

The relationship between productivity and multiple aspects of biodiversity in six grassland communities

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Received: 4 March 2008 / Accepted: 28 August 2008 / Published online: 24 September 2008
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Abstract Biodiversity is a multifaceted concept but most studies examining the association between the biodiversity of a community and its productivity focus only on species richness. Consequently, studies are needed to examine how other facets of biodiversity vary with productivity if we want to have a better understanding of the distribution of biodiversity across our planet. We evaluated how a number of biodiversity measures (species richness, evenness, dominance, rarity, Simpson's diversity, and Shannon–Weiner diversity) varied across natural productivity gradients at 6 grassland sites in the continental US. Variation in productivity did not account for a substantial amount of variation in any measure of biodiversity at small spatial scales ($\approx 1 \text{ m}^2$) at most sites. When productivity accounted for substantial variation in biodiversity, different measures of biodiversity responded to productivity in different ways. For example, dominance changed in a U-shaped fashion along a productivity gradient whereas richness increased in an asymptotic fashion. Consequently, diversity indices, which account for both species richness and evenness, varied in a hump-shaped fashion along the productivity gradient. Our results highlight that an exclusive focus on the association between species richness and productivity provides an incomplete picture of how a community's biodiversity is related to its functioning.

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Keywords Biodiversity · Productivity · Species richness · Species evenness · Diversity indices · Grasslands

Abbreviations

ANPP	Annual aboveground net primary productivity
CDR	Cedar Creek LTER
E	Species evenness
KBS	Kellog Biological Station LTER
PH	Parkhill prairie
S	Species richness
SGS	Short Grass Steppe LTER
T	Temple oldfield
TP	Temple prairie

Introduction

Understanding how the functioning of an ecosystem is related to its biodiversity has been a topic of great interest to ecologists for quite some time. Recently, a number of books (Kinzig et al. 2001; Loreau et al. 2002) and major review articles (Waide et al. 1999; Gessner et al. 2004; Giller et al. 2004; Hooper et al. 2005) have summarized research on the topic. Three common points in these reviews are that (1) biodiversity is a multifaceted concept that can be assessed at multiple levels of biological organization, (2) most studies examining the biodiversity-ecosystem function relationship focus on only one aspect of biodiversity, species richness, and (3) significant associations commonly exist between species richness and some aspects of ecosystem function. These points beg the question: what are the associations between the functioning of ecosystems and aspects of biodiversity other than species richness? Here, we quantify how multiple aspects of biodiversity at the level of species are associated with a commonly measured ecosystem function, net primary productivity. Although productivity and biodiversity likely affect each other through reciprocal feedback mechanisms (Loreau et al. 2001), we focus on the potential causal effect of productivity on multiple facets of biodiversity.

The concept of biodiversity at the species level is best presented graphically by plotting the relative abundance (or biomass) of each species by its rank order (Whittaker 1972; Kempton 1979; May 1981; Magurran 1988; Tokeshi 1993). A number of different quantitative measures can be derived from such representations (e.g., richness, dominance, evenness, and rarity; Fig. 1). Although some of these measures may be correlated with each other (Stevens and Willig 2002; Wilsey et al. 2005), each represents a different concept (Table 1). Alternatively, we could use an index of biodiversity (e.g., Simpson's or Shannon–Weiner) that reflects two or more of these concepts (e.g., richness and evenness; Pielou 1977; Magurran 1988) into a single number. From an empirical perspective, richness and evenness have direct and independent effects on the magnitude of diversity indices and have important indirect effects that result from synergisms between them (Stirling and Wilsey 2001).

Given that each biodiversity measure represents a different conceptual attribute of the relative abundance distribution of a community, each biodiversity measure may vary with productivity in a different way. Theories predict positive monotonic, negative monotonic or hump-shaped relationships between richness and productivity, with empirical support

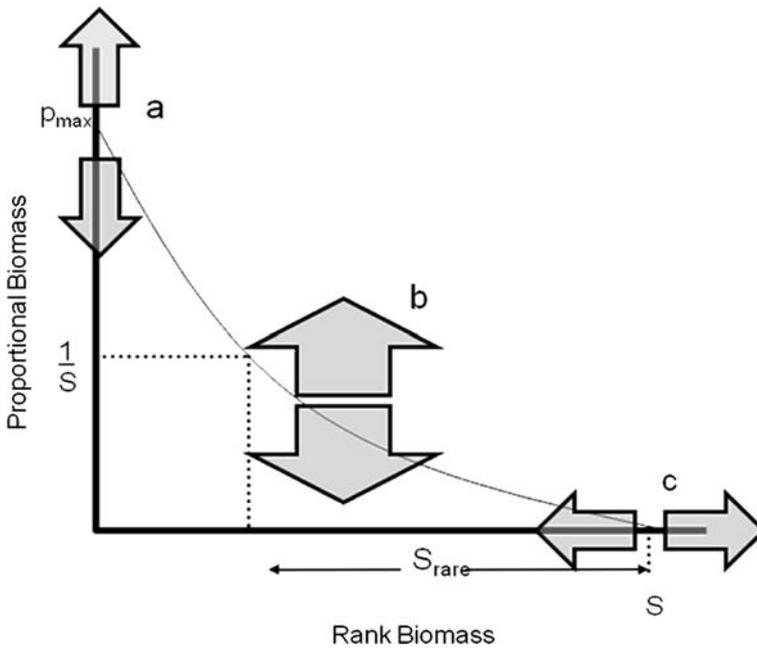


Fig. 1 A graphical depiction of biodiversity as portrayed by the relative biomass distribution of species. Species richness (S) represents the total number of species and dominance (p_{max}), following Berger–Parker (1970), represents the relative biomass of the species with the greatest biomass in the focal unit. We define the number of rare species within a community (S_{rare}) as the number of species that have a relative biomass that is less than the average relative biomass ($1/S$) for all species within a plot or field. Rarity is represented by the proportion of species that are rare. Evenness is a measure of the degree to which each species is equally represented in the community (i.e., flatness of the relative abundance distribution). Grey arrows indicate the potential independent influences that productivity may have on biodiversity by (a) altering the extent to which the most dominant species usurps resources from other species, (b) altering how similar species are in terms of their proportional biomass (as reflected by the slope of the relative biomass distribution line), and (c) a change in the number of species present in the community. Most biodiversity studies only focus on changes in species richness (c)

Table 1 Four conceptual aspects of the relative abundance distribution

Term	Concept
Evenness	A measure of how equally resources are partitioned among all species within the community
Dominance	The extent to which the most common species sequesters resources away from other species
Rarity	The fraction of species in an ecosystem that use less than their fair share of resources
Richness	The number of species partitioning resources

Although some of these concepts may be closely related, they are not necessarily strongly correlated (Wilsey et al. 2005)

for all patterns, including no relationship (see reviews by Waide et al. 1999; Grime 2001; Mittelbach et al. 2001; Scheiner and Willig 2005). Species evenness is expected to decline with productivity because (1) unproductive environments cannot support sustainable populations of rare species which increases species evenness and (2) productive environments can support sustainable populations of rare species and enhance the growth of

competitively dominant species but the growth of the competitive dominants suppresses the population size of rare species which decreases evenness (Drobner et al. 1998). On the other hand, evenness can increase with productivity if subdominant/rare species are better able to acquire resources than dominant species when resources are more common (Nijs and Roy 2000). Empirical work has demonstrated that species evenness declines linearly with increasing productivity (Vermeer and Verhoeven 1987; Drobner et al. 1998) or does not change significantly with a change in productivity (Weiher and Keddy 1999). We are not aware of any theoretical or empirical work that addresses how other measures of biodiversity should or do vary with productivity. Nonetheless, productivity could alter biodiversity through mechanisms that alter the proportional abundance of dominant and subdominant species (e.g., arrows a and b in Fig. 1) in addition to mechanisms (arrow c in Fig. 1) that alter species richness.

Examining the relationship between productivity and multiple measures of biodiversity is important for at least two reasons. First, such examinations can indicate if some facets of biodiversity have stronger associations with productivity than does richness. Measures of biodiversity that consider aspects of abundance (e.g., evenness) may be more sensitive to changes in productivity than measures that only consider the presence/absence of species (e.g., richness). Such a finding would suggest that anthropogenic changes in productivity can alter community structure before any species are lost by changing the manner in which resources are partitioned among species. Second, simultaneous consideration of multiple facets of biodiversity in a single measure (e.g., Simpson's diversity) may provide broad understanding of the relationship between ecosystem structure and function. For example, the productivity-Simpson's diversity relationship may be stronger than the productivity-richness relationship, because residual scatter in the latter that is caused by variation in evenness is reflected in Simpson's diversity. Furthermore, the form and parameterization of the productivity-Simpson's diversity relationship may be stronger than the productivity-richness relationship because the former should reflect the simultaneous responses of both richness and evenness to productivity.

We evaluated how multiple measures of herbaceous plant biodiversity at the plot scale varied with productivity within each of six grassland sites located in the United States (Table 2). Wilsey et al. (2005) found substantial spatial variation in biodiversity measures within each of these sites and that the different diversity measures were often weakly correlated. Here, we examine whether within site variation in diversity measures reported at these sites by Wilsey et al. (2005) is associated with variation in productivity.

Methods

We analyzed data on the associations between plant biodiversity and productivity within each of six grassland sites for which we had (1) data access and (2) information on the relative abundances of taxa. Three of these sites are Long-Term Ecological Research sites; sites selected to examine long-term changes within representative ecosystems (Hobbie et al. 2003). Details of the sampling design differed among sites (Table 2) but sampling often occurred at multiple spatial scales within sites, with several small plots nested within a larger location and several locations dispersed within each site. The larger locations at Short Grass Steppe represented different localities within the same open rangeland, whereas the larger locations at the other sites represented different fields within each site. The size of fields differed among sites: Cedar Creek (1.9–11.3 ha), Kellog Biological Station (0.9 ha), Parkhill (21 ha), and Temple-oldfield and Temple-prairie (0.4–3 ha).

Table 2 Description of the six grassland sites, including aspects of sampling design, used for the assessment of the relationship between measures of biodiversity and ANPP

Site	Site code	Location	Site description	Years studied	Number of fields	Number of plots per field	Plot size (m ²)
Cedar Creek LTER (MN)	CDR	45°24' N, 93°12' W	Oldfield	1988–1996	14	4	0.3
Kellog Biological Station LTER (MI)	KBS	42°24' N, 85°24' W	Oldfield	1989–2001	6	5	1
Short Grass Steppe LTER (CO)	SGS	40°49' N, 104°48' W	Short grass steppe	1992–1998	7	15	0.25
Parkhill (TX)	PH	33°15' N, 95°53' W	Texas blackland prairie	2001	1	12	0.5
Temple (TX)	T	31°05' N, 97°20' W	Oldfield	2001	4	10	0.5
Temple-Prairie (TX)	TP	31°05' N, 97°20' W	Texas blackland prairie	2001	1	10	0.5

Despite this nested design, the number and size of plots per location at each site were small, which reduced the effectiveness of estimating biodiversity at larger spatial scales by aggregating plots within a location (e.g., Chalcraft et al. 2004). Consequently, we only present results from the focal scale of a plot ($\leq 1 \text{ m}^2$), as this is the scale that researchers commonly use to assess variation in species richness and productivity in grassland communities (see Gross et al. 2000). Furthermore, differences in the size and number of plots at each site (Table 2), and differences in interplot distances among sites (e.g., $>50 \text{ m}$ at Parkhill and $>5 \text{ m}$ at Temple-oldfield and Temple-prairie), argue against pooling of data from multiple sites for a cross-site analysis. A description of the study sites is provided in Wilsey et al. (2005).

Site investigators provided data on the amount of dry aboveground biomass of each species found in particular plots. Amount of dry aboveground biomass of each species was obtained by clipping all of the vegetation within a plot at the end of a growing season, sorting the vegetation by species, and recording the total dry mass of each species. Summing this peak aboveground biomass of all plants in a plot in a particular year provided an estimate of aboveground net primary production (ANPP). Although this approach assumes that herbivory is minimal, it is a common way of estimating ANPP when researchers examine associations between biodiversity and productivity (e.g., see Gross et al. 2000 for review). We also used this information to estimate six different measures of biodiversity: species richness (S); Simpson's diversity ($D = 1/\sum p_i^2$), where p_i is the proportional biomass of species i ; Simpson's evenness ($E = D/S$); Shannon–Weiner diversity ($H' = -\sum p_i \ln(p_i)$); Berger–Parker dominance, the proportional biomass of the species with greatest biomass within a plot (Berger and Parker 1970); and rarity, the proportion of species having less than the average proportional biomass ($1/S$) within the plot (Camargo 1993). Although H' is correlated positively with D , we present results for both indices because (1) H' is reported more frequently in the ecological literature and (2) the evenness index associated with D is mathematically independent of species richness, whereas the evenness index associated with the H' is not (Smith and Wilson 1996).

Compared to D , H' is more sensitive to the biomasses of species in the right hand tail of the rank biomass distribution.

Analyses of spatial associations

We assessed how spatial variation in each measure of biodiversity was related to spatial variation in ANPP within each site using ordinary least square regression analysis. Because S -productivity relationships may be positive linear, negative linear, or unimodal (Waide et al. 1999; Mittelbach et al. 2001), we included both linear (L) and quadratic (Q) components of ANPP in regression models. To reduce collinearity between linear and quadratic components of ANPP, we centered the values of ANPP by their grand mean prior to regression analysis (Neter et al. 1996). At three sites (Cedar Creek, Kellog Biological Station, and Short Grass Steppe), data were available for multiple years (Table 2). Consequently, we include a temporal effect (Y), as well as its interactions with linear and quadratic components of ANPP (i.e., $L \times Y$ and $Q \times Y$) in analyses. Importantly, the same plots within a location were not sampled each year. Thus, observations in the analysis are not interdependent. A significant $L \times Y$ or $Q \times Y$ interaction indicates that the spatial association between a biodiversity measure and productivity differs among years. We used type III sums of squares (SS) for regression analyses (SAS Proc GLM; SAS 1999) because no rationale exists for determining the order of parameters in the regression model (e.g., should a year effect be specified before or after the linear component of productivity). Thus, the significance of a predictor was evaluated after other predictors were entered into the model. As such, we did not assign a priori preferences to linear versus quadratic components, or to main effects versus interactive effects in assessing significance.

Do significant quadratic associations represent modal versus asymptotic associations?

A significant quadratic term in a polynomial regression can indicate either a modal (e.g., hump-shaped or U-shaped) association between two variables or a non-linear but saturating association between two variables (i.e., asymptotic). The Mitchell-Olds and Shaw (MOS) test often is used to distinguish asymptotic and modal trends when quadratic components of regression analyses are significant (Mitchell-Olds and Shaw 1987). We employed MOS at each of three sites (Parkhill, Temple-prairie, and Temple-oldfield). We did not do so for spatial associations at the other three sites (Cedar Creek, Kellog Biological Station, Short Grass Steppe) because components other than the linear and quadratic representations of ANPP (e.g., Y , $Y \times L$, or $Y \times Q$) were integral to the regression analyses, preventing the application and interpretation of the MOS test. In those cases, asymptotic and modal relationships were distinguished in a qualitative way by visual examination of scatter plots.

Assessing the independence of responses to productivity by S and E

S and E are correlated at these sites but the magnitude of the association ($r \leq -0.46$) is rather weak (Wilsey et al. 2005). Nonetheless, the association between ANPP and E could represent a direct response of E to ANPP or it could be the result of ANPP indirectly influencing E through a common process or association with S . Similarly, the association between ANPP and S could represent a direct response of S or it could be an indirect response produced by ANPP altering E . To assess the independence of responses to ANPP by S and E , we performed similar analyses to those outlined in the section on spatial

associations but in this case we (1) included terms for S and an interaction between S and year when testing the association between ANPP and E and (2) we included terms for E and an interaction between E and year when testing the association between ANPP and S. We retained use of type III SS because a significant ANPP term suggests that ANPP has an independent effect on either S or E despite any possible shared association between the two measures. Such a finding indicates that ANPP affects the different biodiversity measures through different mechanisms or each biodiversity measure responds to the same mechanism in different ways.

Results

Although variation in ANPP had a significant effect on variation in all measures of biodiversity, the effect on a particular measure of biodiversity was significant at only a few sites (Table 3). ANPP was not associated significantly with any measure of biodiversity at 2 (Temple-oldfield and Temple-prairie) of the 6 sites, and was only associated significantly with all measures of biodiversity at one site (Short Grass Steppe). Furthermore, the direction of the relationship (as portrayed by the sign of regression coefficients) between ANPP and a particular measure of biodiversity often differed among sites. Significant annual variation characterized the association between ANPP and dominance (Cedar Creek) and E (Cedar Creek and Short Grass Steppe) at some sites (Table 3).

Despite the frequent detection of statistically significant associations between ANPP and measures of biodiversity, ANPP generally did not account for much of the variation in any measure of biodiversity. In most cases, the sum of linear and quadratic components of ANPP as well as their interactive effects with year accounted for less than 9% of the variation in any aspect of biodiversity (Table 3). ANPP accounted for substantial variation in several biodiversity measures at Parkhill: dominance evinced a U-shaped relationship (MOS test: predicted peak < maximum observed ANPP— $F_{1,9} = 14.62$, $P = 0.004$; predicted peak > minimum observed ANPP— $F_{1,9} = 5.97$, $P = 0.037$), S increased linearly, and both diversity indices evinced a humped relationship ([D] MOS test: predicted peak < maximum observed ANPP— $F_{1,9} = 8.71$, $P = 0.016$; predicted peak > minimum observed ANPP— $F_{1,9} = 5.45$, $P = 0.044$; [H'] MOS test: predicted peak < maximum observed ANPP— $F_{1,9} = 19.53$, $P = 0.002$; predicted peak > minimum observed ANPP— $F_{1,9} = 11.33$, $P = 0.008$) with ANPP (Table 3; Fig. 2). Because the most productive plot may have been an outlier, we quantified regression models for Parkhill using least trimmed squares robust regression. This approach identifies and reduces the influence of outlying data (SAS Institute, Cary, North Carolina, 2002). No outliers were detected using this procedure, and results consistently corroborated patterns documented by ordinary least square regression, with the exception that the effect of the quadratic component of ANPP on S became significant ($\chi^2 = 3.98$, $DF = 1$, $P = 0.046$; Fig. 2b).

Including S and the S * Y interaction in models examining spatial variation in E did not substantially alter how any component of productivity (either linear or quadratic components, or their interactions with year) was associated with E at any site, except at Parkhill. Inclusion of S in the analysis of E at Parkhill produced a significant quadratic relationship between ANPP and residual variation in E (linear component: $F_{1,8} = 1.24$, $P = 0.299$, $r^2 = 7\%$; quadratic component: $F_{1,8} = 6.94$, $P = 0.030$, $r^2 = 39\%$; Fig. 3b). The inclusion of S in the analysis evaluating the effect of linear and quadratic components of evenness on ANPP, however, did not substantially alter prior results.

Table 3 Results from regression analyses evaluating the effect of year (Y), linear (L) and quadratic (Q) components of ANPP, and their interactions, on measures of biodiversity at the small focal scale for each of six sites

Factor	CDR	KBS	SGS	PH	T	TP
<i>Dominance</i>						
Year (Y)	0.04*	0.16***	0.08***			
ANPP (L)	-0.00	+0.00	+0.00	-0.01	+0.04	+0.15
ANPP (Q)	-0.00	-0.01*	-0.01*	+0.46**	-0.00	-0.07
ANPP (L) × Y	0.01	0.05	0.02			
ANPP (Q) × Y	0.03*	0.04	0.02			
<i>Rarity</i>						
Year (Y)	0.02	0.10*	0.01			
ANPP (L)	-0.000	+0.01	+0.02*	-0.04	-0.04	-0.00
ANPP (Q)	-0.00	-0.03**	-0.00	+0.22	-0.01	-0.00
ANPP (L) × Y	0.02	0.06	0.02			
ANPP (Q) × Y	0.02	0.07	0.01			
<i>Evenness</i>						
Year (Y)	0.01	0.10**	0.01			
ANPP (L)	+0.01 [Ⓢ]	-0.00	-0.02**	+0.00	-0.02	-0.08
ANPP (Q)	+0.02**	+0.04**	+0.00	-0.22	+0.03	+0.03
ANPP (L) × Y	0.04**	0.06 [Ⓢ]	0.02*			
ANPP (Q) × Y	0.03*	0.06	0.01			
<i>Richness</i>						
Year (Y)	0.05**	0.17***	0.11***			
ANPP (L)	-0.00	-0.00	-0.01*	+0.35*	-0.01	-0.13
ANPP (Q)	+0.00	+0.00	-0.00	-0.27 [Ⓢ]	-0.02	+0.01
ANPP (L) × Y	0.02	0.05 [Ⓢ]	0.00			
ANPP (Q) × Y	0.01	0.02	0.00			
<i>Simpson's diversity</i>						
Year (Y)	0.03 [Ⓢ]	0.20***	0.10***			
ANPP (L)	-0.00 [Ⓢ]	-0.00	-0.00	+0.07	-0.05	-0.35 [Ⓢ]
ANPP (Q)	+0.00	+0.01 [Ⓢ]	+0.01*	-0.44*	+0.01	+0.10
ANPP (L) × Y	0.01	0.05	0.01			
ANPP (Q) × Y	0.03 [Ⓢ]	0.04	0.02			
<i>Shannon–Weiner Diversity</i>						
Year (Y)	0.04*	0.19***	0.12***			
ANPP (L)	-0.01 [Ⓢ]	-0.00	-0.00	+0.07	-0.05	-0.23
ANPP (Q)	+0.00	+0.01 [Ⓢ]	+0.01*	-0.60**	+0.00	+0.03
ANPP (L) × Y	0.01	0.05	0.00			
ANPP (Q) × Y	0.03*	0.03	0.01			

Levels of significance are represented by: ***, highly significant ($P < 0.001$); **, very significant ($P < 0.01$); *, significant ($P < 0.05$); and [Ⓢ], marginally non-significant ($P < 0.10$). The sign associated with an R^2 represents whether the coefficients for linear (L) or quadratic (Q) components of ANPP were positive or negative in regression models. Site codes are as in Table 2

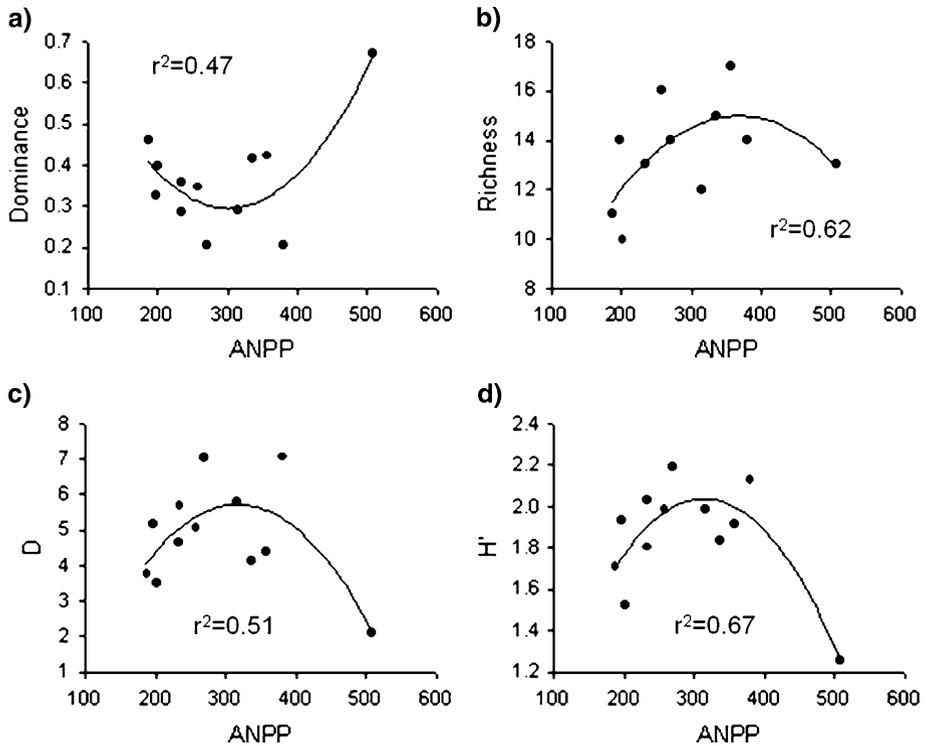


Fig. 2 Variation in (a) species dominance, (b) species richness, (c) Simpson's diversity (D) and (d) Shannon–Weiner's (H') index across a gradient of annual aboveground net primary production (ANPP; g/m^2) at Parkhill. Lines represent the results of regression analyses when ANPP accounted for a significant ($P < 0.05$) amount of variation in a measure of diversity

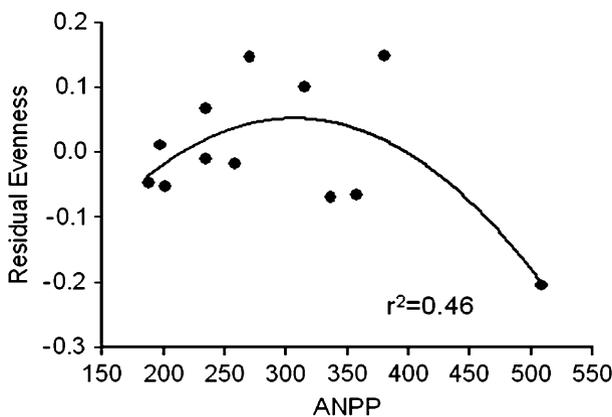


Fig. 3 Variability in species evenness across a gradient of annual aboveground net primary production (ANPP; g/m^2) at Parkhill after the effect of species richness on species evenness was removed. Residual values represent the extent to which species richness either overestimated or underestimated species evenness. Lines represent the results of regression analyses when ANPP explained a significant ($P < 0.05$) amount of variation in species evenness

Including E and the E * Y interaction in models explaining spatial variation in S did not substantially alter how any component of ANPP was associated with S at any site, except at Parkhill. At Parkhill, the inclusion of E in the analysis produced an increasing (linear component: $F_{1,8} = 6.50$, $P = 0.034$; quadratic component: $F_{1,8} = 7.98$, $P = 0.022$) but saturating association between S and ANPP. Furthermore, the amount of variation in S at Parkhill accounted for by linear and quadratic components of ANPP increased from 62% to 80%. Ordinary least square regression results for Parkhill were corroborated by least trimmed squares robust regression.

Discussion

Diversity-productivity associations are generally weak at small spatial scales

Considerable attention has been directed toward the relationship between S and productivity, but the relationship between productivity and other aspects of biodiversity has received considerably less attention. At all sites, spatial variation in at least one measure of biodiversity was associated significantly with productivity. No single measure of biodiversity, however, was significantly associated with productivity at all sites. Furthermore, the form of the association between a particular measure of biodiversity and productivity differed among sites as well as among years within a site. Nonetheless, spatial variation in productivity generally explained only a small proportion of the variation in any measure of biodiversity. In these cases, statistical significance may not indicate biological significance.

Weak associations between aspects of biodiversity and productivity are not unusual. For example, approximately 25% of the studies reviewed by Waide et al. (1999, Table 1) and Grace (1999), Table 2) reported non-significant S-productivity relationships or weak relationships (i.e., productivity explained <10% of the variation in S). Gross et al. (2000) and Chalcraft et al. (2004) reported spatial scale-dependence in S-productivity relationships at several LTER sites, and both reported that the strength of the association was weakest at the spatial scale considered here. Non-experimental studies reporting the strength of the association between natural variation in productivity and measures of biodiversity other than S are rare and have produced mixed results. Two studies (Vermeer and Verhoeven 1987; Weiher and Keddy 1999) reported weak associations between E and productivity ($r^2 < 8\%$), whereas one (Drobner et al. 1998) reported a stronger ($r^2 = 51\%$) association. Laird et al. (2003) found moderate associations between E and productivity at three sites ($r^2 > 28\%$), but their study focused on how spatial variation in E affected productivity, rather than how spatial variation in productivity affected E. Our results, in conjunction with prior studies, suggest that either spatial variation in productivity often has no appreciable effect on spatial variation in biodiversity when measured at small spatial scales, or that its effects are diminished by other environmental characteristics that evince considerable spatial variation (e.g., soil type or elevation, Grace et al. 2007).

Factors influencing the strength of biodiversity-productivity associations

Despite the general absence of strong associations between different measures of biodiversity and productivity, strong associations did occur at Parkhill. Consequently, it is important to identify factors that predispose some sites to evince such strong relationships. Prior studies report that the strength of S-productivity associations can change with the spatial scale of analysis (Gross et al. 2000; Scheiner and Jones 2002; Chalcraft et al. 2004),

but it is unlikely that such scale dependence is important here because the size of study plots at all six sites were similar ($\approx 1 \text{ m}^2$) albeit not identical. Furthermore, it is unlikely that disturbance history was important in causing variation in the strength of biodiversity-productivity associations. Although Laird et al. (2003) found that the association between S and productivity is weaker in sites that have not been disturbed by plowing recently than in sites recently disturbed by plowing, we found weak associations at sites with recent disturbances (Cedar Creek, Kellogg Biological Station and Temple-oldfield were previously cultivated) and sites (Short Grass Steppe and Temple-prairie were not previously cultivated) that were relatively undisturbed. Our strongest association between S and productivity occurred at Parkhill, a location that has never been cultivated.

So, what are characteristics of Parkhill that distinguish it from the other sites and that might contribute to the detection of strong productivity gradients of biodiversity? Parkhill differed from all sites except Temple-prairie, in that it is a remnant of a tall grass prairie that has never been plowed and has been managed by burning. Parkhill, however, has been managed by burning for a longer time period and is larger in size (21 vs 3 ha) than Temple-prairie (Wilsey et al. 2005). Consequently, some combination of community type, size of the habitat, and management history may play an important role in affecting biodiversity-productivity associations. Unfortunately, differences in the spatial scale at which data were collected at the six grassland sites for which we had data prevent making direct comparisons among sites. Alternatively, among site variation in associations between biodiversity and productivity could be due to among site variation in the history of community assembly (Fukami and Morin 2003), niche specialization (Kassen et al. 2000), and role of consumers (Leibold et al. 1997; Worm et al. 2002). Identifying the conditions that mitigate the influence of productivity on biodiversity is an important goal for future studies and future efforts should (1) attempt to collect data in similar ways in different sites so as to facilitate cross site comparisons and (2) conduct experiments at each site to examine the importance of assembly history, niche specialization, and consumers on the strength of the association between measures of biodiversity and productivity. Such information is essential to explain geographic variation in relationships between biodiversity and productivity.

Biodiversity measures vary in their response to productivity at Parkhill

Generally, strong associations existed between biodiversity measures and productivity at Parkhill but the form of the association differed among biodiversity measures. Increasing productivity was associated with an increase in S but dominance initially decreased and then increased after a threshold productivity level was surpassed (Fig. 2a, b). Although both S and dominance were correlated with productivity, they were not strongly associated ($r = -0.11$) with each other at Parkhill (Wilsey et al. 2005). The change in dominance with an increase in productivity may not be the result of partitioning resources among more species (i.e., adding more species steals resources away from dominant species). Rather an increase of productivity in unproductive areas is associated with coexisting subdominant and rare species acquiring a greater portion of the available resources than dominant species and an increase in productivity in intermediate or more productive areas tends to be associated with dominant species acquiring a greater portion of the available resources than coexisting subdominant species. In other words, the identity of the species that is better able to acquire resources changes across the productivity gradient. This supposition that productivity alters how resources are distributed among species independently of any changes in the number of species present is supported by the fact that evenness varied in a hump shaped fashion along a productivity gradient after removing the influence of S on E at Parkhill (Fig. 3).

In contrast, productivity was associated with a hump-shaped change in both D and H' (Fig. 2c, d) at Parkhill, and explained a comparable amount of variation in these diversity indices (51% and 67%, respectively) as it did for S (62%). This was surprising given that neither linear nor quadratic components of D or H' accounted for a large amount of variation in S (all P -values >0.59). Consequently, changes in a diversity index with productivity were not being primarily driven by changes in S . Instead, changes in diversity indices with productivity were greatly influenced by changes in E , as E is strongly correlated with D ($r = 0.90$, $P < 0.001$) and H' ($r = 0.77$, $P = 0.004$). These results suggest that productivity can have important associations with measures of biodiversity other than richness. More attention should be directed to studying the conditions in which productivity affects the relative abundance distributions of species and the mechanisms by which these changes take place.

The hump-shaped change in E with productivity at PH has not been predicted by any theory or reported by another empirical study of which we are aware, but Scheiner and Willig (2005) do consider circumstances (i.e., tradeoffs) required to produce modal relationships in biodiversity along environmental gradients. One possible explanation for this pattern is that an increase in productivity in unproductive locations tends to favor growth of subdominant species, whereas an increase in productivity of more productive locations tends to favor growth of dominant species. Alternatively, different mechanisms may be differentially important at different portions of the productivity gradient. For example, in areas with low productivity, dominant species may competitively suppress the relative abundances of sub-dominant species and herbivores avoid feeding in such unproductive areas. Herbivores may be attracted to areas with intermediate productivities, however, and preferentially consume competitive dominants. At high productivities, either herbivore suppression of dominants is insufficient to prevent the dominant competitors from suppressing the growth of sub-dominant or dominant species can use more of the available resource supply to invest in anti-predator defenses and force herbivores to leave the area or forage on subdominant vegetation. Further work is needed, however, to differentiate between these and possibly other mechanisms that could cause a hump-shaped change in E along a productivity gradient.

Summary

Understanding how biodiversity is distributed across our planet and identifying how anthropogenic influences alter biodiversity are important goals in ecology. Although a great deal of work focuses on species richness, much less attention has been directed at other conceptual aspects of biodiversity. Our work has demonstrated that there is substantial spatial variation in the different measures of biodiversity, and that these measures of biodiversity are often weakly correlated with each other (Wilsey et al. 2005). Furthermore, spatial variation in productivity accounts for a substantial amount of variation in biodiversity measures in some locations but not others and different measures of biodiversity respond to productivity in different ways. We believe that future studies should expand their focus of biodiversity to include measures of biodiversity that focus on abundance, and conduct experiments to identify the conditions in which these biodiversity measures will change predictably along productivity gradients.

Acknowledgements This study would not have been possible without the provision of data by the Cedar Creek LTER (J. Knopps and D. Tilman), the Kellogg Biological Station LTER (K. Gross), and the Shortgrass Steppe LTER (D. Milchunas and J. Moore) programs. The research group at SGS is a partnership between

Colorado State University, United States Department of Agriculture, Agricultural Research Service, and the U.S. Forest Service Pawnee National Grasslands. The National Science Foundation's Long-Term Ecological Research program provided significant funding for the collection of data (DEB-9632852). Analytical portions of this work were supported by the Knowledge and Distributed Intelligence Program (NSF Grant DEB 99-80154) and the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant DEB-0072909), the University of California, and the Santa Barbara campus. Additional support was provided by Texas Tech University and a USDA-ARS specific cooperative agreement no. 58-6206-0-023 faculty development grant from Iowa State University (BJW). We thank S. Andelman, I. Castro, J. Knopps, D. Milchunas, W. Polley, S. Presley, M. Smith, D. Tilman, H. Vance-Chalcraft and J. Williams for thoughtful comments on drafts of this manuscript.

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