.15	11.072	0.000	0.000	0.296	0.16	0.770

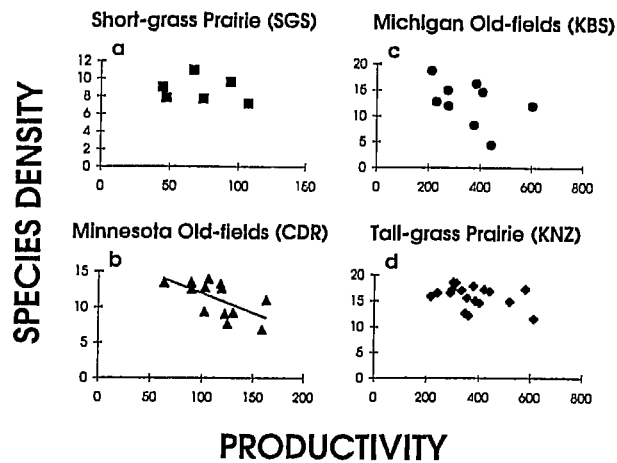


Fig. 2. The relationship between species density ( $D$ ) and ANPP ( $\text{g m}^{-2} \text{yr}^{-1}$ ) at the scale of fields (= focus) within a community type (= extent) in the four grassland sites. Significant relationships are plotted as solid lines (see Table 2). Note that the range for ANPP differs for each site. Unique symbols are used for each LTER sites in this and following figures.

was a five-fold range in mean ANPP among the four types of grasslands, from 72.4 for short grass prairie to 360.1  $\text{g m}^{-2} \text{yr}^{-1}$  for the tall grass prairie site. Overall

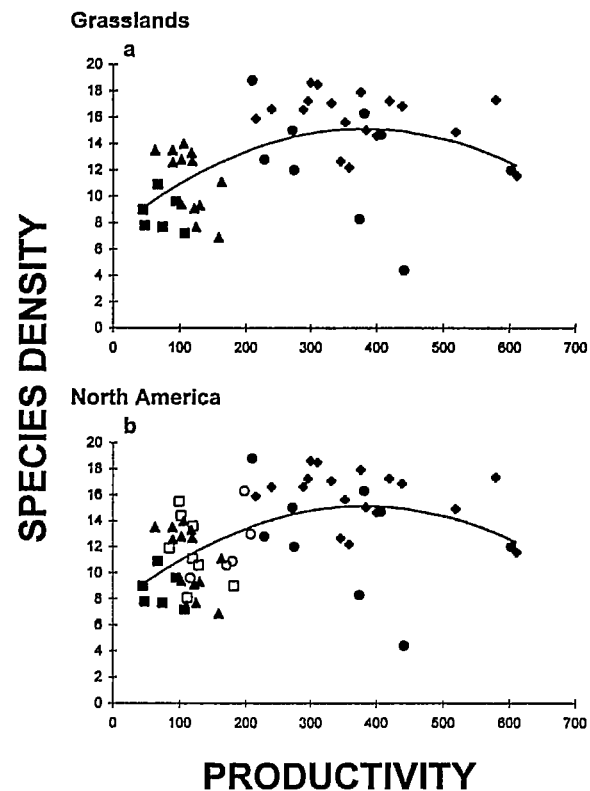


Fig. 3. The relationship between species density ( $D$ ) and ANPP ( $\text{g m}^{-2} \text{yr}^{-1}$ ) at the scale of fields (= focus) within biomes or biogeographic regions (extent = grasslands or North America). Data for fields from the grassland sites are indicated by unique closed symbols as in Fig. 2; data from the two tundra sites (NWT and ARC) are indicated by unique open symbols.

the arctic and alpine tundra sites had less variation in ANPP (approximately two-fold) among community types than did the grasslands (Table 1). Mean ANPP for the two tundra sites was intermediate to low relative to the grassland sites.

Mean species density varied approximately two-fold (8.7–16.3  $m^{-2}$ ) across the 17 community types (Table 1). The range in species density among the four grassland communities (8.7–13.2  $m^{-2}$ ) was similar to that measured in the 13 communities at the two tundra sites (9.0–16.3  $m^{-2}$ ).

### Patterns among fields within community types

In the four grassland communities, we only detected one significant relationship between species density and ANPP (Fig. 2). Among the Minnesota old-fields (CDR; Fig. 2b), species density decreased linearly as ANPP increased, and productivity accounted for 38% of the variation in species density among fields. There was no evidence for a unimodal relationship at this scale in any of the grassland communities (Table 2).

### Patterns among fields within biomes and biogeographic regions

When we expanded the extent of the analysis to broader biogeographic regions (grasslands or North America), but maintained field as the focus, the relationship between species density and productivity was consistently significant and unimodal (Fig. 3). Specifically, 29% and 26% of the variation in species density among fields was accounted for by variation in ANPP

when grasslands (Fig. 3a) or North America (Fig. 3b) were the extent of the analysis, respectively. The peak of the unimodal curve occurred at approximately the same point for grasslands and North America (381 or 387  $g\ m^{-2}\ yr^{-1}$ , respectively; Fig. 3a, b).

### Among community types within biogeographic regions

When we shifted the focus of analysis to community types, we did not detect a significant unimodal or linear relationship for any of the four biogeographic regions we examined (Fig. 4a–d). For grasslands and alpine tundra, this may have been a consequence of the limited sample size ( $n = 4$  and 5 community types, respectively) for these regions. However, for both the arctic tundra and North America we had a larger number of community types ( $n = 8$  and 17, respectively) and still there was no indication of a significant relationship (linear or unimodal) for either of these biogeographic regions (Fig. 4c, d, Table 2).

### Discussion

Based on current theory, and the emphasis in the literature, we had expected to observe unimodal relationships between plant species density and productivity at all the scales we examined (cf. Grime 1973, Tilman and Pacala 1993, Huston 1994). In fact, Huston (1994, 1999) recently asserted that the unimodal pattern is “ubiquitous” and expected at all spatial scales. Although unimodal patterns have been detected over a broad range of spatial scales in plant communities (see Mittelbach et al. unpubl.), few published studies have examined this relationship at different spatial scales. Our study is unique in that we had a data set that allowed us to examine this relationship for communities dominated by a similar life form (vascular herbaceous plants) at both local and broad regional scales. In our analysis, we found that the form of the species density–productivity relationship depended on the spatial scale at which the pattern was analyzed (i.e., the focus and extent of the data used to examine the relationship).

Mittelbach et al. (unpubl.) also found that the spatial extent of a study influenced the form of the relationship between productivity and species richness. For studies in vascular plant communities, they found that a unimodal relationship was detected most frequently when patterns were analyzed across community types. In studies conducted within a community type, unimodal and positive relationships were detected equally in the literature (33 and 30% of studies, respectively). Negative relationships (which are often interpreted as unimodal; see Grace 1999) were reported in 18% of studies (Mittelbach et al. unpubl.). Moreover, the geographic

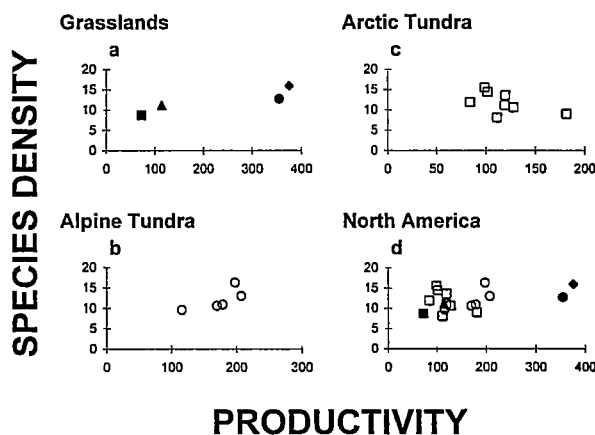


Fig. 4. The relationship between species density ( $D$ ) and ANPP ( $g\ m^{-2}\ yr^{-1}$ ) at the scale of community types (focus) within different biogeographic regions (extent = grasslands, alpine tundra, arctic tundra, or North America). Data for each grassland community is indicated by unique symbols (Fig. 2). Note that the range for ANPP differs for each biogeographic region.

extent of a study influenced the pattern detected. Although unimodal relationships were the most common pattern observed for vascular plants at geographical scales smaller than continental scales (< 4000 km), they accounted for only 31–45% of the relationships at any spatial scale. Positive relationships between productivity and species richness were the next most commonly observed pattern (20–28%), and this was the predominant pattern at the continental scale (60%; Mittelbach et al. unpubl.). Similarly, Grace (1999) also found that unimodal patterns were commonly detected in studies examining local patterns of species density in plant communities.

Our results based on data from a broad range of herbaceous communities at six LTER sites from a broad geographic gradient in North America are not consistent with those reported in these two recent literature reviews (Grace 1999, Mittelbach et al. unpubl.). Using data from the local scale (sites within 20 km) at the four grassland sites, we did not detect a significant unimodal relationship at any site. In fact, the only significant relationship we detected was negative linear (Minnesota old-fields). Foster (1996 and unpubl.) also found a negative linear relationship between species density and productivity (measured as live biomass and live plus litter) across a different set of nine old-field sites at the KBS site. Some studies have interpreted a negative relationship as evidence for a unimodal pattern (observing only the descending portion of the curve; see Grace 1999). However, we have no evidence for an ascending portion for this relationship within a community type at either of these sites.

Although we only observed significant unimodal relationships when data were combined across sites, and so encompassed a large geographic extent, we also found that changes in the focus of analysis (i.e., fields or community types) resulted in different patterns at the same extent. When we used community type as the focus of analysis, we failed to detect a significant relationship between species density and productivity. Although the sample sizes for communities within grasslands and alpine tundra were limited in our data set, we also saw no relationship among communities in the arctic tundra or in all of North America where our sample sizes were larger. This result underscores the importance of controlling for differences in extent and focus of analysis when making comparisons among studies examining the relationship between any component of species diversity (e.g. density, richness) and productivity.

### Patterns at different spatial scales

Only a few other studies have examined explicitly the relationship between species density and productivity at different spatial scales. Consistent with our results,

these studies also have found that the form of the relationship depends on the focus and extent of the analysis. For example, Moore and Keddy (1989) found no relationship between species density and productivity among plots within 15 wetland communities. However, when they combined plot data from all communities sampled (a change in extent) a unimodal pattern was observed. They also observed a unimodal pattern when community means (a change in focus) were used to examine the pattern (see also Ter Heerdt et al. 1991).

The failure to detect a unimodal (or any) relationship at the within community scale is argued to be due, in part, to the more limited range in ANPP (or *D*) at this scale (Rosenzweig 1995, Grace 1999). Although studies done in communities dominated by a single life form (e.g. herbaceous perennials) are likely to encounter less variation in ANPP than those that cross community boundaries (e.g. grasslands to savannas to forests), there is no clear indication that limited ANPP alone accounts for the failure to detect significant patterns in our study. There was a two- to three-fold range in ANPP among fields within community types in our data set (Table 1, Fig. 2). Several studies in the literature that report a unimodal relationship have examined a similar range in ANPP (see Grace 1999). Moreover, Mittelbach et al. (unpubl.) found that range in ANPP was not related to detection of a significant unimodal pattern in their literature review. Although limited sample size certainly can affect the ability to detect a significant unimodal (or any) relationship, we had reasonable sample sizes ( $n = 6-18$  fields per community type) for this scale of analyses. Thus, it is unlikely that either of these factors per se limited our ability to detect unimodal patterns.

Combining data over community types reduced both the range in ANPP and the sample sizes for our analyses. This may have reduced our power to detect significant relationships of any form at the largest spatial extent (biomes and continental). Sample size in our data set was particularly small when focus was among community types at the extent of grasslands ( $n = 4$ ). However, several recent studies examining diversity-productivity relationships in grasslands have also reported finding no relationship. For example, Harrison (1999) found that species density ranged from 10–15 species per  $m^2$ , and was independent of productivity (measured as peak standing biomass) across 40 meadows sampled in serpentine and non-serpentine grasslands in California. Zobel and Liira (1997) also found that species density per  $m^2$  was independent of standing biomass across a broad gradient of productivity (32–812  $g\ m^{-2}$ ) in Estonian grasslands. Similarly, Stohlgren et al. (1999) reported species density of 9–11 per  $m^2$  across a broad range of grazed and ungrazed grasslands in the Rocky Mountains.



With North America as the extent, our among-community types analysis combines data from a broad geographic gradient for a range of herbaceous community types. Analyses across such a broad geographic extent may be confounded by changes in the size and composition of the regional species pool (Huston 1999, Waide et al. 1999). Although we did not detect a significant relationship between species density and ANPP at this broad biogeographic scale, when we combined data from all fields of a community type to estimate species richness ( $S$ ), we found a positive linear relationship across sites ( $S = 0.063 \times \text{ANPP} + 20.32$ ;  $n = 17$ ,  $p = 0.087$ ,  $R^2 = 0.18$ ). This result is consistent with patterns observed in other analyses at the between biome (sensu Mittelbach et al. unpubl.) and geographical provinces (Rosenzweig 1995) scale.

### The pattern accumulation hypothesis

One explanation for the failure to detect unimodal patterns in some of our analyses could be a consequence of the total range of ANPP in a particular data set (i.e., small extent). That is, in each data set we may be sampling ascending, flat, or descending portions of a true unimodal relationship that exist across a broader range of ANPP (Rosenzweig 1995, Scheiner et al. 2000). This would result in a mix of significant positive, non-significant, and significant negative slopes for the restricted data from each field along a broader ANPP gradient (cf. Moore and Keddy 1989, Guo and Berry 1998). This situation has been termed the "pattern accumulation hypothesis" by Scheiner et al. (2000), because the overall unimodal pattern is the result of a sequence of linear relationships at smaller extents whose slopes vary with ANPP. Guo and Berry's (1998) analysis of species richness across five microhabitats in a New Mexico grassland provides evidence for this hypothesis.

We tested if the pattern accumulation hypothesis accounted for the mix of significant and non-significant linear relations, as well as the significant unimodal relationships, we detected by examining variation in slopes (among plots within fields) at three spatial extents: fields within each site, fields from the grassland biome, and fields from North America. We used Spearman rank correlation to test this hypothesis by evaluating if there was a negative association between the slopes from the linear regressions of species density and ANPP at each scale. This test assessed if the slopes from each of the linear regressions vary with ANPP in the way suggested by the tangents of segments from a unimodal distribution (e.g., positive at low ANPP, non-significant, and then negative with increasing ANPP).

None of these analyses were significant (smallest  $p > 0.164$ ) at any level, regardless of whether the slopes were derived from regressions of plots within fields or

fields within communities. This is important, for two reasons. First, it suggests that our failure to detect unimodal patterns in this data set was not necessarily because of low power. Second, it indicates that the unimodal patterns we did detect (Fig. 3), are not a consequence of the pattern accumulation hypothesis. This suggests that different processes may be operating to produce linear or non-significant relationships between species density and ANPP when fields or community types are the extent, compared to those which operate at larger spatial extents such as grasslands or all of North America.

The size and composition of the local or regional species pool (sensu Zobel 1997) can also influence local species density (cf. Pärtel et al. 1996, Zobel and Liira 1997, Grace 1999). Unfortunately our data set was not sufficient to assess how much of the variation we see in local species density among fields within a community type or among community types is due to variation in the local or regional species richness among sites. However, it is interesting to note that several of the successional old-fields in Michigan and Minnesota have species density lower than we would expect given their productivity (see Fig. 3a). The species composition in successional communities certainly reflects the species pool in the surrounding landscape, but it may take considerable time for the local and regional influences on species density to sort out (cf. Holt 1993). Clearly the frequency of disturbance, time since last disturbance, and the colonization potential of species in the surrounding landscape all can influence (along with productivity) the observed species density in a field or community.

### Conclusions

In this paper we have shown that changes in two attributes of scale – focus and extent – can affect the relationship between productivity and species density in herbaceous vascular plant communities. When we used fields as the focus and examined the pattern over large-scale extents such as biomes or biogeographic regions (grasslands or North America), we consistently observed the expected unimodal relationship. Moreover, it is noteworthy that we observed a significant unimodal relationship among communities dominated by a single life form, herbaceous vascular plants. This suggests that mechanisms other than strong asymmetries in competitive abilities associated with changes in life form may determine the "hump" in these plant communities.

A second noteworthy point revealed by our analysis is the relative constancy in species density per  $\text{m}^2$  for herb-dominated communities across a wide range of productivity in North America. Across these 17 plant communities, species density ranged from 8–15 per  $\text{m}^2$

over a nearly eight-fold range in above ground biomass production. The constancy of species density we report for the four LTER grassland sites (9–13 species per m<sup>2</sup>) is remarkably similar to that which has been reported for other North American grasslands (see Harrison 1999, Leach and Givnish 1999, Stohlgren et al. 1999). We know of no particular reason why species density per m<sup>2</sup> would be relatively constant across a broad productivity and geographic gradient of North American grasslands. It is unlikely (though possible) that the local and regional species pools across this broad spectrum of sites is constant and so raises intriguing questions regarding the mechanisms that operate to determine local species density in grasslands, and perhaps herb-dominated communities in general.

Clearly, further documentation of the observed patterns of species density and richness at different spatial scales across a wide range of productivity is needed. Such surveys need to be sufficiently replicated and include the full productivity gradient at a site and coupled with experimental studies examining the mechanisms proposed to underlie these relationships at these same scales (Rosenzweig 1995, Mittelbach et al. unpubl.). As Gough et al. (2000) point out, simple fertilization experiments that increase productivity are of limited value for examining the mechanisms that underlie species density patterns at different scales. Experiments that directly manipulate resource heterogeneity or other factors likely to vary with productivity, or the potential species pool, may better reveal mechanisms that determine local and regional patterns of diversity over a range of spatial scales.

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