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Title: Sensitivity of grassland plant community composition to spatial versus 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.

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 U.S., 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 U.S., 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.
2010), and no studies that have investigated how species composition varies
temporally versus 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,
Similar patterns are observed globally 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 versus spatial responsiveness in production have been largely viewed as differences in short-term versus 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 U.S., 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 ANPP 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
influence the sensitivity of species richness to environmental change
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-weighed 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 vary with MAP across sites due to life-history characteristics of the dominant species. In particular we expected that 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 (Figure 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 non-linear, 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 m² 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 m² scale. For Konza (KNZ), Sevilleta (SEV) and Shortgrass Steppe (SGS) we utilized visually-estimated percent cover data collected using a common methodology (30, 1 m² 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 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, 1m² plots from Field D (Figure 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
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 composition 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: \((\text{Number of species gained} + \text{Number of species lost}) / \text{Total number of species observed in both the focal year and previous year combined}\) \((\text{Rusch and van der Maarel 1992})\). This calculation is based on the original formulation by MacAurthur 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.

To incorporate aspects of species composition associated with shifting species abundances independent from species richness, we calculated Bray-Curtis dissimilarity \((\text{Bray and Curtis 1957})\) 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 \((\text{McCune and Grace 2002})\). 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, using the Laplace method for maximum likelihood estimation (Littell et al. 2006). To demonstrate the relative influence of annual versus 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 non-parametric 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 versus 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 (Figure 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 (Figure 2B, 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 (Figure 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 (Figure 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 (Figure 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 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 5 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 \( (R^2 \).
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).
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 (Figure 3A). These sites generally had a high proportion of annual species in their species pools (35-75%, Figure 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 m²) 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 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 co-vary 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 deposition across our focal sites (see Supplementary material). 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 semi-arid 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 & 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 inter-annual variability in
precipitation, unlike primary productivity where ecosystems with
intermediate levels of MAP were most responsive to inter-annual 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 (Oksanen 1996, Goldberg and Miller 1990).

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 datasets 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
454differences in response to climate-change induced by future shifts in
455precipitation patterns.
456
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variability, carbon cycling, and plant species diversity in a mesic grassland. Science **298**:2202-2205.


Table 1. Summary of datasets included in this cross-site synthesis.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Location</th>
<th>Years</th>
<th>Plot size (m²)</th>
<th># of plots sampled each year</th>
<th>Mean total area</th>
<th>Dataset description, notes, and citation</th>
</tr>
</thead>
<tbody>
<tr>
<td>CDR</td>
<td>Cedar Creek LTER</td>
<td>1982-2004</td>
<td>0.3</td>
<td>5</td>
<td>1.5</td>
<td>Prairie grassland. Data from experiment e001, only field D and Nrt (no nutrients added) plots (Tilman 1993)</td>
</tr>
<tr>
<td>HAY</td>
<td>Hayes, Kansas</td>
<td>1937-1972</td>
<td>1</td>
<td>15-23</td>
<td>19</td>
<td>Kansas Prairie, earliest years of data were not used because some species were lumped (Adler et al. 2007)</td>
</tr>
<tr>
<td>JRG</td>
<td>Jasper Ridge Biological Preserve</td>
<td>1983-2010</td>
<td>1</td>
<td>18</td>
<td>18</td>
<td>Serpentine grassland plots where herbivores were not excluded (Hobbs et al. 2007)</td>
</tr>
<tr>
<td>JRN</td>
<td>Jornada Basin LTER</td>
<td>1989-2008</td>
<td>1</td>
<td>49</td>
<td>49</td>
<td>Desert grassland. Long-term study on patterns of net primary productivity; data from Grassland Basin site only (Huenneke et al. 2002)</td>
</tr>
<tr>
<td>KBS</td>
<td>Kellogg Biological Station LTER</td>
<td>1996-2009</td>
<td>1</td>
<td>30</td>
<td>30</td>
<td>Old-field. Dataset ID: KBS019. T7 plots, we used data starting in 1996 when there was one consistent harvest per year (Huberty et al. 1998)</td>
</tr>
<tr>
<td>MON</td>
<td>Miles City, Montana</td>
<td>1933-1945</td>
<td>1</td>
<td>7-14</td>
<td>11</td>
<td>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)</td>
</tr>
<tr>
<td>NWT</td>
<td>Niwot Ridge LTER</td>
<td>2002-2010</td>
<td>1</td>
<td>7</td>
<td>7</td>
<td>Alpine tundra. Control plots from an experiment (Suding et al. 2008)</td>
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<tr>
<td>SEV</td>
<td>Sevilleta LTER</td>
<td>1989-2010</td>
<td>0.1</td>
<td>40</td>
<td>8</td>
<td>Desert grassland. Permanent line transects in 10 x 0.02 m segments. Dataset ID: SEV004, only the &quot;deep well&quot; site was used (Chen et al. 2006)</td>
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<tr>
<td>SGS</td>
<td>Short Grass Steppe LTER</td>
<td>1992-2008</td>
<td>0.1</td>
<td>119-163</td>
<td>14</td>
<td>Ungrazed short grass steppe grassland, Dataset ID: ARS #32 Grazing and Soil Texture experiment</td>
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</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Site</th>
<th># years</th>
<th>S vs AP</th>
<th>S vs AP prior yr</th>
<th>T vs AP</th>
<th>T vs AP prior yr</th>
<th>BC vs AP</th>
<th>BC vs AP prior yr</th>
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</thead>
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<tr>
<td>CDR</td>
<td>22</td>
<td>ns</td>
<td>ns</td>
<td>p=0.03, pos, r²=0.20</td>
<td>ns</td>
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<td>ns</td>
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<td>p=0.008, pos, r²=0.47</td>
<td>ns</td>
<td>ns</td>
<td>p=0.01, pos, r²=0.50</td>
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<td>ns</td>
</tr>
</tbody>
</table>
Figure 1. Map of the locations of the 10 sites superimposed on mean annual precipitation (MAP) in mm derived from the Prism dataset.

Figure 2. A) Species richness at the 1-m² scale is positively predicted by spatial variation in MAP (P = 0.02, R² = 0.46). B) Species richness is sensitive to temporal variation in annual precipitation only at the driest sites.

Figure 3. A) Interannual turnover in species composition (see Methods for definition) is lower for sites with higher MAP (P = 0.05, R² = 0.44). B) Sites with low MAP have a higher proportion of annual species in the local species pool (P =0.006, R² = 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, R² = 0.26). 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.
Figure 1.
Figure 2.
Figure 3.