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EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

Sensitivity of grassland plant community composition to spatial vs. temporal variation in precipitation

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Abstract. Climate gradients shape spatial variation in the richness and composition of plant communities. Given future predicted changes in climate means and variability, and likely regional variation in the magnitudes of these changes, it is important to determine how temporal variation in climate influences temporal variation in plant community structure. Here, we evaluated how species richness, turnover, and composition of grassland plant communities responded to interannual variation in precipitation by synthesizing long-term data from grasslands across the United States. We found that mean annual precipitation (MAP) was a positive predictor of species richness across sites, but a positive temporal relationship between annual precipitation and richness was only evident within two sites with low MAP. We also found higher average rates of species turnover in dry sites that in turn had a high proportion of annual species, although interannual rates of species turnover were surprisingly high across all locations. Annual species were less abundant than perennial species at nearly all sites, and our analysis showed that the probability of a species being lost or gained from one year to the next increased with decreasing species abundance. Bray-Curtis dissimilarity from one year to the next, a measure of species composition change that is influenced mainly by abundant species, was insensitive to precipitation at all sites. These results suggest that the richness and turnover patterns we observed were driven primarily by rare species, which comprise the majority of the local species pools at these grassland sites. These findings are consistent with the idea that short-lived and less abundant species are more sensitive to interannual climate variability than longer-lived and more abundant species. We conclude that, among grassland ecosystems, xeric grasslands are likely to exhibit the greatest responsiveness of community composition (richness and turnover) to predicted future increases in interannual precipitation variability. Over the long term, species composition may shift to reflect spatial patterns of mean precipitation; however, perennial-dominated systems will be buffered against rising interannual variation, while systems that have a large number of rare, annual species will show the greatest temporal variability in species composition in response to rising interannual variability in precipitation.

Key words: annual species; climate variability; community composition; LTER; mean annual precipitation; species richness; species turnover.

INTRODUCTION

Plant community composition, including number and identity of species, abundance, temporal variability (turnover), and life history traits, plays a key role in controlling net primary production and ecosystem

stability (Tilman 1999, Hooper et al. 2012, Reich et al. 2012). For example, habitat structure, biogeochemical cycles, and ecosystem productivity are influenced by species richness and community structure (Cardinale et al. 2012, Hooper et al. 2012). Given the magnitude of environmental and land-use changes worldwide, there is a growing likelihood that the species composition of many ecosystems will shift in response to global environmental change (Smith et al. 2009), ultimately altering ecosystem processes such as food web structure and net primary production.

The relationship between climate and species composition is a cornerstone of plant ecology at regional to global scales (Schimper 1903, Whittaker 1975). For instance, the combination of precipitation and temperature define the distribution of biomes in terrestrial systems (Whittaker 1975). Precipitation is also strongly correlated with species richness along latitudinal gradients both globally (Hawkins et al. 2003, Kreft and Jetz 2007) and regionally (Richerson and Lum 1980, O'Brien 1993, Adler and Levine 2007). The amount and distribution of precipitation are predicted to change in the coming decades as a consequence of rising atmospheric greenhouse gases and associated warming trends (Cusbasch et al. 2001, Meehl 2007). Though models differ in the predicted magnitude and direction of these changes, there is general agreement that interannual precipitation variability and the frequency of extreme precipitation events have and will continue to increase in many regions (Easterling et al. 2000, Christensen and Hewitson 2007, Min et al. 2011, Durack et al. 2012). The southwestern United States, in particular, has been identified as a future climate change "hot spot" due to predicted increases in interannual climate variability (Diffenbaugh et al. 2008, Gutzler and Robbins 2011).

Ideally plant community sensitivity to precipitation variability could be predicted on the basis of long-term observations. It is unclear, however, whether changes in community composition across spatial precipitation gradients are similar to patterns of community change within a location over time in response to interannual variation in precipitation. For instance, Adler and Levine (2007) found a positive spatial relationship between species richness and precipitation across five grassland sites in the United States, but no temporal relationship between annual rainfall and species richness across years at one site at the midpoint of their spatial precipitation gradient. In contrast, in a Chihuahuan Desert grassland a positive temporal relationship between rainfall and species richness was found (Xia et al. 2010), suggesting that species richness may be more sensitive to interannual variation in precipitation in more water-limited systems. To date, there have been few studies that have investigated how species richness varies with interannual variation in precipitation (but see Tilman and El Haddi 1992, Peco et al. 1998), and no studies that have investigated how species composition

varies temporally vs. spatially across multiple sites in relation to variability in precipitation.

There may be important parallels between community composition and primary production in their responses to precipitation variability, given that both have been shown to respond to increasing variation in rainfall (Knapp et al. 2002). For example, productivity has differing spatial compared to temporal relationships with precipitation (Sala et al. 2012). Across the North American grassland biome there is a strong positive relationship between net primary production and mean annual precipitation (MAP) (Sala et al. 1988, Knapp and Smith 2001). Similar patterns are observed across global grasslands where regions of higher precipitation support higher net primary production (Huxman et al. 2004). In contrast, within a site over time, primary production is far less sensitive to interannual variation in precipitation (Lauenroth and Sala 1992, Knapp and Smith 2001, Adler and Levine 2007, Hsu et al. 2012, Sala et al. 2012). Differences in temporal vs. spatial responsiveness in production have been largely viewed as differences in short-term vs. longer-term dynamics, respectively, relating to turnover in species composition.

Prior work aimed at understanding regional patterns of productivity can also inform our expectations about compositional responsiveness across spatial gradients of precipitation. Across the United States, the maximum sensitivity of production to interannual precipitation variability has been found at sites with intermediate levels of precipitation (Knapp and Smith 2001, Hsu et al. 2012). In arid sites, the low temporal sensitivity of production has been attributed to life history attributes of the dominant species that often exhibit low responsiveness to resource pulses (Lauenroth and Sala 1992, Ladwig et al. 2012). In mesic systems, the response of productivity to interannual precipitation variability may be constrained by nutrient and/or light limitation, or by storage mechanisms in the dominant species (Knapp and Smith 2001). Grasslands with intermediate levels of precipitation tend to have the highest sensitivity of production to interannual variation in precipitation. These grasslands are dominated by species capable of fast growth from abundant dormant meristems (Knapp and Smith 2001, Dalgleish and Hartnett 2006), pointing to the importance of the perennial bud bank (sensu Harper 1977) in determining sensitivity to interannual climate variation.

Sensitivity in species composition to interannual precipitation variation might be expected to follow patterns similar to sensitivity in production because above-ground net primary productivity represents an aggregate response of species in a community. However, mechanisms that operate at the community level, such as variation among species in their response to environmental fluctuations (Houlahan et al. 2007) may cause these patterns to differ. For instance, differences in species life history traits along bioclimatic gradients may
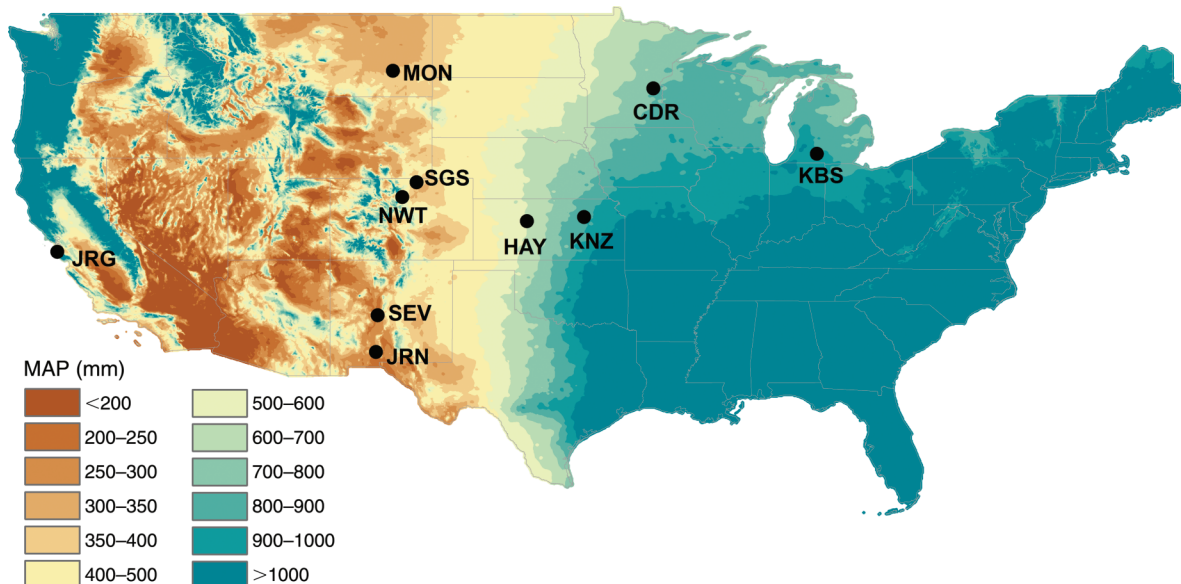
FIG. 1.   Map of the locations of the 10 sites superimposed on mean annual precipitation (MAP) derived from the Prism data set.

influence the sensitivity of species richness to environmental change (Eriksson 1993, Gough et al. 1994, Zobel 1997). Species richness in mesic grasslands may be buffered to interannual precipitation variability because of dominance by long-lived, bud-banking species (Benson and Hartnett 2006), compared to arid systems that contain a higher proportion of seed banking annual species (Aronson and Shmida 1992, Angert et al. 2009), with the potential for high interannual variation in species composition due to the appearance and disappearance of rare species. Alternatively, species that dominate in less fertile sites are often found to be slow growing, long lived, and stress tolerant, leading to lower predicted turnover in the composition of the dominant species in response to climate variation (Grime et al. 2000, Grime et al. 2008).

Here, we used long-term data on plant species composition in 10 grasslands to document spatial and temporal patterns of species composition (richness, turnover, and abundance-weighted community dissimilarity) in herbaceous plant communities that span a precipitation gradient across the United States. We tested the following hypotheses: (1) Across sites, species richness increases with MAP, but this relationship may be dampened within sites by the abundance of perennials, as found in analyses of production sensitivity to interannual variation in rainfall. (2) Temporal turnover in species composition will decline with MAP across sites due to life-history characteristics of the dominant species. Specifically, we expected that arid and semiarid sites with a high proportion of short-lived, fast growing annual species would be most sensitive to interannual variation in precipitation.

METHODS

Data set

To evaluate the relationship between interannual variation in species richness and precipitation, we identified data sets from 10 grassland sites (Fig. 1, Table 1) where plant species composition had been documented in replicated plots for at least 10 consecutive years, and where both measurement techniques and management regimes had remained consistent over the period of data collection. We focused on North American grasslands where prior work has evaluated spatial and temporal patterns of primary production (Knapp and Smith 2001, Hsu et al. 2012). Data collection techniques varied among studies: species composition for most sites was monitored on permanent plots, but destructive biomass harvests were performed for species composition measurements at Cedar Creek (CDR) and Kellogg Biological Station (KBS). Furthermore, the plot size and replication for measurements of species composition varied among locations (Table 1). Because species–area relationships are nonlinear, variation in plot size and replication presents a major challenge for cross-site synthesis efforts (e.g., Gross et al. 2000). Six sites measured species composition at the 1-m^2 scale but, for those that used a different plot size, we identified supplementary data from the same location in order to calculate a mean value for species richness at the 1-m^2 scale. For Konza (KNZ), Sevilleta (SEV), and Shortgrass Steppe (SGS) we utilized visually estimated percent cover data collected using a common methodology (30 1-m^2 plots sampled in 2007), as part of the Nutrient Network Research Collective (Adler et al. 2011). While there is a Nutrient Network site at CDR, it

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was not located in Field D where the long-term community composition data were collected. Hence, for CDR, we used published richness values in 120 1-m^2 plots from Field D (Fig. 2a in Tilman et al. 1996).

Annual precipitation for each site was obtained from the closest available weather station, and was calculated as the water year that contributed to the growing season (October of the previous year to September of the calendar year). This calculation allowed a common water year across sites; all of these sites have a summer growing season except for Jasper Ridge (JRG), which has a Mediterranean-type climate and a winter growing season cued by the onset of fall rains in October or November, with almost no precipitation during summer months.

Data analysis

Unless otherwise indicated, all data analysis was performed in R v. 2.12 (R Core Development Team 2011). We examined three aspects of species composition: richness, temporal turnover, and Bray-Curtis dissimilarity in community composition from one year to the next. The spatial richness–precipitation relationship was evaluated using a linear model to predict average species richness per 1 m^2 at each site based on MAP. Due to variation among sites in plot size, number, and the methodology used to collect species composition, we first calculated the number of unique species (S) found across all plots within a site in a given year. To evaluate the temporal richness–precipitation relationship, we subsequently predicted yearly site-level richness with annual precipitation at each site. Prior analyses have identified time lags in community response to precipitation (i.e., Adler and Levine 2007), so we performed these analyses using both precipitation in the current and previous year. The slope of this relationship was then compared across sites as an index of sensitivity to interannual variation in precipitation (Knapp and Smith 2001).

Turnover in species identities from year to year can mask changes in species composition as measured solely by species richness (Collins et al. 2008). To address this problem, we calculated the proportion of species turnover from one year to the next as ([number of species gained] + [number of species lost])/(total number of species) observed in both the focal year and previous year combined (Rusch and van der Maarel 1992). This calculation is based on the original formulation by MacArthur and Wilson (1963) for evaluating species turnover on islands, as modified by Diamond (1969) to express proportional turnover in order to compare sites that differ in starting species richness. As for yearly site-level richness, turnover was calculated by combining all plots in a location to minimize potential bias introduced by variation in sampling area and method across sites. Abundance does not factor into these calculations, and all species richness values are positive.

To incorporate aspects of species composition associated with shifting species abundances independent from species richness, we calculated Bray-Curtis dissimilarity (Bray and Curtis 1957) in community composition between years. Briefly, Bray-Curtis dissimilarity is the sum of the absolute value of the difference in species abundances between year 1 and 2, divided by the sum of the total number of species observed in each year; this metric is most influenced by the dynamics of abundant species (McCune and Grace 2002). As with our other metrics of species composition, Bray-Curtis dissimilarity was calculated using average species abundances across all plots in a site in a given year (including zero values for plots where a species was not found). To evaluate spatial relationships between annual precipitation and turnover or Bray-Curtis dissimilarity, we utilized mean values averaged across all years within a site.

To evaluate whether annual species played a disproportionate role in yearly species turnover as opposed to perennial species, we performed repeated-measures logistic regressions predicting the likelihood of individual species loss or gain in a given year at each site, on the basis of duration (annual or perennial), species relative abundance (in the prior year for loss, in the current year for gain), and their interaction (all fixed effects). Site was included as a random effect and species was the subject of repeated measures across year. These analyses were conducted using PROC GLIMMIX in SAS v.9.2 (SAS Institute 2008), using the Laplace method for maximum likelihood estimation (Littell et al. 2002). To demonstrate the relative influence of annual vs. perennial species for turnover across sites we calculated the proportion of annual species in the species pool at each location. We estimated the species pool as the number of unique species identified across all years and plots in a location, excluding species where the taxonomy was not resolved to the species level. The proportion of annuals was the number of those unique species with an annual life history divided by the total number of species in the species pool. Finally, to evaluate whether annual species were more likely than perennial species to be rare across our sites we calculated the mean relative abundance of annual and perennial species at each site, and performed a Wilcoxon signed-rank test (a nonparametric test to compare paired samples). Data from the Montana (MON) site were excluded from the Bray-Curtis dissimilarity analysis and the Wilcoxon signed-rank test because abundances were monitored using different methods for annual vs. perennial species (Anderson et al. 2011).

RESULTS

We found a positive relationship between species richness at the 1-m^2 scale and MAP across sites (Fig. 2A, $P = 0.02$, $R^2 = 0.46$). Within sites there were few significant temporal relationships between mean site-level richness and annual precipitation in the current year or with previous year's precipitation (Fig. 2B,

TABLE 1.   Summary of data sets included in this cross-site synthesis.

Abbreviation	Location	Years	Plot size (m²)	No. plots sampled each year	Mean total area (m/yr)	Data set description, notes, and citation
CDR	Cedar Creek LTER	1982–2004	0.3	5	1.5	Prairie grassland; data from experiment e001, only field D and Ntrt (no nutrients added) plots (Tilman 1993)
HAY	Hayes, Kansas	1937–1972	1	15–23	19	Kansas Prairie; earliest years of data were not used because some species were lumped (Adler et al. 2007)
JRG	Jasper Ridge Biological Preserve	1983–2010	1	18	18	Serpentine grassland plots where herbivores were not excluded (Hobbs et al. 2007)
JRN	Jornada Basin LTER	1989–2008	1	49	49	Desert grassland; long-term study on patterns of net primary productivity, data from Grassland Basin site only (Huenneke et al. 2002)
KBS	Kellogg Biological Station LTER	1996–2009	1	30	30	Old-field; data set ID: KBS019, T7 plots; we used data starting in 1996 when there was one consistent harvest per year (Huberty et al. 1998)
KNZ	Konza Prairie LTER, unburned watershed	1983–2007	10	20	200	Tallgrass prairie; data set ID: PVC02, using only uplands in unburned watershed 20b (Collins 2000)
MON	Miles City, Montana	1933–1945	1	7–14	11	Grazed pastures, using only the lowest stocking rate; these data were not analyzed for abundance because annuals and perennials were counted using different methods (Anderson et al. 2011)
NWT	Niwot Ridge LTER	2002–2010	1	7	7	Alpine tundra; control plots from an experiment (Suding et al. 2008)
SEV	Sevilleta LTER	1989–2010	0.1	40	8	Desert grassland; permanent line transects in 10 × 0.02 m segments; data set ID: SEV004; only the "Deep Well" site was used (Chen et al. 2005)
SGS	Short Grass Steppe LTER	1992–2008	0.1	119–163	14	Ungrazed short grass steppe grassland; data set ID: ARS #32 grazing and soil texture experiment

statistics summary in Table 2). Two sites with low MAP had significantly positive temporal richness–precipitation relationships (Jornada Basin [JRN] and MON), while KBS with intermediate MAP displayed a significant negative relationship between richness and precipitation the prior year.

Across sites MAP was a significant negative predictor of species turnover when one site with unusually low turnover was excluded (Fig. 3A, $P = 0.05$, $R^2 = 0.44$, if Jasper Ridge is included the relationship is not significant). Interannual precipitation variability (coefficient of variation of MAP) did not predict mean turnover ($P = 0.35$, results not shown). Sites with low MAP had a high proportion of annual species in their species pools (Fig. 3B, $P = 0.04$, $R^2 = 0.38$; if the outlier

Jasper Ridge, which is an annual-dominated grassland, is removed, this relationship is highly predictive: $P = 0.006$, $R^2 = 0.64$. The proportion of annual species in the species pool positively predicted turnover across sites, but this relationship is only marginally significant (Fig. 3C, $P = 0.09$, $R^2 = 0.26$). Annual species tend to have lower relative abundances across these focal sites than perennial species (Wilcoxon signed-rank test $P = 0.01$). Species were more likely to contribute to turnover via loss if they were annual (duration, $P = 0.01$, $F_{1,4147} = 6.01$) or had low abundance in the prior year ($P < 0.0001$, $F_{1,4147} = 23.1$). In addition there was a duration by abundance interaction ($P = 0.02$, $F_{1,4147} = 5.5$), whereby rare annual species were more likely to be lost than rare perennial species. Similarly, rare species were
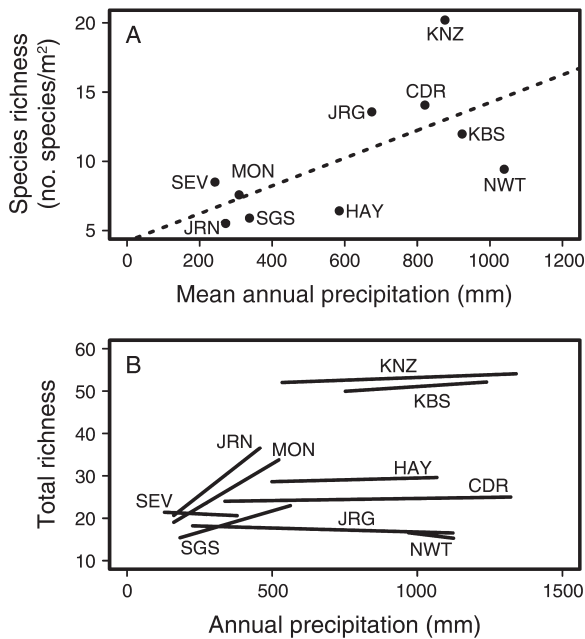
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FIG. 2. (A) Species richness at the 1-m² scale is positively predicted by spatial variation in MAP ($P = 0.02$, $R^2 = 0.46$; values are means). (B) Species richness is sensitive to temporal variation in annual precipitation only at the driest sites.

more likely to contribute to turnover via gains in a given year ($P < 0.0001$, $F_{1,4183} = 16.2$), and rare annuals were more likely to be gained than rare perennial species (duration by abundance interaction $P < 0.0001$, $F_{1,4183} = 17.5$). As with richness, there were few significant temporal relationships between turnover and annual precipitation within sites (Table 2), with the exception of CDR where annual precipitation positively predicted turnover, and MON where there was a positive relationship between turnover and precipitation in the previous year.

As the total area sampled at a site decreases, there is an increasing chance of undersampling the species pool and introducing random sampling error from year to year (Nilsson and Nilsson 1982). The area sampled at KNZ was nearly five times greater than the site with the next greatest area sampled, and was 130 times greater than the site with the least area sampled. While KNZ did sample the largest number of species and had low turnover, total area sampled was a poor predictor of turnover across sites ($R^2 = 0.08$, $P = 0.43$), suggesting that differences in plot area across site did not introduce a systematic bias to these results.

Mean Bray-Curtis dissimilarity between years was unrelated to MAP across sites, and was also unrelated to the proportion of annuals in the species pool across sites. Within sites, Bray-Curtis dissimilarity between years had a positive temporal relationship with annual precipitation only at JRN (Table 2).

DISCUSSION

We found that the relationship between species richness and precipitation depended on whether we examined the relationship focusing on temporal (within a site) or spatial variation (across sites). While plot-scale species richness was positively related to mean annual precipitation across our sites, site-scale species richness was not related to interannual variation in precipitation in 8 of the 10 sites, consistent with the findings of Adler and Levine (2007). However, we found a positive temporal richness–precipitation relationship at two of the driest sites in our analysis. Turnover driven by the appearance of more annual species in wet years may account for this relationship (Polis et al. 1997). We did not find evidence that lag effects were important in predicting richness-precipitation relationships, unlike previous studies which focused on within site relationships (Adler and Levine 2007).

TABLE 2. Summary of within-site temporal relationships between species composition (measured as species richness [S], species turnover [T], or Bray-Curtis [BC] dissimilarity to the prior year) and precipitation (measured as annual precipitation [AP] or annual precipitation in the prior year).

Site	No. years	S vs. AP	S vs. AP prior year	T vs. AP	T vs. AP prior year	BC vs. AP	BC vs. AP prior year
CDR	22	ns	ns	$P = 0.03$, pos, $r^2 = 0.20$	ns	ns	ns
HAY	35	ns	ns	ns	ns	ns	ns
JRG	27	ns	ns	ns	ns	ns	ns
JRN	19	$P = 0.003$, pos, $r^2 = 0.41$	ns	ns	ns	$P = 0.04$, pos, $r^2 = 0.23$	ns
KBS	11	ns	$P = 0.01$, neg, $r^2 = 0.50$	ns	ns	ns	ns
KNZ	24	ns	ns	ns	ns	ns	ns
MON	12	$P = 0.008$, pos, $r^2 = 0.47$	ns	ns	$P = 0.01$, pos, $r^2 = 0.50$	NA	NA
NWT	8	ns	ns	ns	ns	ns	ns
SEV	21	ns	ns	ns	ns	ns	ns
SGS	14	ns	ns	ns	ns	ns	ns

Notes: The slope of significant relationships was characterized as positive (pos) or negative (neg). Nonsignificant relationships are labeled "ns." Relationships labeled "NA" are not applicable at that site.

While most of our sites displayed little variation in species richness across years, there was remarkable species turnover across years. The four driest sites displayed the highest levels of species turnover, with an average of 35–53% of species turning over each year (Fig. 3A). These sites generally had a high proportion of annual species in their species pools (35–75%, Fig. 3B), consistent with the idea that annual species represent an important reservoir of temporally rare species that might be exceptionally sensitive to future climate change (Xia et al. 2010). Dominance by annual species, however, does not necessarily mean a site will have high turnover. For example, JRG had the lowest average species turnover (11%), but had the highest proportion of annual species (80%). Serpentine grasslands like those at JRG contain many endemic species adapted to the unusual chemistry of their soils, and they tend to occur in relatively small patches with large distances between patches. This may result in lower rates of dispersal from adjacent communities than other more continuous habitat types (Harrison 1997). Indeed, recent work has documented extremely low year-to-year variability in species composition in serpentine sites as compared with more fertile sandy soils in California (Fernandez-Going et al. 2012).

Unlike the presence–absence metrics of richness and turnover, our abundance-weighted measure of species composition (Bray-Curtis dissimilarity between years) was unrelated to precipitation on both spatial and temporal scales, with the exception of JRN where there was a positive relationship between precipitation and dissimilarity from the previous year. High interannual variation in community composition in relation to climate has been documented at other Chihuahuan desert sites (Guo and Brown 1997). The general lack of a response of abundant species to interannual variation in rainfall across our data sets, and the increased likelihood of species loss for rare species, indicate that the dynamic nature of turnover we observed in these communities is likely due to substitutions among rare species (Benedetti-Cecchi et al. 2008). A temporal analysis of tallgrass prairie communities at KNZ showed that a small number of dominant species occurred in almost all years, but over half of the species were found only once or a few times over the 15-year time period (Collins 2000). This high level of turnover occurred despite the fact that the plots sampled were large (10 m^2) and there was high replication (20 plots per year), suggesting that high turnover is common and is an important mechanism by which a large regional species pool buffers site-level diversity from interannual variation in climate. Although dominant species tend to have the greatest influence on ecosystem functioning (i.e., the mass ratio hypothesis; Grime 1998), rare species can nevertheless influence ecosystem functions such as invasion resistance (Lyons and Schwartz 2001) and provide important resources for specialist consumers (Ehrlich and Murphy 1987) and mutualists (Kearns et al. 1998), making it
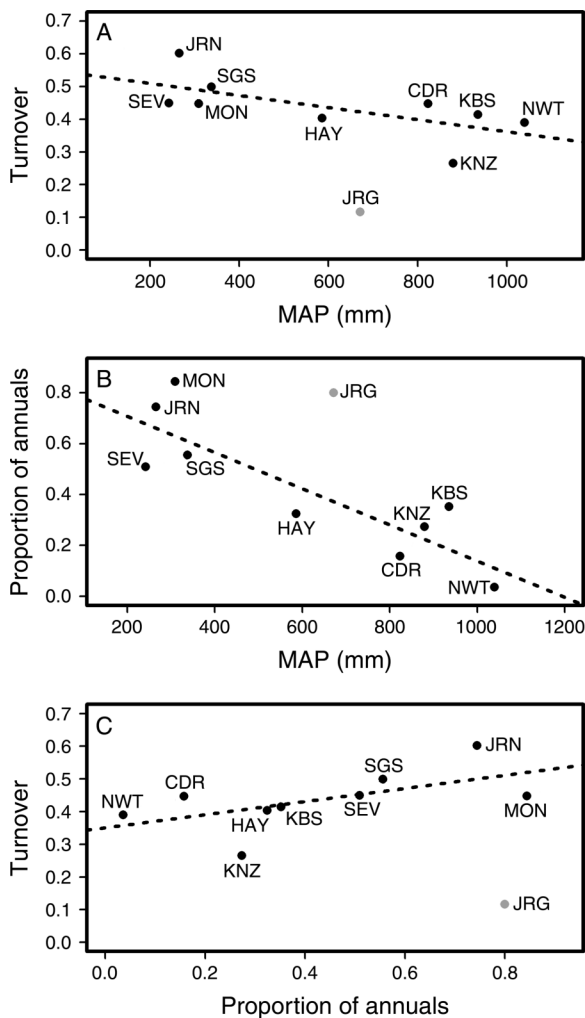

FIG. 3. (A) Interannual turnover in species composition (see *Methods* for definition) is lower for sites with higher MAP ($P = 0.05$, $R^2 = 0.44$; values are means). (B) Sites with low MAP have a higher proportion of annual species in the local species pool ($P = 0.006$, $R^2 = 0.64$). (C) Sites with high proportions of annual species tend to have high turnover across years, although this relationship is only marginally significant ($P = 0.09$, $R^2 = 0.26$; values are means). When fitting these linear models, we excluded Jasper Ridge (shown in gray) because it was identified as an outlier, having much lower turnover than any other site.

important to document both the temporal dynamics of rare and abundant species in ecosystems.

While we have documented patterns relating species richness and composition to annual precipitation, it is possible that other factors that covary with precipitation ultimately drive this interannual variation in species composition. For instance, annual precipitation is highly correlated with annual rates of wet N deposition, an aspect of environmental change that can have a great influence over species composition in plant communities (Suding et al. 2005, Bobbink et al. 2010); however, species richness was not predicted by rates of N

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deposition across our focal sites (Appendix: Fig A1). Other factors, which likely vary across sites and could play a large role in determining interannual species composition, include the timing and temperature at the onset of the rainy season. In arid and semiarid environments, these are important cues to break dormancy for species in the seed bank and bud bank because of their combined effects on soil moisture availability (Chesson et al. 2004). Seed banks can differ strikingly from the community composition of the surrounding vegetation (e.g., Rabinowitz and Rapp 1980), and are likely the source of the high interannual turnover in species composition we observed in our xeric sites. In contrast, bud banks are often reflective of the extant community (Lee 2004), potentially acting to stabilize community composition in response to interannual climate variation, similar to their role as a reservoir of potential vegetative regrowth, allowing communities to recover quickly following disturbance (reviewed in Klimešová and Klimeš 2007). It has been argued that species composition in North American tallgrass prairie, for instance, is determined largely by the dynamics of vegetative growth from perennial species rather than by dynamics of seed production and dispersal (Benson and Hartnett 2006). Perennial meristems increase across a precipitation gradient that includes several of our focal sites (Dalgleish and Hartnett 2006), consistent with our observations of lower interannual turnover in response to interannual precipitation variability in mesic compared with xeric sites.

Over the longer timescales necessary for species to disperse to new habitats, we expect that areas with consistent increases in precipitation will have increased local species richness while regions with prolonged decreases in precipitation will experience declining local species richness. Our analysis demonstrated that plant community structure in arid ecosystems showed the greatest responsiveness to interannual variability in precipitation, unlike primary productivity where ecosystems with intermediate levels of MAP were most responsive to interannual variation in precipitation (Knapp and Smith 2001). Based on our analysis we can conclude that among grassland ecosystems, arid grasslands are likely to demonstrate the greatest short-term response of species richness to changing precipitation regimes, due to the dynamics of short-lived annual species capable of responding on the same time scale as year-to-year variation in precipitation. We also found that across our sites annual species were more likely to be rare compared to perennial species, and sites with a greater number of rare species are more likely to see richness declines with increasing environmental variation due to stochastic demographic events (Goldberg and Miller 1990, Oksanen 1996).

Plant ecology has a strong tradition of documenting patterns in species composition in relation to climatic factors (i.e., von Humboldt 1858, Schimper 1903, Whittaker 1975), but this work has primarily focused on spatial variation. Few studies have monitored community composition and climatic variables for long enough (10+ years) to be able to evaluate how communities respond to temporal climate variation. Differences in the methodology used to monitor species composition present a significant hurdle for cross-site analyses due to the influence of scale, extent, and grain on patterns of species richness and turnover (Gross et al. 2000). Species richness does not scale linearly with area, while primary production usually does, and perhaps as a consequence our knowledge of spatial and temporal variation in production-climate relationships has progressed further (e.g., Knapp and Smith 2001, Hsu et al. 2012). The advent of consistent cross-site sampling efforts at continental to global scales, such as NEON (Keller et al. 2008) and the Nutrient Network Research Collective (Adler et al. 2011), will eventually provide invaluable data sets for identifying how species composition changes both over space and over time in relation to climate variability. Nevertheless, our cross-site analysis demonstrated that interannual variation in species identity and richness is high in North American grasslands, and there are likely to be predictable regional differences in response to climate change induced by future shifts in precipitation patterns.

LITERATURE CITED

Adler, P. B., and J. M. Levine. 2007. Contrasting relationships between precipitation and species richness in space and time. Oikos 116:221–232.

Adler, P. B., et al. 2011. Productivity is a poor predictor of plant species richness. Science 333:1750–1753.

Adler, P. B., W. R. Tyburczy, and W. K. Lauenroth. 2007. Long-term mapped quadrats from Kansas prairie: demographic information for herbaceous plants. Ecology 88:2673–2673.

Anderson, J., L. Vermeire, and P. B. Adler. 2011. Fourteen years of mapped, permanent quadrats in a northern mixed prairie, USA. Ecology 92:1703.

Angert, A. L., T. E. Huxman, P. Chesson, and D. L. Venable. 2009. Functional tradeoffs determine species coexistence via the storage effect. Proceedings of the National Academy of Sciences USA 106:11641–11645.

Aronson, J., and A. Shmida. 1992. Plant species diversity along a Mediterranean-desert gradient and its correlation with interannual rainfall fluctuations. Journal of Arid Environments 23:235–247.

Benedetti-Cecchi, L., I. Bertocci, S. Vaselli, E. Maggi, and F. Bulleri. 2008. Neutrality and the response of rare species to environmental variance. PLoS One 3:e2777.

Benson, E. J., and D. C. Hartnett. 2006. The role of weed and vegetative reproduction in plant recruitment and demography in tallgrass prairie. Plant Ecology 187:163–177.

Bobbink, R., et al. 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. Ecological Applications 20:30–59.

Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of Southern Wisconsin. Ecological Monographs 27:326–349.

Cardinale, B. J., et al. 2012. Biodiversity loss and its impact on humanity. Nature 486:59–67.

Chen, X., B. Li, and S. L. Collins. 2005. Multiscale monitoring of a multispecies case study: two grass species at Sevilleta. Plant Ecology 179:149–154.

Chesson, P., R. L. E. Gebauer, S. Schwinning, N. Huntly, K. Wiegand, M. S. K. Ernest, A. Sher, A. Novoplansky, and J. F. Weltzin. 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. Oecologia 141:236–253.

Christensen, J., and B. Hewitson. 2007. Regional climate projections. Pages 847–940 in S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, editors. Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate change. Cambridge University Press, Cambridge, UK.

Collins, S. L. 2000. Disturbance frequency and community stability in native tallgrass prairie. American Naturalist 155:311–325.

Collins, S. L., K. N. Suding, E. E. Cleland, M. Batty, S. C. Pennings, K. L. Gross, J. B. Grace, L. Gough, J. E. Fargione, and C. M. Clark. 2008. Rank clocks and community dynamics. Ecology 89:3534–3541.

Cusbasch, U., G. A. Meehl, G. J. Boer, R. J. Stouffer, M. Dix, A. Noda, C. A. Senior, S. Raper, and K. S. Yap. 2001. Projections of future climate change. Pages 525–582 in J. R. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell, and C. A. Johnson, editors. Climate change 2001: the scientific basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Dalgleish, H. J., and D. C. Hartnett. 2006. Below-ground bud banks increase along a precipitation gradient of the North American Great Plains: a test of the meristem limitation hypothesis. New Phytologist 171:81–89.

Diamond, J. M. 1969. Avifaunal equilibria and species turnover rates on the Channel Islands of California. Proceedings of the National Academy of Sciences 64:57–63.

Diffenbaugh, N. S., F. Giorgi, and J. S. Pal. 2008. Climate change hotspots in the United States. Geophysical Research Letters 35:L16709.

Durack, P. J., S. E. Wijffels, and R. J. Matear. 2012. Ocean salinities reveal strong global water cycle intensification during 1950 to 2000. Science 336:455–458.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate extremes: observations, modeling, and impacts. Science 289:2068–2074.

Ehrlich, P. R., and D. D. Murphy. 1987. Conservation lessons from long-term studies of checkerspot butterflies. Conservation Biology 1:122–131.

Eriksson, O. 1993. The species-pool hypothesis and plant community diversity. Oikos 68:371–374.

Fernandez-Going, B. M., B. L. Anacker, and S. P. Harrison. 2012. Temporal variability in California grasslands: soil type and species functional traits mediate response to precipitation. Ecology 93:2104–2114.

Goldberg, D. E., and T. Miller. 1990. Effects of different resource additions on species diversity in an annual plant community. Ecology 71:213–225.

Gough, L., J. B. Grace, and K. L. Taylor. 1994. The relationship between species richness and community biomass: the importance of environmental variables. Oikos 70:271–279.

Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. Journal of Ecology 86:902–910.

Grime, J. P., V. K. Brown, K. Thompson, G. J. Masters, S. H. Hillier, I. P. Clarke, A. P. Askew, D. Corker, and J. P. Kielty. 2000. The response of two contrasting limestone grasslands to simulated climate change. Science 289:762–765.

Grime, J. P., J. D. Fridley, A. P. Askew, K. Thompson, J. G. Hodgson, and C. R. Bennett. 2008. Long-term resistance to simulated climate change in an infertile grassland. Proceedings of the National Academy of Sciences USA 105:10028–10032.

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

Guo, Q., and J. H. Brown. 1997. Interactions between winter and summer annuals in the Chihuahuan Desert. Oecologia 111:123–128.

Gutzler, D., and T. Robbins. 2011. Climate variability and projected change in the western United States: regional downscaling and drought statistics. Climate Dynamics 37:835–849.

Harper, J. L. 1977. Population biology of plants. Academic Press, London, UK.

Harrison, S. 1997. How natural habitat patchiness affects the distribution of diversity in Californian serpentine chaparral. Ecology 78:1898–1906.

Hawkins, B. A., et al. 2003. Energy, water, and broad-scale geographic patterns of species richness. Ecology 84:3105–3117.

Hobbs, R. J., S. Yates, and H. A. Mooney. 2007. Long-term data reveal complex dynamics in grassland in relation to climate and disturbance. Ecological Monographs 77:545–568.

Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. K. Byrnes, B. A. Hungate, K. L. Matulich, A. Gonzalez, J. E. Duffy, L. Gamfeldt, and M. I. O'Connor. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486:105–108.

Houlahan, J. E., et al. 2007. Compensatory dynamics are rare in natural ecological communities. Proceedings of the National Academy of Sciences USA 104:3273–3277.

Hsu, J. S., J. Powell, and P. B. Adler. 2012. Sensitivity of mean annual primary production to precipitation. Global Change Biology 18:2246–2255.

Huberty, L., K. Gross, and C. Miller. 1998. Effects of nitrogen addition on successional dynamics and species diversity in Michigan old-fields. Journal of Ecology 86:794–803.

Huenneke, L. F., J. P. Anderson, M. Remmenga, and W. H. Schlesinger. 2002. Desertification alters patterns of above-ground net primary production in Chihuahuan ecosystems. Global Change Biology 8:247–264.

Huxman, T. E., et al. 2004. Convergence across biomes to a common rain-use efficiency. Nature 429:651–654.

Kearns, C. A., D. W. Inouye, and N. M. Waser. 1998. Endangered mutualisms: the conservation of plant–pollinator interactions. Annual Review of Ecology and Systematics 29:83–112.

Keller, M., D. S. Schimel, W. M. Hargrave, and F. M. Hoffman. 2008. A continental strategy for the National Ecological Observatory Network. Frontiers in Ecology and the Environment 6:282–284.

Klimešová, J., and L. Klimeš. 2007. Bud banks and their role in vegetative regeneration—a literature review and proposal for simple classification and assessment. Perspectives in Plant Ecology, Evolution and Systematics 8:115–129.

Knapp, A. K., P. A. Fay, J. M. Blair, S. L. Collins, M. D. Smith, J. D. Carlisle, C. W. Harper, B. T. Danner, M. S. Lett, and J. K. McCarron. 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. Science 298:2202–2205.

Knapp, A. K., and M. D. Smith. 2001. Variation among biomes in temporal dynamics of aboveground primary production. Science 291:481–484.

Kreft, H., and W. Jetz. 2007. Global patterns and determinants of vascular plant diversity. Proceedings of the National Academy of Sciences USA 104:5925–5930.

Ladwig, L., S. Collins, A. Swann, Y. Xia, M. Allen, and E. Allen. 2012. Above- and belowground responses to nitrogen addition in a Chihuahuan Desert grassland. Oecologia 169: 177–185.

Lauenroth, W. K., and O. E. Sala. 1992. Long-term forage production of North American shortgrass steppe. Ecological Applications 2:397–403.

Lee, P. 2004. The impact of burn intensity from wildfires on seed and vegetative banks, and emergent understory in aspen-dominated boreal forests. Canadian Journal of Botany 82:1468–1480.

Littell, R. C., W. W. Stroup, and R. J. Freund. 2002. SAS for linear models. Fourth edition. SAS Institute, Cary, North Carolina, USA.

Lyons, K., and M. Schwartz. 2001. Rare species loss alters ecosystem function—invasion resistance. Ecology Letters 4: 358–365.

MacArthur, R. H., and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. Evolution 17:373–387.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Glenedon Beach, Oregon, USA.

Meehl, G. A., et. al. 2007. Global climate projections. Pages 747–845 in S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, editors. Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Min, S.-K., X. Zhang, F. W. Zwiers, and G. C. Hegerl. 2011. Human contribution to more-intense precipitation extremes. Nature 470:378–381.

Nilsson, I. N., and S. G. Nilsson. 1982. Turnover of vascular plant species on small islands in lake Möckeln, South Sweden 1976–1980. Oecologia 53:128–133.

O'Brien, E. M. 1993. Climatic gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa's woody flora. Journal of Biogeography 20: 181–198.

Oksanen, J. 1996. Is the humped relationship between species richness and biomass an artefact due to plot size? Journal of Ecology 84:293–295.

Peco, B., T. Espigares, and C. Levassor. 1998. Trends and fluctuations in species abundance and richness in Mediterranean annual pastures. Applied Vegetation Science 1:21–28.

Polis, G. A., S. D. Hurd, C. T. Jackson, and F. S. Piñero. 1997. El Niño effects on the dynamics and control of an island ecosystem in the Gulf of California. Ecology 78:1884–1897.

R Core Development Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.com

Rabinowitz, D., and J. K. Rapp. 1980. Seed rain in a North American tallgrass prairie. Journal of Applied Ecology 17: 793–802.

Reich, P. B., D. Tilman, F. Isbell, K. Mueller, S. E. Hobbie, D. F. B. Flynn, and N. Eisenhauer. 2012. Impacts of biodiversity loss escalate through time as redundancy fades. Science 336:589–592.

Richerson, P. J., and K. Lum. 1980. Patterns of plant species diversity in California: relation to weather and topography. American Naturalist 116:504–536.

Rusch, G., and E. van der Maarel. 1992. Species turnover and seedling recruitment in limestone grasslands. Oikos 63:139–146.

Sala, O., L. Gherardi, L. Reichman, E. Jobbagy, and D. Peters. 2012. Legacies of precipitation fluctuations on primary production: theory and data synthesis. Philosophical Transactions of the Royal Society B 367:3135–3144.

Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the United States. Ecology 69:40–45.

SAS Institute. 2008. SAS version 9.2. SAS Institute, Cary, North Carolina, USA.

Schimper, A. F. W. 1903. Plant geography upon a physiological basis. Clarendon Press, Oxford, UK.

Smith, M. D., A. K. Knapp, and S. L. Collins. 2009. A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. Ecology 90:3279–3289.

Suding, K. N., I. W. Ashton, H. Bechtold, W. D. Bowman, M. L. Mobley, and R. Winkleman. 2008. Plant and microbe contribution to community resilience in a directionally changing environment. Ecological Monographs 78:313–329.

Suding, K. N., S. L. Collins, L. Gough, C. Clark, E. E. Cleland, K. L. Gross, D. G. Milchunas, and S. Pennings. 2005. Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. Proceedings of the National Academy of Sciences USA 102:4387–4392.

Tilman, D. 1993. Species richness of experimental productivity gradients: How important is colonization limitation? Ecology 74:2179–2191.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80: 1455–1474.

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

Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379:718–720.

von Humboldt, A. 1858. Kosmos: Entwurf einer physischen Weltbeschreibung. Cotta, Stuttgart/Tübingen, Germany.

Whittaker, R. H. 1975. Communities and ecosystems. Macmillan, New York, New York, USA.

Xia, Y., D. I. Moore, S. L. Collins, and E. H. Muldavin. 2010. Aboveground production and species richness of annuals in Chihuahuan Desert grassland and shrubland plant communities. Journal of Arid Environments 74:378–385.

Zobel, M. 1997. The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? Trends in Ecology and Evolution 12: 266–269.

CONCEPTS & SYNTHESIS

SUPPLEMENTAL MATERIAL

Appendix

Supplementary analysis of the relationships among mean annual precipitation, nitrogen deposition, and species richness at our focal sites (*Ecological Archives* E094-154-A1).