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SCALE DEPENDENCE IN THE SPECIES-RICHNESS–PRODUCTIVITY RELATIONSHIP: THE ROLE OF SPECIES TURNOVER

David R. Chalcraft,[1,2,3] John W. Williams,[1] Melinda D. Smith,[1] and Michael R. Willig[2]

[1]*National Center for Ecological Analysis and Synthesis, 735 State Street Suite 300, Santa Barbara, California 93101 USA*
[2]*Ecology Program, Department of Biological Sciences and The Museum, Texas Tech University,*
Lubbock, Texas 79409 USA

Abstract. Recent research in aquatic systems suggests that productivity–richness relationships change with spatial scale and that species turnover (i.e., spatial and temporal variation in species composition) plays an important role in generating this scale dependence. The generality of such scale dependence and the effects of variation in temporal scale remain unknown. We examined the extent to which the richness–productivity relationship in terrestrial plant communities depends on spatial or temporal scale and evaluated how spatial and temporal turnover (i.e., species turnover in space and time) generates scale dependence in these relationships using data from two Long-Term Ecological Research (LTER) sites (Jornada and Konza). We found a weak hump-shaped relationship (Jornada) and no relationship (Konza) between richness and productivity at the smallest focal scale (1 m^2 at Jornada and 50 m^2 at Konza) at each site, but strong hump-shaped relationships at the largest focal scale (49 m^2 at Jornada and 200 m^2 at Konza) for each site. Relationships between spatial turnover and productivity at each site mirrored the productivity–richness relationships that emerged at the larger spatial scale (i.e., a significant hump-shaped pattern). In contrast, temporal turnover was unrelated to productivity, and hence increasing temporal scale did not appreciably change the form of the productivity–richness relationship. Our study suggests that the way in which productivity–richness relationships change with spatial or temporal scale depends on the form and strength of the underlying relationship between species turnover and productivity. Moreover, we contend that a dominant effect of increasing productivity is the generation of dissimilarity in species composition among localities that comprise a region, rather than increasing the number of species that occur within local communities. Thus, understanding the mechanisms that cause species turnover to vary with productivity is critical to understanding scale dependence in richness–productivity relationships.

Key words: biodiversity; environmental heterogeneity; grasslands; LTER; productivity; scale; species composition; species richness; species turnover; stability; terrestrial plants.

Introduction

A critical challenge for ecology is to understand the mechanisms linking ecosystem function and community dynamics (Loreau et al. 2001). The relationship between species richness and net primary productivity, key measures of biodiversity and ecosystem function, has been particularly controversial, with disagreement over whether productivity controls or is controlled by species richness (Waide et al. 1999, Loreau et al. 2001, Bond and Chase 2002). Theories predict positive monotonic, negative monotonic, or hump-shaped relationships, with empirical support for all three (see reviews by Waide et al. 1999, Mittelbach et al. 2001). Although some claim that the hump-shaped relationship is often invariant with spatial scale (Rapson et al. 1997, Huston 1999, Dodson et al. 2000), others (Moore and Keddy 1989, Rosenzweig 1995, Pastor et al. 1996, Waide et al. 1999, Weiher 1999, Gross et al. 2000, Loreau 2000, Loreau et al. 2001, Mittelbach et al. 2001, Whittaker et al. 2001, Chase and Leibold 2002, Scheiner and Jones 2002) argue that the shape of the relationship is scale dependent.

The relationship between richness and any environmental variable likely depends on focal scale (i.e., the inference space represented by each datum in an analysis; Scheiner et al. [2000], Whittaker et al. [2001]), because species richness changes with area in nonlinear ways (see Rosenzweig [1995] for review). Indeed, regional (γ diversity) richness, the number of species in a large focal area, is always greater than or equal to local richness (α diversity), the number of species in a smaller constituent focal area, due to differences in species composition (species turnover or β diversity) among localities (Whittaker 1972, Veech et al. 2002 for review). Recent studies (Whittaker et al. 2001, Chase and Leibold 2002) have hypothesized that focal scale dependence in the richness–productivity relationship results from the way in which species turnover changes with productivity. Although this idea is not

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[3] Present address: Department of Biology, East Carolina University, Greenville, North Carolina 27858 USA. E-mail: chalcraftd@mail.ecu.edu

new (Holt et al. 1994, Leibold 1996, Leibold et al. 1997, Grover and Holt 1998), only a few studies (Leibold 1999, Chase et al. 2000, Chase and Leibold 2002, Stevens and Willig 2002) have empirically examined the relationship between spatial species turnover and productivity or correlates of productivity (e.g., precipitation or latitude). All of these studies suggest that species turnover increases with productivity. Furthermore, Pastor et al. (1996) and Weiher (1999) demonstrated that parameters of the species–area curve can vary with productivity as well.

Species turnover occurs not only in space but also in time (e.g., MacArthur and Wilson 1967). Locations with higher temporal turnover will accumulate more species within a given time period than will locations with lower temporal turnover. As a result, the richness–productivity relationship will depend on temporal scale as well if temporal turnover is related to productivity. Dodson et al. (2000) found evidence for temporal scale-dependence in the richness–productivity relationship for lake communities, but did not quantify how temporal turnover varied with productivity.

We present a synthetic study that examines spatial, temporal and spatiotemporal scale dependence in the species-richness–productivity relationship in terrestrial plant communities. We independently aggregated species occurrence data from the Jornada and Konza Prairie Long-Term Ecological Research (LTER) sites at two different spatial and temporal focal scales, and then compared richness-productivity relationships across scales within each site. We consider scale dependence to occur if either the form or parameterization (with the exception of the *y* intercept) of the richness–productivity relationship changed significantly as focal scale increased (as in Waide et al. 1999, Gross et al. 2000, Mittelbach et al. 2001, Lyons and Willig 2002). We also evaluated how variance in productivity (a measure of environmental heterogeneity) and temporal changes in species composition, two of three mechanisms proposed by Chase and Leibold (2002) that may cause turnover to change with productivity, were related to productivity.

METHODS

The Jornada LTER site is located in southern New Mexico (32°30′ N, 106°48′ W; elevation ~1300 m), at the northern terminus of the Chihuahuan Desert. The Konza LTER site is located in the Flint Hills of northeastern Kansas (39°05′ N, 96°35′ W; elevation ~400 m). Both sites are dominated by low-stature vascular plants. For each site, we assembled information about species composition and net primary productivity from long-term monitoring plots. Aboveground net primary productivity (ANPP) was measured as the amount of dry aboveground plant biomass that accumulated within a 1-m^2 area during one year. A more detailed description of the sites and data are provided in the Appendix.

For each site, we considered two spatial scales: (1) a small (local) scale in which the focus was the smallest sampling unit for species composition (1-m^2 plots at Jornada, 50-m^2 plots at Konza), and (2) a large (regional) scale in which the focus was extended to a cluster of replicate plots (49 plots representing an area of 49 m^2 at Jornada, four plots representing an area of 200 m^2 at Konza). Although the size of the area applied to ''local'' and ''regional'' may differ among studies, we use these terms to identify our two relatively different scales of analysis within each site. As such, ecologists should be cautious when comparing patterns between any study sites using the terms ''local'' or ''regional.'' Because ''local'' and ''regional'' scales differed between our two studies sites (i.e., local at Konza is 50 m^2, local at Jornada is 1 m^2), we restricted our comparisons between scales to only within a study site and made only qualitative comparisons among study sites. Data were compiled for nine shrubland regions and six grassland regions at Jornada, and upland and lowland regions in eight different watersheds at Konza. We also defined two temporal scales: (1) an annual scale in which the focus was one year and (2) a multiannual scale in which the focus was the entire time interval of data collection (10 yr at Jornada, 5 yr at Konza).

Estimating richness, turnover, and productivity across space and time

The smallest focal scale in time and space is represented by annual local richness (α_S) and productivity ($\mathrm{ANPP}_{\mathrm{Loc}}$) for each plot. Because multiple years of data characterize each plot, we used the mean of the annual values of richness and productivity for each plot (i.e., $\bar{\alpha}_S$ and $\overline{\mathrm{ANPP}}_{\mathrm{Loc}}$; Fig. 1A). Species richness, turnover in species composition, mean productivity, and variance of productivity (a measure of environmental heterogeneity, Chase and Leibold 2002) were estimated for larger focal scales by independently aggregating plot data in space and time (Fig. 1). Importantly, estimates of species richness at large focal scales represent the cumulative number of unique species that occur within an aggregated set of plots (as in Chase and Leibold 2002) rather than the mean number of species that occur across an aggregated set of plots (as in Gross et al. 2000). We chose this measure because it accounts for greater richness at larger spatial scales due to among locality differences in species composition.

Annual regional focus.—The annual regional focus is presented in Fig. 1B. Annual regional richness ($\bar{\gamma}_S$) was calculated as the mean annual richness for each region, where the annual richness for each region is the number of unique taxa in a species list compiled from all plots in that region for a particular year. Spatial turnover (β_S) within a region was measured as the mean Jaccard dissimilarity index (Legendre and Legendre 1998) between all possible pairs of plots in a region

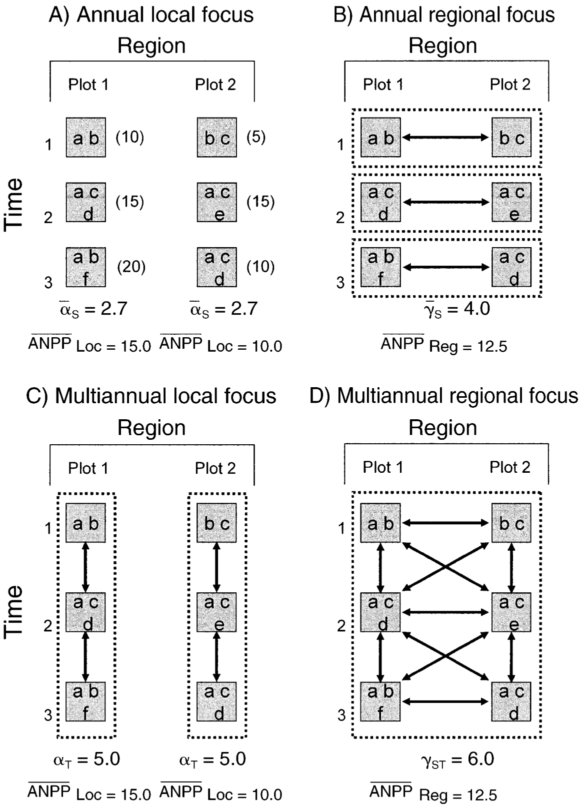

FIG. 1. Diagrammatic representation of protocols for aggregating data in analyses involving considerations of spatial and temporal scale. Two plots (gray squares) are illustrated within a single region, with three years (times 1, 2, and 3) of species composition and productivity data for each plot. Lowercase letters within each box identify the species that occur with each plot. Productivity values for particular plots are shown in parentheses in (A) only, but the same values apply to the plots in (B), (C), and (D). Four combinations of temporal and spatial foci were analyzed: (A) a short-term local focus in which there was no aggregation of plots, (B) a short-term regional focus in which plots within a region are aggregated within years (indicated by dashed box outlines), (C) a long-term local focus in which plots are aggregated in time but not space (indicated by dashed box outlines), and (D) a long-term regional focus in which all plots within a region are aggregated in time and space (indicated by dashed box outline). Arrows identify plots that were compared in deriving turnover estimates. The identities of the derived variables and the methods for their calculation are described in *Methods: Estimating richness, turnover, and productivity across space and time.*

for each year (arrows in Fig. 1B). Regional productivity ($\overline{\text{ANPP}}_{\text{Reg}}$), the mean annual productivity of a region, was calculated across all plots and years. Variance in regional productivity ($\overline{\text{ANPPVar}}_{\text{Reg}}$) was calculated as the annual mean of the variance in productivity among plots within each region.

Multiannual local focus.—The multiannual local focus is presented in Fig. 1C. Multiannual local richness (α_T) was the number of unique species in each plot across all yearly censuses. Temporal turnover (β_T) was calculated separately for each plot as the mean Jaccard dissimilarity between adjacent years, a measure that is functionally similar to Diamond and May's (1977) measure of temporal turnover. The productivity measure assigned to the multiannual local focus is the same as that applied to the annual local focus ($\overline{\text{ANPP}}_{\text{Loc}}$). Variance in temporal productivity (ANPPVar_T) was calculated as the variance of productivity for each plot across all years.

Multiannual regional focus.—The multiannual regional focus is presented in Fig. 1D. Multiannual regional richness (γ_{ST}) was measured as the total number of unique species in any plot within a region across all years. Temporal turnover at a regional focus ($\beta_{T,\ \text{Reg}}$) was calculated as the mean Jaccard dissimilarity across adjacent years for each region. We also calculated spatiotemporal turnover (β_{ST}), a combined index of spatial and temporal turnover, by calculating the mean Jaccard dissimilarity between all pairs of plots within a region within each year or adjacent years (but not non-adjacent years). The productivity measure assigned to the multiannual regional focus is the same as that applied to the annual regional focus ($\overline{\text{ANPP}}_{\text{Reg}}$), whereas the variance in spatiotemporal productivity (ANPPVar_{ST}) comprises the variance among all plots and years.

Analyses

The size of sampling units, distance among sampling units, and the spatial sampling structure (e.g., number of localities within a region) differed between the study sites. Consequently, we conducted statistical analyses separately for each site and qualitatively compared results. To improve the statistical power at the regional focus, we used data from different habitats (i.e., shrublands and grasslands) in Jornada and different topographic locations (i.e., upland and lowland) at Konza. We analyzed the species turnover-productivity relationship and the productivity variance-productivity relationship in each spatial and temporal dimension to determine if species turnover or productivity variance were functions of productivity and if scale dependence was attributable to these characteristics (Chase and Leibold 2002). Our results using Jaccard's dissimilarity index as a measure of species turnover were qualitatively similar to results obtained using an alternate measure of species turnover (β_{sim}) advocated by Koleff et al. (2003).

Relationships were evaluated using multiple regression analyses with a linear and quadratic term for productivity. To reduce collinearity between linear and quadratic terms, we centered the independent variable prior to regression (Neter et al. 1996). Regressions with significant quadratic terms subsequently were evaluated with the Mitchell-Olds and Shaw (MOS) test (Mitchell-Olds and Shaw 1987) for unimodality. The MOS test determines whether the predicted peak or minimum of a quadratic relationship occurs before or

TABLE 1. Regression analyses for the Jornada and Konza LTER sites.

Response variable	Error df	Linear component: Importance	Linear component: *P*	Quadratic component: Importance	Quadratic component: *P*	R^2	MOS
Jornada							
Species richness							
$\bar{\alpha}$s	732	0.001	0.399	0.046	<**0.001**	0.047	unimodal
$\bar{\gamma}$s	12	0.009	0.700	0.334	**0.030**	0.343	unimodal
α_T	732	<0.001	0.660	0.049	<**0.001**	0.049	unimodal
γ_{ST}	12	0.016	0.593	0.336	**0.028**	0.352	unimodal
Turnover							
β_S	12	<0.001	0.934	0.303	**0.041**	0.303	unimodal
β_T	732	0.003	0.148	<0.001	0.626	0.003	NA
β_{ST}	12	<0.001	0.996	0.483	**0.006**	0.483	unimodal
Heterogeneity							
$\overline{\text{ANPPVar}}_S$	12	0.146	0.143	0.143	0.147	0.289	NA
ANPPVar_T	732	0.431	<**0.001**	0.003	**0.035**	0.434	unimodal
ANPPVar_{ST}	12	0.676	<**0.001**	0.002	0.768	0.678	NA
Konza							
Species richness							
$\bar{\alpha}_S$	61	0.060	0.053	0.007	0.499	0.067	NA
$\bar{\gamma}_S$	13	0.012	0.626	0.337	**0.022**	0.349	unimodal
α_T	61	0.008	0.483	0.025	0.214	0.033	NA
γ_{ST}	13	0.000	0.983	0.348	**0.021**	0.348	unimodal
Turnover							
β_S	13	0.007	0.666	0.507	**0.003**	0.514	unimodal
β_T	61	0.173	0.743	0.025	0.211	0.027	NA
β_{ST}	13	0.000	0.989	0.264	**0.050**	0.264	unimodal
Heterogeneity							
$\overline{\text{ANPPVar}}_S$	13	0.230	0.056	0.095	0.200	0.324	NA
ANPPVar_T	61	0.351	<**0.001**	0.000	0.965	0.351	NA
ANPPVar_{ST}	13	0.477	**0.004**	0.002	0.825	0.479	NA

Notes: Probabilities (*P*) are for *F* tests evaluating whether linear or quadratic components of productivity explain a significant amount of variation of a response variable. Bold lettering identifies those *P* values that are significant ($\leq$0.05). Importance of linear and quadratic components is estimated by the proportion of the total sums of squares attributable to each component. The MOS column indicates whether the quadratic component reflects a significant unimodal relationship based on the Mitchell-Olds Shaw (MOS) test. NA indicates that the MOS test is not applicable because the quadratic component was not significant.

after the lowest or highest observed productivity value used in the regression analysis. Type I sums of squares were used for all analyses and linear terms were always entered into the model first. All analyses were conducted using SAS statistical software, version 8.1 (SAS Institute 1999).

RESULTS

Annual local and regional focus

The relationship between $\bar{\alpha}_S$ and $\overline{\text{ANPP}}_{\text{Loc}}$ was weak but significant at Jornada, with the linear and quadratic terms accounting for a small fraction of the variation in $\bar{\alpha}_S$ (Table 1A, Fig. 2). At Konza, the relationship was not significant (Table 1B, Fig. 2). A significant unimodal relationship characterized $\bar{\gamma}_S$ and $\overline{\text{ANPP}}_{\text{Reg}}$ at Jornada and at Konza (Table 1, Fig. 3A, B). At each site, the quadratic component of the model accounted for ~35% of the variation in $\bar{\gamma}_S$ (Table 1). Removing the one outlier with low species richness at Konza (Fig. 3B) did not qualitatively change the results. The relationship between β_S and $\overline{\text{ANPP}}_{\text{Reg}}$ was unimodal (Tables 1, Fig. 3C, D) and peaked at a productivity that was similar to that detected for the $\bar{\gamma}_S$–$\overline{\text{ANPP}}_{\text{Reg}}$ curve at Jornada and at Konza. Variation in β_S at each site was explained mostly by quadratic components (Table 1), although the overall fit of the model was better for Konza ($R^2 = 0.51$) than for Jornada ($R^2 = 0.30$). No significant relationship existed between $\overline{\text{ANPPVar}}_S$ and $\overline{\text{ANPP}}_{\text{Reg}}$ at either site (Table 1, Fig. 3E, F).

Multiannual local focus

A weak unimodal relationship existed between α_T and $\overline{\text{ANPP}}_{\text{Loc}}$ at Jornada, whereas the relationship was not significant at Konza (Table 1, Fig. 4A, B). Hence, the relationship was more similar to that of $\bar{\alpha}_S$ and $\overline{\text{ANPP}}_{\text{Loc}}$ (Fig. 2) than to that of $\bar{\gamma}_S$ and $\overline{\text{ANPP}}_{\text{Reg}}$ (Fig. 3A, B). Linear and quadratic components of the model explained a small fraction of the variation in species richness at Jornada (Table 1). Variation in β_T was not associated with variation in $\overline{\text{ANPP}}_{\text{Loc}}$ at either site (Ta-

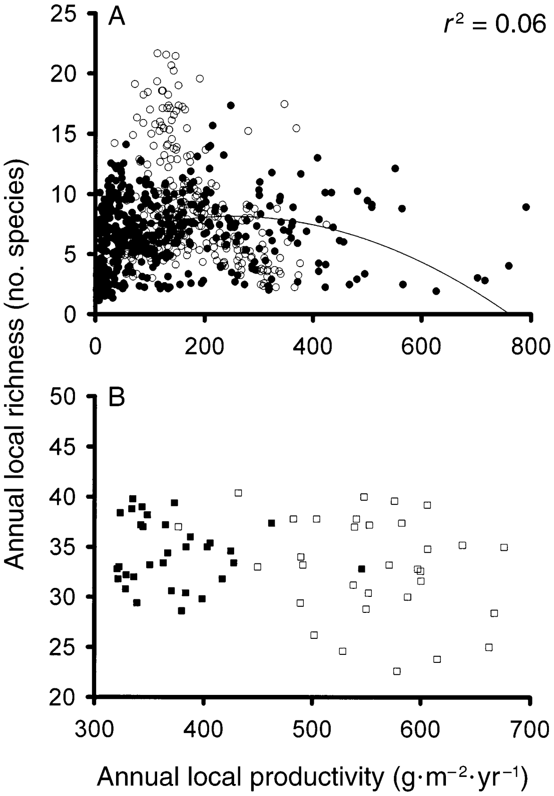

FIG. 2. The relationship between annual local species richness and productivity at (A) the Jornada and (B) the Konza LTER sites. Solid symbols represent data from shrubland (Jornada, $n = 441$) or from upland (Konza, $n = 32$) habitats, whereas open symbols represent data from grassland (Jornada, $n = 294$) or from lowland (Konza, $n = 32$) habitats. Lines are plotted only if the linear or quadratic components from a regression analysis were significant ($P \leq 0.05$). The local scale is 1 m^2 at Jornada and 50 m^2 at Konza.

ble 1, Fig. 4C, D) despite a strong positive relationship between $\text{ANPPVar}_{\text{T}}$ and $\overline{\text{ANPP}}_{\text{Loc}}$ (Table 1, Fig. 4E, F).

Multiannual regional focus

At broader spatial and temporal foci, the relationships among productivity, richness, and turnover closely matched the patterns observed for the short-term regional analyses (Fig. 3A–D). γ_{ST} was associated significantly with $\overline{\text{ANPP}}_{\text{Reg}}$ at Jornada and at Konza, and was significantly unimodal (Table 1). The quadratic component of the model explained ~34% of the variation in γ_{ST} (Table 1). Also, the relationship between β_{ST} and $\overline{\text{ANPP}}_{\text{Reg}}$ was unimodal at each site, with peak turnover and maximum species richness occurring at a similar productivity (Table 1). The quadratic component of the β_{ST}–$\overline{\text{ANPP}}_{\text{Reg}}$ relationship explained more of the variation in β_{ST} than did the linear component (Table 1). $\text{ANPPVar}_{\text{ST}}$ was correlated positively and linearly with $\overline{\text{ANPP}}_{\text{Reg}}$ (Table 1), reflecting the form of the relationship between $\text{ANPPVar}_{\text{T}}$ and $\overline{\text{ANPP}}_{\text{Loc}}$ (Fig. 4E, F) rather than that between $\text{ANPPVar}_{\text{S}}$ and $\overline{\text{ANPP}}_{\text{Reg}}$. No evidence existed for a relationship between $\beta_{\text{T,Reg}}$ and $\overline{\text{ANPP}}_{\text{Reg}}$ at Jornada (error df = 12, linear $P = 0.966$, quadratic $P = 0.185$) or Konza (error df = 13, linear $P = 0.759$, quadratic $P = 0.538$).

DISCUSSION

Our study supports the hypothesis that the richness–productivity relationship is dependent on spatial scale, and that variation in species turnover along productivity gradients is key to the generation of scale dependence. We observed either a weak hump-shaped relationship (Jornada) or no relationship (Konza) between species richness and productivity at the smallest focal scale at each site (Fig. 2), whereas we observed strong hump-shaped relationships between species richness and productivity at the largest focal scale at each site (Fig. 3A, B). In contrast, the relationship between species richness and productivity did not change with increasing temporal focus (Fig. 4A, B). The existence of scale dependence when increasing spatial focus but not temporal focus is due to spatial turnover changing with productivity (Fig. 3C, D) but not temporal turnover (Fig. 4C, D). Thus, the existence of scale dependence and the form of the richness–productivity relationship is influenced strongly by the turnover–productivity re-

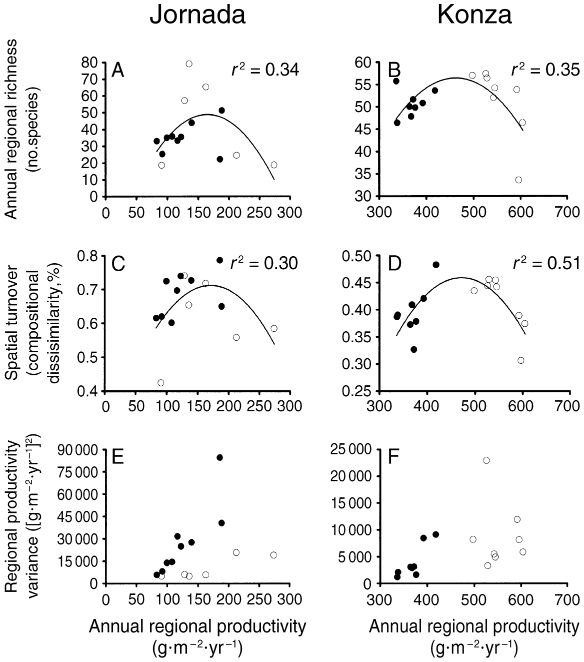

FIG. 3. Relationships between productivity and annual regional species richness, spatial turnover, and variance in regional productivity at Jornada (A, C, and E) or Konza (B, D, and F) LTER sites. Solid symbols represent data from shrubland (Jornada, $n = 9$) or from upland (Konza, $n = 8$) habitats, whereas open symbols represent data from grassland (Jornada, $n = 6$) or from lowland (Konza, $n = 8$) habitats. Lines are plotted only if the linear or quadratic components from a regression analysis were significant ($P \leq 0.05$). The regional scale is 49 m^2 at Jornada and 200 m^2 at Konza.

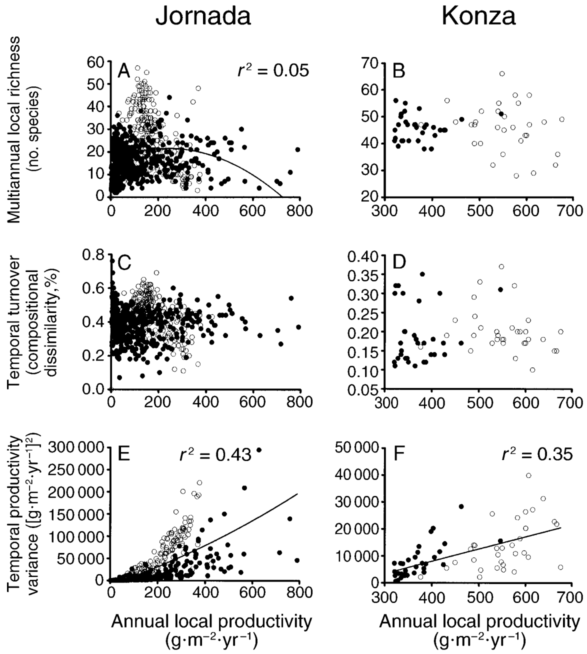

FIG. 4. Relationships between productivity and multiannual local species richness, temporal turnover, and variance in temporal productivity at Jornada (A, C, and E) or Konza (B, D, and F) LTER sites. Solid symbols represent data from shrubland (Jornada, $n = 441$) or from upland (Konza, $n = 32$) habitats, whereas open symbols represent data from grassland (Jornada, $n = 294$) or from lowland (Konza, $n = 32$) habitats. Lines are plotted only if the linear or quadratic components from a regression analysis were significant ($P \leq 0.05$). The local scale is 1 m^2 at Jornada and 50 m^2 at Konza. Jornada data were compiled for 10 years, and Konza data were compiled for 5 years.

lationship (Whittaker et al. 2001, Chase and Leibold 2002).

In contrast to previous studies showing species turnover increasing with productivity (Leibold 1999, Chase et al. 2000, Chase and Leibold 2002), spatial turnover at Jornada and Konza peaked at intermediate values of productivity and temporal turnover did not vary with productivity. Furthermore, we found either no evidence or weak evidence for a hump-shaped pattern between local richness and productivity. We also observed different patterns when comparing the regional richness–productivity relationship at Jornada (hump-shaped) to the local richness–productivity relationship at Konza (absent) even though the area represented by each scale was the same (i.e., 50 m^2) at each site. These discrepancies are not surprising as the shape of the richness–productivity relationship also can depend on the historical sequence in which communities assemble (Fukami and Morin 2003). Hence, the richness–productivity relationship and the species-turnover–productivity relationship manifest differently in different locations or times. Understanding the conditions that predispose one type of pattern (e.g., hump-shaped) to emerge over others is a fertile ground for research.

Mechanisms

Chase and Leibold (2002) proposed three mechanisms that could cause species turnover to vary with productivity. One mechanism is that environmental heterogeneity, measured as variance in productivity, causes species turnover and that environmental heterogeneity is correlated positively with productivity (environmental heterogeneity hypothesis). Together, these result in a positive relationship between species turnover and productivity and generate scale dependence. We found that variance in productivity was not correlated with mean productivity in space, but was correlated positively in time at each LTER site. Similarly, spatiotemporal turnover and variance in productivity were each associated with mean productivity, but the form of the association (Table 1) was different for each (hump-shaped for spatiotemporal turnover and positively linear for productivity variance). Because the form of the relationship between productivity variance and mean productivity consistently differed from the turnover–productivity relationships (Figs. 3, 4), it appears that environmental heterogeneity did not play an important role in causing species turnover to change with productivity in space or time. Heterogeneity in environmental factors that do not affect productivity could influence species turnover, but unless these factors are correlated with productivity (and not linked causally), this heterogeneity would not cause species turnover to change with productivity. Chase and Leibold (2002) reached the same conclusion in their study of ponds but were unable to evaluate other mechanisms causing turnover to change with productivity.

We found no support for Chase and Leibold's (2002) hypothesis that productivity affects species turnover by altering the probability of species extinction or colonization (stability hypothesis). Specifically, temporal changes in species composition were not associated with variation in productivity (Table 1, Fig. 3C–F).

Although lack of support for either the environmental heterogeneity or stability hypothesis indirectly supports Chase and Leibold's (2002) alternate stable state hypothesis, this hypothesis cannot be evaluated directly with current information, and other mechanisms may cause turnover to change with productivity. Future experiments should strive to quantify the strength and relative importance of mechanisms that cause turnover to vary with productivity. Concurrently, there is need to evaluate the conditions that cause turnover to peak at intermediate versus high productivity.

Effects of focus and extent on detecting scale dependence

The ability to detect scale dependence is, in part, determined by the difference in size between small and large focal scales. If the difference between spatial focal scales is small, then differences between local and regional richness across a gradient of productivity likely will be small because of only small changes in species turnover. Similarly, the degree to which differences in temporal focal scale (i.e., the temporal period represented by each datum) affects temporal scale dependence will depend on the longevity of species and rate of species turnover within and between years.

Detection of scale dependence also can depend on differences in another aspect of scale—extent—the inference space represented by the collection of data in an analysis (e.g., the spatial area or temporal domain over which all samples are collected; Scheiner et al. 2000, Whittaker et al. 2001). If the spatial or temporal extent is limited, then only a portion of broader relationships between productivity, turnover, and richness at local and regional foci may be captured (Guo and Berry 1999, Scheiner et al. 2000). Indeed, it is likely that increasing the number of years included in the analysis (if data were available), would increase the chance of including data from years with extreme values of productivity or high levels of species loss (e.g., drought; Tilman and El Haddi 1992). This could affect the form of the richness-productivity relationship at larger temporal scales and hence detection of scale dependence.

Detection of focal scale dependence in the productivity–richness relationship at Konza was influenced by spatial extent. If we had not included upland and lowland habitats, common elements of the landscape at Konza, in our examination (Figs. 2–4), we might have reported a positive (upland) or negative (lowland) relationship between regional richness–productivity rather than the hump-shape reported here. It is unclear whether the unimodal relationship between regional richness and productivity at Konza is the result of including multiple habitats in the analysis or of increasing the range of productivity included in the analysis (different habitats at Konza differ in productivity). In contrast, productivity only differed slightly between the habitats at Jornada (Figs. 2–4), so that the unimodal relationship between regional richness and productivity was likely the result of increasing productivity rather than including multiple habitats.

Conclusions

The relationship between species richness and productivity at two grassland sites was dependent on spatial but not temporal focal scale. Scale dependence in the richness–productivity relationship results from either spatial or temporal turnover of species changing with productivity. The lack of temporal scale dependence was the result of no change in temporal turnover of species with a change in productivity. Although no interaction between spatial and temporal focal scale was observed, our study reveals the need to separate the two in future studies. The nature of the cause and effect relationship between species richness and productivity was not addressed in this study, but our results suggest that the primary effect of increased productivity at Jornada and Konza was in the generation of dissimilarity in species composition among localities that compose a region, rather than in altering the number of species that occur within a particular locality. Although regions with intermediate productivity were comprised of localities that were more dissimilar in species composition, it is currently not known whether this dissimilarity is the result of intermediate productivity regions being comprised of mixes of community types from high and low productivity regions or whether it is the result of regions with intermediate productivity being comprised of many unique community types that do not occur in regions with low or high productivity. Hence, to better understand scale dependence in patterns involving species richness, future studies should strive to identify the mechanisms that cause species turnover to change with productivity or other driving environmental factors, and determine how the composition of communities change along productivity gradients.

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LITERATURE CITED

Bond, E. M., and J. M. Chase. 2002. Biodiversity and ecosystem functioning at local and regional spatial scales. Ecology Letters **5**:467–470.

Chase, J. M., and M. A. Leibold. 2002. Spatial scale dictates the productivity–biodiversity relationship. Nature **416**: 427–430.

Chase, J. M., M. A. Leibold, A. L. Downing, and J. B. Shurin. 2000. The effects of productivity, herbivory, and plant species turnover in grassland food webs. Ecology **81**:2485–2497.

Diamond, J. M., and R. M. May. 1977. Species turnover rates on islands: dependence on census interval. Science **197**: 266–270.

Dodson, S. I., S. E. Arnott, and K. L. Cottingham. 2000. The relationship in lake communities between primary productivity and species richness. Ecology **81**:2662–2679.

Fukami, T., and P. J. Morin. 2003. Productivity–biodiversity relationships depend on the history of community assembly. Nature **424**:423–426.

Gross, K. L., M. R. Willig, L. Gough, R. Inouye, and S. B. Cox. 2000. Patterns of species density and productivity at different spatial scales in herbaceous plant communities. Oikos **89**:417–427.

Grover, J. P., and R. H. Holt. 1998. Disentangling resource and apparent competition: realistic models for plant–herbivore communities. Journal of Theoretical Biology **191**: 353–376.

Guo, Q., and W. L. Berry. 1998. Species richness and biomass: dissection of the hump-shaped relationships. Ecology **79**:2555–2559.

Holt, R. H., J. Grover, and D. Tilman. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. American Naturalist **144**:741–771.

Huston, M. A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. Oikos **86**:393–401.

Koleff, P., K. J. Gaston, and J. J. Lennon. 2003. Measuring beta diversity for presence–absence data. Journal of Animal Ecology **72**:367–382.

Legendre, L., and P. Legendre. 1998. Numerical ecology. Elsevier Scientific Publications, Amsterdam, The Netherlands.

Leibold, M. A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. American Naturalist **147**:784–812.

Leibold, M. A. 1999. Biodiversity and nutrient enrichment in pond plankton communities. Evolutionary Ecology Research **1**:73–95.

Leibold, M. A., J. M. Chase, J. B. Shurin, and A. L. Downing. 1997. Species turnover and the regulation of trophic structure. Annual Review of Ecology and Systematics **28**:467–494.

Loreau, M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. Oikos **91**:3–17.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Rafaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science **294**:804–808.

Lyons, S. K., and M. R. Willig. 2002. Species richness, latitude, and scale sensitivity. Ecology **83**:47–58.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

Mitchell-Olds, T., and R. G. Shaw. 1987. Regression analysis of natural selection: statistical inference and biological interpretation. Evolution **41**:1149–1161.

Mittelbach, G. G., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, S. I. Dodson, and L. Gough. 2001. What is the observed relationship between species richness and productivity? Ecology **82**: 2381–2396.

Moore, D. R. J., and P. A. Keddy. 1989. The relationship between species richness and standing crop in wetlands: the importance of scale. Vegetatio **79**:99–106.

Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied linear statistical models. Fourth edition.Times Mirror Higher Education Group, Inc. Chicago, Illinois, USA.

Pastor, J., A. Downing, and H. E. Erickson. 1996. Species–area curves and diversity–productivity relationships in beaver meadows of voyageurs National Park, Minnesota, USA. Oikos **77**:399–406.

Rapson, G. L., K. Thompson, and J. G. Hodgson. 1997. The humped relationship between species richness and biomass—testing its sensitivity to sample quadrat size. Journal of Ecology **85**:99–100.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, UK.

SAS Institute. 1999. SAS/SYST STAT user's guide. SAS Institute, Cary, North Carolina, USA.

Scheiner, S. M., S. B. Cox, M. R. Willig, G. Mittelbach, C. W. Osenberg, and M. Kaspari. 2000. Species richness, species–area curves, and Simpson's paradox. Evolutionary Ecology Research **2**:791–802.

Scheiner, S. M., and S. Jones. 2002. Diversity, productivity and scale in Wisconsin vegetation. Evolutionary Ecology Research **4**:1097–1117.

Stevens, R. D., and M. R. Willig. 2002. Geographical ecology at the community level: perspectives on the diversity of New World bats. Ecology **83**:545–560.

Tilman, D., and A. El Haddi. 1992. Drought and biodiversity in grasslands. Oecologia **89**:257–264.

Veech, J. A., K. S. Summerville, T. O. Crist, and J. C. Gering. 2002. The additive partitioning of species diversity: recent revival of an old idea. Oikos **99**:3–9.

Waide, R. B., M. R. Willig, C. F. Steiner, G. Mittelbach, L. Gough, S. I. Dodson, G. P. Juday, and R. Parmenter. 1999. The relationship between productivity and species richness. Annual Review of Ecology and Systematics **30**:257–300.

Weiher, E. 1999. The combined effects of scale and productivity on species richness. Journal of Ecology **87**:1005–1011.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon **21**:213–251.

Whittaker, R. J., K. J. Willis, and R. Field. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. Journal of Biogeography **28**:453–470.

APPENDIX

Descriptions of study sites and procedures for measuring productivity are available in ESA's Electronic Data Archive: *Ecological Archives* E085-084-A1.