



Contrasting relationships between precipitation and species richness in space and time

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Future changes in precipitation regimes are likely to impact species richness in water-limited plant communities. Regional, spatial relationships between precipitation and richness could offer information about how altered rainfall will impact local communities, assuming that processes driving the regional relationship are also dominant at fine spatial and short temporal scales. To test this assumption, we compared spatial and temporal relationships between precipitation and both species richness and species turnover in central North American grasslands. Across a broad geographic gradient, mean plant species richness in 1-m² plots increased significantly with mean annual precipitation. In contrast, over a 36-yr period at one mixed-grass prairie in the center of the regional gradient, single-year precipitation and richness were poorly correlated, and consecutive wet years had little effect on richness. Instead, richness increased most in wet years that followed dry years. Geographically dispersed sites receiving different levels of mean annual precipitation displayed strong differences in species composition, whereas temporal variation in precipitation at one site was not related to compositional dissimilarity, indicating that species turnover plays a key role in generating the regional relationship. Analyses of individual species' presence-absence suggest that the lagged temporal responses reflect environmental germination cues more than resource competition. These complex cues may dampen the initial impact of altered precipitation on diversity, but over the long term, turnover in species composition should lead to changes in richness, as in the regional, spatial relationship. How quickly this long-term response develops may depend on the colonization rates of species better adapted to the altered rainfall regime.

The influence of resource availability on species richness is a classic problem in community ecology (Connell and Orias 1964, Grime 1979, Tilman 1988, Huston 1994), involving fundamental questions about how species interactions regulate diversity. Anthropogenic changes in resource supply have now made this problem relevant to conservation. For example, nitrogen deposition has led to sustained increases in resource supply with widespread effects on plant species richness (Stevens et al. 2004, Suding et al. 2005). Alteration of precipitation regimes under climate change is also likely to influence species richness, especially in arid and semiarid plant communities where water is a primary limiting resource (Noy-Meir 1973, Sala et al. 1988) and spatial correlations between rainfall and species richness are common (Richerson and Lum 1980, Linder 1991,

Pausas and Austin 2001). Such spatial relationships could be used to predict how communities will respond to changing resources. However, this approach assumes that the effect of resource supply on richness is constant across spatial and temporal scales, contrary to recent findings (Gough et al. 1994, Grace and Pugsek 1997, Leibold et al. 1997, Weiher 1999, Chase and Leibold 2002).

The traditional explanations for the effect of resource availability, or productivity, on diversity (Waide et al. 1999, Mittelbach et al. 2001) focus on short-term, local interactions involving population growth and resource competition. Increasing resources may elevate species richness by allowing a greater number of species to physiologically tolerate the environment and attain a minimum viable population

size (Preston 1962, Wright 1983). In other locations, increasing resources may reduce richness through some form of competitive exclusion: the species best-adapted to the high resource conditions monopolize limiting resources and drive other species extinct, though the precise mechanisms remain controversial (Grime 1979, Huston 1994). Under these traditional explanations, resource supply influences richness via its effects on the competitive interactions and growth rates of species already present in the local community. However, over long time-scales, these same processes drive immigration and extinction, producing communities that differ dramatically in the composition (Leibold et al. 1997, Weiher 1999, Chase and Leibold 2002) and size of species pools (Zobel 1992, Eriksson 1993, Gough et al. 1994, Grace and Pugsek 1997). This recent work suggests that the response of species richness to changing resource supply may depend less on short-term, local interactions than on the availability of immigrant species better adapted to the new resource conditions.

The Central Grasslands Region of North America provides an ideal case study for comparing short and long-term effects of precipitation variability on species diversity. A strong rainfall gradient spans the region, with mean annual precipitation increasing from about 300 mm in eastern Colorado to more than 800 mm in eastern Kansas (Fig. 1). These long-term differences in water availability have created distinct plant communities, ranging from shortgrass steppe in the semi-arid west to mixed-grass prairie and then tallgrass prairie in the mesic east (Küchler 1964). Primary production increases with precipitation across this

gradient (Sala et al. 1988), as does species richness at fine (Gross et al. 2000) and broad spatial scales (Withers et al. 1998).

At individual locations along the regional gradient, large interannual fluctuations in precipitation occur, in some cases exceeding the 500 mm difference in mean annual precipitation between eastern Colorado and eastern Kansas (Fig. 1). Yet the ability of individual communities to respond to this variability is constrained in the short term by the pool of species present in the community: one extremely wet year cannot turn shortgrass steppe into tallgrass prairie. Research on primary production illustrates this point, showing that the relationship between interannual variability in precipitation and temporal variability in production at a given site is much weaker than the spatial relationship between mean annual precipitation and mean production (Lauenroth and Sala 1992, Paruelo et al. 1999, Knapp and Smith 2001). Furthermore, lagged effects of precipitation are important, with higher production after consecutive wet years than in a wet year that follows a dry year (Oesterheld et al. 2001, Yahdjian and Sala 2006). Interannual variation in species richness could be similarly constrained by past conditions, yet few studies have examined the processes controlling variation in richness through time (Tilman and El Haddi 1992, Peco et al. 1998).

Current climate models forecast increasing precipitation in some portions of the Central Grasslands and decreases in others, with considerable uncertainty (National Synthesis Assessment Team 2001). Regardless of the direction of future changes, understanding how precipitation influences richness via processes

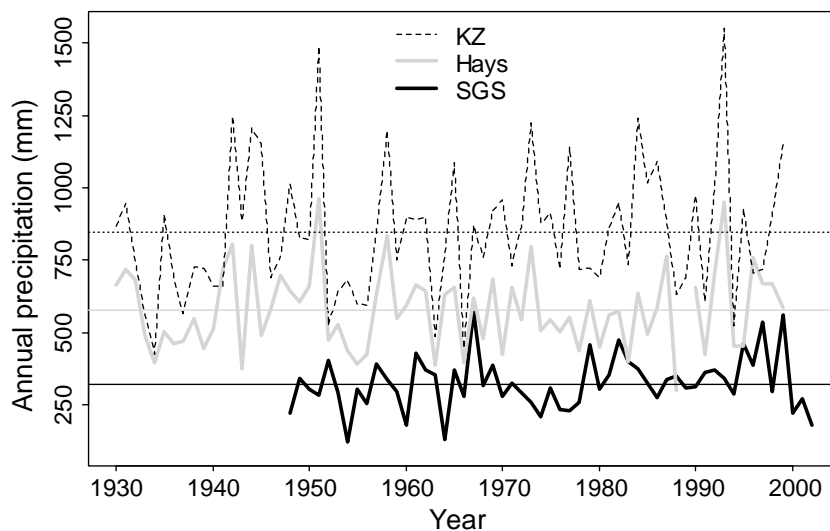


Fig. 1. Precipitation regimes in the Central Grasslands Region of North America. Mean annual precipitation (horizontal lines) increases moving east from the Shortgrass Steppe Long-Term Ecological Research (LTER) site (SGS), to mixed-grass prairie in western Kansas (Hays), to tallgrass prairie in eastern Kansas at the Konza Prairie LTER site (KZ).

operating at both long and short time scales (Camill and Clark 1998) will be critical for predicting the ecological impacts of altered precipitation. As a first step towards this goal, we compared spatial and temporal relationships between precipitation and species richness in the Central Grasslands Region. We had three specific objectives. First, we confirmed that the previously reported positive relationship (Withers et al. 1998, Gross et al. 2000) between mean annual precipitation and species richness across the regional gradient holds at 1-m² scales. Second, we used a 36-yr time series from one site in the center of the regional gradient to describe the temporal relationship between precipitation and richness, including lagged effects. Third, we analyzed turnover in species composition to show that the regional comparison involves distinct plant communities, whereas the temporal relationship holds composition relatively constant. These results suggest that compositional turnover, driven by immigration and extinction, constrains the long-term response of communities to changes in precipitation.

Methods

Spatial analysis of precipitation effects on species richness

To compare species richness across a regional gradient of mean annual precipitation, we assembled census data from 1-m² plots in six sites across the central grasslands region. Mean annual precipitation (MAP) for these sites ranges from 321 mm for Colorado shortgrass steppe to 835 mm for Kansas tallgrass prairie. We limited our analysis to data collected at the 1-m² scale to avoid the confounding effects of sampled area, and to match the spatial scale of the temporal analysis (below). For shortgrass steppe in northeastern Colorado (SGS), a northern mixed-grass prairie site at the High Plains Experimental Range in southeastern Wyoming (HP), a northern mixed-grass prairie site at Wind Cave National Park in South Dakota (WC), and a tallgrass prairie at Pipestone National Monument (PI) in southwestern Minnesota, we used data from Stohlgren et al. (1999). At each of these study areas, four groups of ten quadrats were sampled during 1996. Except for PI, where there was no grazing, quadrats at these study areas were located across a range of grazing intensities, including protected areas, light, and heavy grazing (Stohlgren et al. 1999). We used data from Adler and Lauenroth (2003) for southern mixed-grass prairie at Hays, Kansas, consisting of 10 grazed plots in a shortgrass community and 10 grazed plots in a little bluestem community, sampled in 2002 (we did not sample any quadrats in the ecotone community). These quadrats

receive light grazing each growing season. Finally, we used data from tallgrass prairie at the Konza Prairie LTER site, consisting of 30 plots in an ungrazed, annually burned treatment, and 40 plots in an ungrazed treatment burned every 20 years (Smith and Knapp 2001). These plots were sampled in 1999 and 2001. Spatial heterogeneity, disturbance regime (grazing and fire), and temporal variability all contribute to high variation in richness within each of these study areas. Our goal was not to explain this spatial variability, but to ask whether mean annual precipitation causes a regional trend in richness despite within-site variability. Therefore, we quantified the relationship between mean annual precipitation and species richness with linear regression based on all data points.

Temporal analysis of precipitation effects on species richness

We analyzed a 36-yr dataset from Hays, KS, to quantify the influence of interannual variation in precipitation on species richness in permanent plots. Hays has a MAP of 577 mm, close to the midpoint of the regional precipitation gradient described above. Variability in annual rainfall received at Hays from 1937–1972 spans the extremes of the regional precipitation gradients, with the driest year, 226 mm, below MAP for Colorado shortgrass steppe, and the wettest year, 1122 mm, above MAP for the Kansas tallgrass prairie site. Like other sites in the region, spring and summer rains contributed 80% of annual precipitation.

The Hays dataset consists of 1-m² permanent quadrats censused annually, with few exceptions, from 1937 to 1972 (Albertson and Tomanek 1965). Most quadrats were located inside livestock enclosures in one of three distinct community types (Albertson 1937). The shortgrass community, dominated by the warm-season perennial grasses *Bouteloua gracilis* and *Buchloe dactyloides*, occurs on the deep, loess soils of level uplands. The little bluestem community, dominated by the warm-season bunchgrass *Schizachyrium scoparium*, occurs on the shallow limestone soils of hillbrows and slopes. The third community is a well-defined ecotone separating the shortgrass and little bluestem areas. We analyzed 21 shortgrass quadrats, grouped on 4 transects, 14 ecotone quadrats grouped on 3 transects, and 12 little bluestem quadrats, grouped on 3 transects. Before analysis, we removed records not identified to species, and grouped by genus some pairs of species difficult to identify in the field.

We used statistical analyses to explain interannual variation in species richness as a function of variation in annual or seasonal precipitation. To account for spatial variability among quadrats, we analyzed each

community type separately (shortgrass, ecotone or little bluestem), and within each community introduced a random effect for individual transects, and a nested random effect for quadrats within each transect. Because observations of species richness on individual quadrats in consecutive years are likely to be correlated, not independent, we used a first-order autoregressive error structure, meaning that error in the current year depends on error the previous year, but is independent of longer lag effects. In addition, we removed long-term directional trends in the data, which were not the focus of our investigation, by introducing calendar year and year-squared as explanatory variables (Table A1 in Appendix 1). These long-term trends likely reflect recovery from the Great Drought of the 1930s (Albertson and Weaver 1944).

We then evaluated the influence of precipitation on species richness by adding climatic variables to these initial statistical models. The simplest regression incorporating precipitation effects, and the one most analogous to the spatial approach, adds annual precipitation as a predictor variable. We defined annual precipitation based on an October-September (fall through summer) annual cycle. We tested more complex regressions that included the effects of precipitation received in previous years (lag effects) or individual seasons, introduced non-linear effects through appropriate transformations, and used grass basal cover as a covariate. We used Akaike's information criteria (AIC) which penalizes against extra parameters (Burnham and Anderson 1998), as the basis for model selection. We ran all analyses in R (R Development Core Team 2005).

We also calculated the residual sums of squares (RSS) at the individual quadrat level for the different regression models. The difference in RSS between regressions with and without precipitation predictor variables, scaled by the total sums of squares and then averaged across quadrats, provides an index of variation explained by precipitation variables. Note that because these mixed-effects models rely on weighted least squares, the most likely statistical model may not be the one that minimizes the overall RSS. Therefore, this index provides only a coarse indication of the amount of variation in richness explained by precipitation variables.

We recognize that our ability to detect and analyze interannual variation in species richness will vary with the size of the permanent plots. Increasing plot size would decrease temporal turnover (Adler and Lauenroth 2003), dampening interannual variability in richness. However, given our interest in how resource availability mediates competitive interactions among plants, which occur at fine spatial scales, 1-m² plots are more appropriate than larger plots.

Response of individual species to precipitation

Richness is an aggregate response of many individual species. Therefore, to explain the temporal patterns of richness at Hays, we analyzed the influence of precipitation on the presence-absence of individual species in each quadrat. We used generalized linear mixed models (function "glmmPQL" in the MASS package of R). Quadrats were included as random effects to incorporate spatial variability. The independent variables were year (in case of temporal trends), presence or absence in the previous year, grass cover in the quadrat, and total precipitation in the current and previous year. We also performed a second set of regressions that included an interaction between current and previous year precipitation. Using the inverse of previous year precipitation had little effect on results. We analyzed all species with at least 20 presences. For each species, we only used data from quadrats in which the species occurred in at least one year.

Turnover in species composition

To compare patterns of species turnover in space, we calculated dissimilarity values for all pairs of quadrats located at the different sites along the regional precipitation gradient. For example, we paired each shortgrass steppe quadrat with every quadrat at all other study sites (the same six sites used for the analysis of regional richness). Before the analysis, we removed all taxa not identified to species and standardized all botanical synonyms.

We also calculated compositional turnover in time for the historical quadrats at Hays, KS. In this case, we compared all pairs of observed years for each quadrat (e.g. quadrat 1 in years 1937 vs 1938, 1937 vs 1939, etc.), but never compared different quadrats to each other.

We chose β_{sim} as our measure of species turnover:

$$\beta_{sim} = \frac{\min(b, c)}{\min(b, c) + a}$$

where a is the number of species found in both quadrats, and b and c are the number of species unique to each of the two quadrats (Koleff et al. 2003). Low values of β_{sim} indicate strong similarity (many shared species), high values strong dissimilarity. β_{sim} controls for bias introduced by differences in species richness (Koleff et al. 2003), meaning that we can safely compare dissimilarity between two quadrats with 10 and 20 species and two quadrats with 10 species each.

After calculating all dissimilarity values, we plotted compositional turnover in space against differences in mean annual precipitation between pairs of sites. Similarly, we plotted values of compositional turnover

in time against the difference in annual precipitation for the corresponding pair of years. We described the relationships between turnover and precipitation differences by fitting a logistic function with non-linear least squares regression.

Results

Spatial precipitation-richness relationship

We found that the regional gradient in mean precipitation affected species richness in a much different way than a similar range in precipitation experienced within a single community. The regional gradient showed a positive relationship between precipitation and richness: moving from semiarid shortgrass steppe to mesic tallgrass prairie, species richness increases from roughly 9 to 15 species per m^2 (Fig. 2; $r^2 = 0.25$, $F = 103.2$, $DF = 1,318$, $p < 0.0001$). The significant effect of precipitation emerged despite considerable variability in richness within each site, due to edaphic factors and management. Management varies across sites as well: none of the tallgrass prairie plots (PI and KZ) were grazed. Nevertheless, when we repeated the regression using only ungrazed and lightly grazed sites, we found a

similar relationship (slope = 1.4 species per 100 mm, $r^2 = 0.21$, $F = 60.8$, $DF = 1,228$, $p < 0.0001$).

Temporal precipitation-richness relationship

Based on the positive relationship between precipitation and richness observed across the regional gradient, we might have expected years of high precipitation to coincide with high richness at Hays, KS. But despite considerable interannual variability in both precipitation and richness (Fig. 3), current year precipitation only weakly affected species richness in the shortgrass and ecotone communities, and had no effect in little bluestem (Table A2). While increasing precipitation by 500 mm led to more than 6 new species per m^2 across the spatial gradient, the same increase from one year to the next at Hays would add only 0.7 new species in shortgrass, about 0.6 species in ecotone, and 0.1 species in little bluestem quadrats (Fig. 2).

The weak influence of precipitation on richness in the temporal analysis could be due to lagged or cumulative effects: richness might be controlled most strongly by precipitation in the previous year. In fact, previous year's precipitation did have a significant effect on species richness, but not in a direction consistent

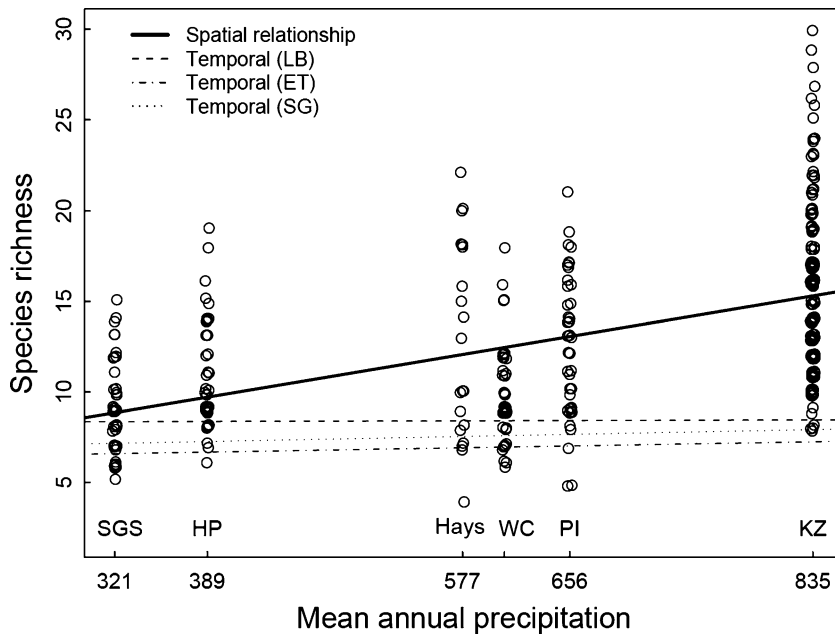


Fig. 2. Species richness increases across a regional gradient of mean annual precipitation. Points show mean species richness in 1- m^2 plots at the Shortgrass Steppe LTER (SGS); the High Plains Grasslands Research Station, WY (HP); Hays KS; Wind Cave National Park, SD (WC); Pipestone National Monument, MN (PI); and the Konza Prairie LTER (KZ). The solid line shows the regression of mean species richness on mean precipitation across this regional, spatial gradient. Temporal analyses of the response of species richness to interannual variation in rainfall in shortgrass (SG), ecotone (ET), and little bluestem (LB) communities at Hays, KS show much weaker relationships. The lower overall richness for the historical analyses relative to the 2002 values reflects recovery from the Great Drought of the 1930s as well as our conservative decisions about species' identities made while processing the original data.

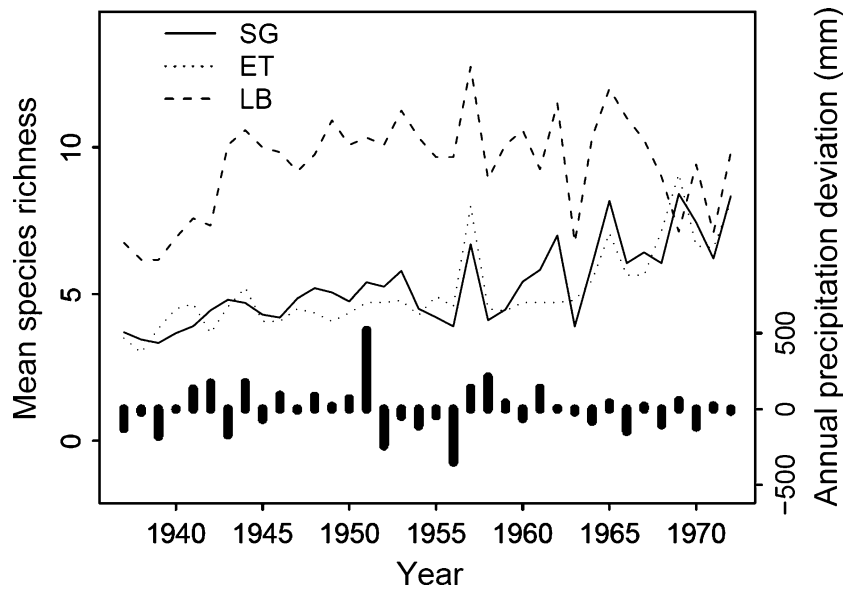


Fig. 3. Changes in mean species richness per 1-m² quadrat from 1937 to 1972 in three community types at Hays, Kansas. Means are from 21 shortgrass (SG), 14 ecotone (ET), and 12 little bluestem (LB) quadrats. Most quadrats, but not all, were sampled in every year. The vertical bars show annual deviations from mean annual precipitation (577 mm).

with the regional, spatial analysis. The effect of previous year precipitation on richness was negative in all three Hays communities, with higher species richness following a dry year than a wet year. In each community, incorporating the effects of precipitation in the previous year improved the models (Table 1), though considering precipitation over lagged periods of two or three years did not (not shown). Based on AIC, previous year precipitation was a better single-variable predictor of species richness than current year precipitation (compare “Current” and “Previous” in Table 1). The effect of precipitation in the previous year was non-linear: substituting previous year precipitation with its inverse improved the regressions considerably (note lower AIC values in Table 1; Table A3).

We also found significant interactions between precipitation in the current and previous year (Table A4). Regressions incorporating this interaction predict that consecutive wet or dry years will have little

effect on richness, but a wet year that follows a very dry year will lead to high richness (Fig. 4).

Although the predicted effects of precipitation on richness in these time series were large in magnitude (Fig. 4), we emphasize that precipitation, which is just one of many contributing factors, explained a small portion of temporal variability in richness. The interactive effects of previous and current year precipitation explained on average 4%, 15%, and 6% of the interannual variation in species richness that remained after accounting for long-term trends in shortgrass, ecotone, and little bluestem quadrats, respectively.

To explore competitive effects, we added the basal cover of perennial grasses to the regressions shown in Fig. 4. Grass cover was positively correlated with species richness in the shortgrass (slope = 0.0002 spp cm⁻² cover, $t = 5.93$, $DF = 666$, $p < 0.0001$) and was not significantly correlated with richness in ecotone (slope = 0.0001 spp cm⁻² cover, $t = 1.50$, $DF = 432$,

Table 1. Comparison of regression models used to describe the influence of precipitation on temporal variation in species richness in three Hays, Kansas plant communities. Shown are values of Akaike’s information criteria (AIC) for each model; the best model (lowest AIC value) for each community is in bold. “Current” refers to Oct.-Sept. total precipitation that includes the growing season when species richness was sampled. “Previous” refers to annual precipitation in the preceding climate year, and its inverse, “Previous⁻¹”, introduces a non-linear effect.

Precipitation variables in model	Shortgrass	Ecotone	Little bluestem
Current	2804.95	1748.58	2086.87
Previous	2809.84	1733.16	2083.91
Previous ⁻¹	2769.13	1679.69	2051.33
Current+previous ⁻¹	2780.07	1695.20	2064.62
Current+previous ⁻¹ + current-previous ⁻¹	2764.86	1669.44	2057.78

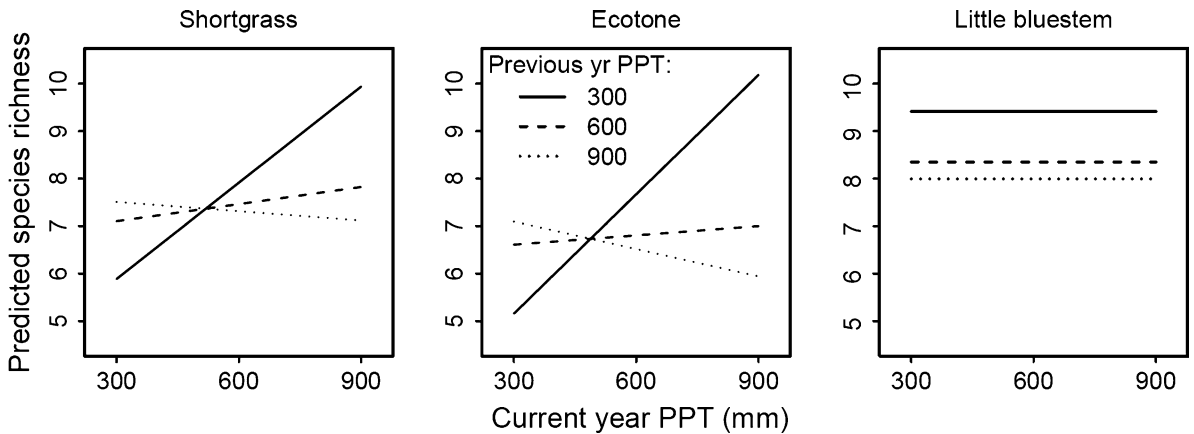


Fig. 4. Predicted species richness as a function of precipitation in the current and previous year for three community types at Hays, Kansas. Predictions are based on fixed effects from the best regression model for each community type, as selected by AIC (Table 1). For the shortgrass and ecotone communities, this was the model incorporating interactive effects of current and previous year precipitation (Table A4). For the little bluestem community, the best model included only the inverse of precipitation received in the previous year (Table A3). Calendar year is a predictor variable in both models; we used '72, the last year of the time series, to generate the values shown here.

$p = 0.13$) and little bluestem quadrats (slope = 0.0001 spp/cm² cover, $t = 0.66$, $DF = 408$, $p = 0.51$). Grass cover in the previous year had no significant effects (all p 's > 0.15).

Temporal response of individual species

We analyzed how precipitation influenced the presence-absence of 57 individual species over time at Hays, KS; 22 responded significantly to precipitation in current or previous years (Table 2). 11 species, including 5 annuals and a biennial, were favored by low precipitation in the previous year. 4 species, all perennials, were favored by high precipitation the previous year. Of these 15 species, 3 were favored by high current year precipitation but low previous year precipitation. Including an interaction between current and previous year precipitation lowered AIC for only 2 of the 22 species listed in Table 2 (not shown); in both cases the interaction led to a higher probability of species presence in wet years following dry years, consistent with results of the richness analysis. Grass cover often had positive effects on forbs and annuals, but had a negative effect on one uncommon perennial grass.

Species turnover in space and time

Quadrats located at different study areas along the regional precipitation gradient shared few species in common. As the difference in mean annual precipitation between study areas increased, compositional turnover increased as well (Fig. 5A). In other words,

shortgrass and tallgrass prairie quadrats differed more than shortgrass and mixed-grass quadrats.

The comparison of permanent quadrats sampled in different years showed a much different pattern. Species turnover was very low, and many plots had identical composition. In addition, there was no clear relationship between turnover and differences in annual precipitation: a dry and a wet year were, on average, no less similar than two dry years (Fig. 5B).

Discussion

The effects of precipitation on species richness across a broad spatial gradient differed greatly from precipitation effects at a single site through time. The spatial analysis showed a positive effect of precipitation on richness, with each 100 mm increase in rainfall adding more than 1 species m⁻², on average. This positive relationship between precipitation and richness, common in grasslands (Cornwell and Grubb 2003, Adler et al. 2005), could be generated by indirect effects of precipitation on a variety of biotic and abiotic variables. However, if we make the simple interpretation that increasing rainfall promotes richness by reducing abiotic stress, we would then expect the temporal relationship to show high richness in wet years, or after a series of wet years. But our analysis of permanent plots at Hays, KS showed a much different pattern: neither a single wet year nor consecutive wet (or dry) years had strong effects on richness. Precipitation in the previous year was a better predictor of richness than current year precipitation but, surprisingly, this lagged effect was negative, meaning high richness following dry years. In

Table 2. Response of individual species to precipitation at Hays, KS. Probability of presence in individual quadrats was increased (+), decreased (–), or not significantly influenced (ns) by total grass cover, precipitation in the current year, and previous year precipitation. Species responding most negatively to previous year precipitation are ranked first. The regressions controlled for quadrat effects, directional temporal trends, and presence in the quadrat the previous year (not shown). “Frequency” refers to the percent of all quadrat-year observations in which the species was present for shortgrass (SG), ecotone (ET), and little bluestem (LB) communities. Species not affected by precipitation ($p < 0.05$) are not shown.

Species	Functional type	Grass cover	Current ppt.	Previous ppt.	Frequency		
					SG	ET	LB
<i>Salsola iberica</i>	Annual	ns	ns	–	1.59	2.66	0.47
<i>Chenopodium album</i>	Annual	ns	ns	–	1.88	6.43	0.94
<i>Sitanion hystrix</i>	Perennial grass	ns	–	–	1.59	8.87	2.35
<i>Helianthus annuus</i>	Annual	ns	ns	–	3.03	8.43	4.23
<i>Coryza canadensis</i>	Annual	ns	ns	–	3.03	2.44	0.23
<i>Panicum virgatum</i>	Perennial grass	ns	ns	–	0.00	0.00	12.91
<i>Lactuca ludoviciana</i>	Biennial	ns	+	–	1.59	3.77	0.00
<i>Polygala verticillata</i>	Annual	ns	+	–	3.03	0.00	0.00
<i>Oxalis stricta</i>	Perennial forb	ns	+	–	6.21	0.22	0.47
<i>Psoralea tenuiflora</i>	Perennial forb	+	–	–	24.71	66.30	40.38
<i>Ambrosia psilostachya</i>	Perennial forb	+	+	–	51.30	59.87	36.62
<i>Aristida spp.</i>	Perennial grass	ns	ns	+	39.74	5.99	3.99
<i>Ratibida columnifera</i>	Perennial forb	+	+	+	26.59	4.66	3.76
<i>Agropyron smithii</i>	Perennial grass	–	ns	+	2.31	2.66	0.00
<i>Helianthus maximiliani</i>	Perennial forb	ns	ns	+	0.58	2.00	2.58
<i>Opuntia macrorhiza</i>	Succulent	ns	–	ns	6.79	0.44	0.70
<i>Liatris punctata</i>	Perennial forb	ns	–	ns	0.87	0.44	15.96
<i>Sporobolus cryptandrus</i>	Perennial grass	+	–	ns	22.11	1.77	7.04
<i>Andropogon gerardii</i>	Perennial grass	ns	+	ns	6.94	32.15	65.02
<i>Gutierrezia sarothrae</i>	Shrub	ns	+	ns	8.53	1.11	11.97
<i>Opuntia humifusa</i>	Succulent	+	+	ns	7.95	1.77	1.88
<i>Chamaesyce spp.</i>	Perennial forb	ns	+	ns	2.75	0.44	0.00

shortgrass and ecotone quadrats, the highest richness occurred in wet years that followed dry years, due to the interactive effect of current and previous year precipitation. Our analyses of precipitation effects on individual species confirmed these results, with many species, especially annuals, responding positively following dry conditions the previous year.

Patterns of species turnover explain the contrasting relationships between precipitation and richness in space and time. Each study area along the regional precipitation gradient had a relatively unique species composition, and the numbers of species shared by sites decreased with larger differences in precipitation. This result emphasizes that current species assemblages represents the outcome of long-term interactions between mean resource availability and immigration, population growth, and extinction (Leibold et al. 1997). In contrast, quadrats sampled through time at Hays had much lower species turnover, and turnover was not related to precipitation differences between years. The year-to-year dynamics, which featured higher richness following dry years, reflect short-term, local processes. Based on previous work (Grime 1979, Sarr et al. 2005), we expected resource competition might play a central role, but as we explain below, we found little evidence that competitive interactions drive temporal variation in richness at Hays.

Population-level processes controlling the temporal relationship

Inter-specific competition offers one potential explanation for the result we observed in the shortgrass and ecotone plots, where richness was especially high in wet years that followed dry years. If the abundance of the dominant perennial grasses is reduced during a very dry year, more resources would be released to the diverse guild of forb species in a subsequent wet year, assuming that the forbs have superior dormancy (Levine and Rees 2004). Under this scenario, we would expect a negative correlation between perennial grass cover and species diversity. Instead, we found a number of positive correlations between grass cover and either richness or individual species' presence, suggesting that conditions favorable for grasses are also favorable for the diverse forbs.

We cannot definitively reject the competition hypothesis. Basal cover may be a poor proxy for resource uptake, or cover measured at the end of the growing season may miss critical interactions occurring early in the growing season. But we can say with confidence that competitive interactions are not strong enough to overwhelm such sources of error. More importantly, it is not clear how measurement error could lead to the observed positive relationships between grass cover and richness or species presence.

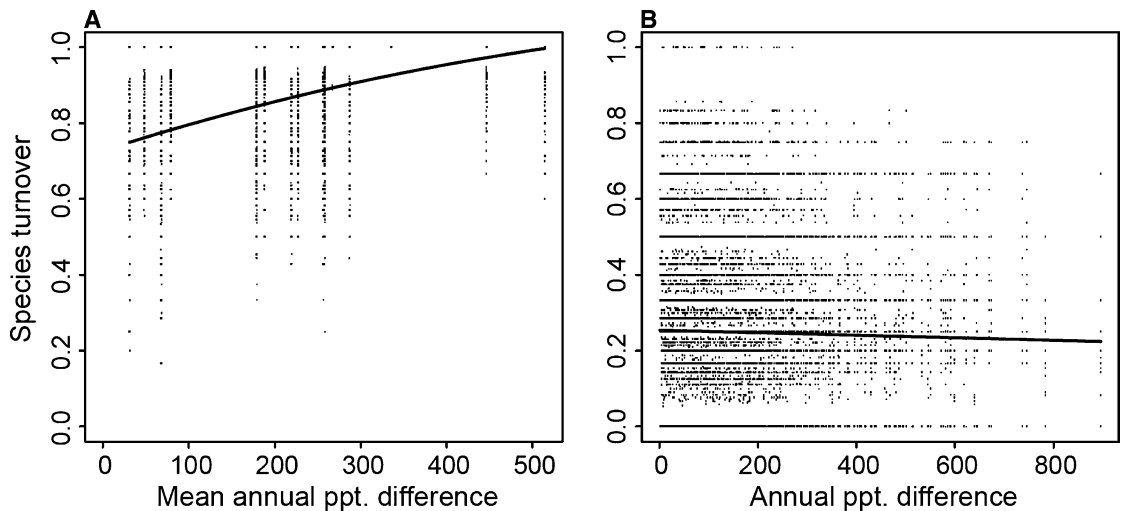


Fig. 5. Species turnover as a function of precipitation differences in space and time. (A) Dissimilarity between all pairs of 1-m² quadrats located at study sites differing in mean annual precipitation (e.g. a Hays plot vs a Konza plot). (B) Dissimilarity for all pairs of permanent 1-m² quadrats at Hays, KS observed in years receiving different precipitation (e.g. the same quadrat in 1939 vs 1955). Dissimilarity was calculated using β_{sim} , which controls for differences in species richness. The lines are best fits for a logistic function.

The positive correlations are consistent with recent work showing the importance of facilitation, especially in stressful environments (Bruno et al. 2003).

The lack of evidence for the competitive release mechanism encourages consideration of alternative hypotheses. One possibility is that richness increases following very dry years because of environmental cues for growth or germination triggered by particular climate conditions (Chesson 2000, Crawley 2004). For example, dry conditions may be necessary to crack the seed coats of some species, releasing them from physical dormancy (Baskin and Baskin 2001). Alternatively, a dry period might lead to a more intense pulse of nitrate upon rewetting (Austin et al. 2004). Since nitrate functions as a germination cue for some species (Baskin and Baskin 2001), such a pulse could be an important trigger.

The response of individual species to precipitation provides indirect evidence for the environmental cueing hypothesis. Six of the eight individual species responding most positively to dry conditions the previous year were annuals or biennials, meaning that their dynamics depend critically on germination. Furthermore, many of these species benefited from drought in the previous year regardless of precipitation the current year, emphasizing the importance of cues rather than total water availability. The annuals appear to play a disproportionate role in driving the temporal pattern of richness, since they contribute only 3.5, 4.6, and 1.2% of average richness in shortgrass, ecotone, and little bluestem quadrats, respectively. The low contribution of annuals to richness in little bluestem quadrats may

explain differences among the three communities in model selection (Table 1).

The potential for precipitation to influence richness through cueing highlights what Grace (2001) refers to as a “nonresource environmental effect.” In other words, the role of precipitation in triggering germination may be independent of precipitation’s effect on total resource availability, at least on ecological time scales (on evolutionary timescales we should expect a relationship). Nonresource environmental effects might also explain why two belowground resources, water and nitrogen, frequently have different effects on species richness (Goldberg and Miller 1990, Cornwell and Grubb 2003). For example, water availability might influence richness primarily through nonresource effects, whereas nitrogen’s resource effects might be dominant. It is tempting to interpret regional relationships between resource variables and richness in terms of local resource competition. However, we should be suspicious of such interpretations for two reasons: First, regional relationships may reflect historical processes involving species turnover more than inter-specific interactions and, second, environmental variables can have both resource and nonresource effects on richness.

Predicting effects of climate change on species richness

The difference between the spatial and temporal precipitation–richness relationships suggests that short and long-term responses to future changes in precipitation

may also differ. The spatial relationship implies that a long-term increase in precipitation at a site will eventually lead to increases in species richness at the 1-m² scale, while decreases in precipitation will decrease richness. The temporal relationship, which was considerably weaker and more complex, indicates that richness may not respond to the initial phase of a change in mean precipitation.

How many years of increased precipitation would be necessary to overcome these short-term processes and increase richness to levels predicted by the spatial relationship? The patterns of species turnover offer a clue: whereas the spatial analysis compares sites that differ dramatically in species composition, the temporal analysis constrains changes in species composition. The implication is that strong relationships between precipitation and richness depend more on turnover of species pools than on short-term resource competition. Therefore, an increase in richness at Hays would require the immigration of species better adapted to mesic conditions. This hypothesis is supported by recent work in a Kansas tallgrass prairie showing that water additions had strong positive effects on richness only when combined with seed additions that increased the size of the species pool (Foster and Dickson 2004). Natural immigration, however, may be quite slow. Increases in diversity following the 1930's drought accumulated over several decades (Fig. 3), the result of slow but steady arrival into the plots of immigrants from either local refugia or regional sources. Immigration rates could be even slower in extremely fragmented habitats, such as the tallgrass prairie. Where such barriers to dispersal exist, the temporal relationship might be more appropriate than the spatial relationship for predicting how altered precipitation will affect species richness.

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Appendix 1.

Table A1. Statistical tables for the initial model, explaining spatial variability among quadrats and long-term trends in species richness for three community types at Hays, Kansas.

Shortgrass community (n = 692), auto-regressive parameter: 0.24

Fixed effects	Parameter estimate	Standard error	DF	T	p
Intercept	-0.56	0.61	670	-0.91	0.36
Year	0.11	0.01	670	13.63	<0.0001

Ecotone community (n = 451), auto-regressive parameter: 0.25

Fixed effects	Parameter estimate	Standard error	DF	T	p
Intercept	-0.48	0.66	436	-0.74	0.46
Year	0.10	0.01	436	9.45	<0.0001

Little bluestem community (n = 426), auto-regressive parameter: 0.35

Fixed effects	Parameter estimate	Standard error	DF	T	p
Intercept	-22.03	5.76	412	-3.83	0.0002
Year	1.14	0.20	412	5.58	<0.0001
Year ²	-0.0099	0.0019	412	-5.31	<0.0001

Table A2. Statistical tables for regression models incorporating the effect of annual precipitation on species richness in the three Hays communities.

Shortgrass community (n = 692), auto-regressive parameter: 0.27

Fixed effects	Parameter estimate	Standard error	DF	T	p
Intercept	-1.47	0.66	669	-2.22	0.027
Year	0.11	0.008	669	13.76	<0.0001
Current PPT	0.0015	0.0004	669	3.67	0.0003

Ecotone community (n = 451), auto-regressive parameter: 0.32

Fixed effects	Parameter estimate	Standard error	DF	T	p
Intercept	-1.30	0.72	435	-1.80	0.07
Year	0.10	0.01	435	9.41	<0.0001
Current PPT	0.0013	0.0005	435	2.82	0.005

Little bluestem community (n = 426), auto-regressive parameter: 0.35

Fixed effects	Parameter estimate	Standard error	DF	T	p
Intercept	-22.	5.76	411	-3.82	0.0002
Year	1.13	0.212	411	5.52	<0.0001
Year ²	-0.0099	0.0019	411	-5.26	<0.0001
Current PPT	0.00019	0.00076	411	0.26	0.80

Table A3. Statistical tables for regression models incorporating the effect of the inverse of the previous year's precipitation on species richness in the three Hays communities.

Shortgrass community (n = 692), auto-regressive parameter: 0.30

Fixed effects	Parameter estimate	Standard error	DF	T	p
Intercept	-1.65	0.66	669	-2.49	0.013
Year	0.11	0.009	669	13.20	<0.0001
1/previous PPT	526.2	102.3	669	5.15	<0.0001

Ecotone community (n = 451), auto-regressive parameter: 0.35

Fixed effects	Parameter estimate	Standard error	DF	T	p
Intercept	-1.98	0.68	435	-2.91	0.004
Year	0.10	0.01	435	9.38	<0.0001
1/previous PPT	810.2	108.1	435	7.50	<0.0001

Little bluestem community (n = 426), auto-regressive parameter: 0.37

Fixed effects	Parameter estimate	Standard error	DF	T	p
Intercept	-24.2	5.85	411	-4.13	<0.0001
Year	1.17	0.21	411	5.67	<0.0001
Year ²	-0.010	0.0019	411	-5.40	<0.0001
1/previous PPT	635.7	191.9	411	3.31	0.001

Table A4. Statistical tables for regression models incorporating interactive effects of annual precipitation in the current year and the inverse of previous year precipitation on species richness in the three Hays communities.

Shortgrass community (n = 692), auto-regressive parameter: 0.29

Fixed effects	Parameter estimate	Standard error	DF	T	p
Intercept	1.58	1.13	667	1.40	0.16
Year	0.11	0.0085	667	13.21	<0.0001
Current PPT	-0.0044	0.0014	667	-3.14	0.002
1/previous PPT	-1728.7	554.7	667	-3.12	0.002
Current PPT × 1/previous PPT	3.33	0.84	667	3.99	<0.0001

Ecotone community (n = 451), auto-regressive parameter: 0.36

Fixed effects	Parameter estimate	Standard error	DF	T	p
Intercept	2.68	1.15	433	2.33	0.02
Year	0.10	0.011	433	9.58	<0.0001
Current PPT	-0.007	0.0014	433	-4.90	<0.0001
1/previous PPT	-2261.6	600.6	433	-3.77	0.0002
Current PPT × 1/previous PPT	4.6	0.89	433	5.20	<0.0001

Little bluestem community (n = 426), auto-regressive parameter: 0.37

Fixed effects	Parameter estimate	Standard error	DF	T	p
Intercept	-17.56	6.50	409	-2.70	0.007
Year	1.09	0.21	409	5.17	<0.0001
Year ²	-0.0095	0.0019	409	-4.92	<0.0001
Current PPT	-0.007	0.0026	409	-2.67	0.008
1/previous PPT	-1904.6	1083.1	409	-1.76	0.080
Current PPT × 1/Previous PPT	3.99	1.62	409	2.47	0.014