

1Title: Sensitivity of grassland plant community composition to spatial versus  
2temporal variation in precipitation

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26Abstract

27Climate gradients shape spatial variation in the richness and composition of  
28plant communities. Given future predicted changes in climate means and  
29variability, and likely regional variation in the magnitudes of these changes,  
30it is important to determine how temporal variation in climate influences  
31temporal variation in plant community structure. Here, we evaluated how  
32species richness, turnover, and composition of grassland plant communities  
33responded to interannual variation in precipitation by synthesizing long-term  
34data from grasslands across the United States. We found that mean annual  
35precipitation (MAP) was a positive predictor of species richness across sites,  
36but a positive temporal relationship between annual precipitation and  
37richness was only evident within two sites with low MAP. We also found  
38higher average rates of species turnover in dry sites that in turn had a high  
39proportion of annual species, although interannual rates of species turnover  
40were surprisingly high across all locations. Annual species were less  
41abundant than perennial species at nearly all sites, and our analysis showed  
42that the probability of a species being lost or gained from one year to the  
43next increased with decreasing species abundance. Bray-Curtis dissimilarity  
44from one year to the next, a measure of species composition change that is  
45influenced mainly by abundant species, was insensitive to precipitation at all  
46sites. These results suggest that the richness and turnover patterns we

47observed were driven primarily by rare species, which comprise the majority  
48of the local species pools at these grassland sites. These findings are  
49consistent with the idea that short-lived and less abundant species are more  
50sensitive to interannual climate variability than longer-lived and more  
51abundant species. We conclude that among grassland ecosystems, xeric  
52grasslands are likely to exhibit the greatest responsiveness of community  
53composition (richness and turnover) to predicted future increases in  
54interannual precipitation variability. Over the long-term, species composition  
55may shift to reflect spatial patterns of mean precipitation; however,  
56perennial dominated systems will be buffered against rising interannual  
57variation, while systems that have a large number of rare, annual species will  
58show the greatest temporal variability in species composition in response to  
59rising interannual variability in precipitation.

60

## 61Introduction

62 Plant community composition, including number and identity of  
63species, abundance, temporal variability (turnover) and life history traits,  
64plays a key role in controlling net primary production and ecosystem stability  
65(Tilman 1999, Hooper et al. 2012, Reich et al. 2012). For example, habitat  
66structure, biogeochemical cycles and ecosystem productivity are influenced  
67by species richness and community structure (Cardinale et al. 2012, Hooper  
68et al. 2012). Given the magnitude of environmental and land-use changes  
69worldwide, there is a growing likelihood that the species composition of

70many ecosystems will shift in response to global environmental change  
71(Smith et al. 2009), ultimately altering ecosystem processes such as food  
72web structure and net primary production.

73       The relationship between climate and species composition is a  
74cornerstone of plant ecology at regional to global scales (Schimper 1903,  
75Whittaker 1975). For instance, the combination of precipitation and  
76temperature define the distribution of biomes in terrestrial systems  
77(Whittaker 1975). Precipitation is also strongly correlated with species  
78richness along latitudinal gradients both globally (Hawkins et al. 2003, Kreft  
79and Jetz 2007) and regionally (Richerson and Lum 1980, O'Brien 1993, Adler  
80and Levine 2007). The amount and distribution of precipitation are predicted  
81to change in the coming decades as a consequence of rising atmospheric  
82greenhouse gases and associated warming trends (Cusbasch et al. 2001,  
83Meehl 2007). Though models differ in the predicted magnitude and direction  
84of these changes, there is general agreement that interannual precipitation  
85variability and the frequency of extreme precipitation events have and will  
86continue to increase in many regions (Easterling et al. 2000, Christensen and  
87Hewitson 2007, Min et al. 2011, Durack et al. 2012). The Southwestern U.S.,  
88in particular, has been identified as a future climate change “hot spot” due  
89to predicted increases in interannual climate variability (Diffenbaugh et al.  
902008, Gutzler and Robbins 2011).

91       Ideally plant community sensitivity to precipitation variability could be  
92predicted on the basis of long-term observations. It is unclear, however,

93whether changes in community composition across spatial precipitation  
94gradients are similar to patterns of community change within a location over  
95time in response to interannual variation in precipitation. For instance, Adler  
96and Levine (2007) found a positive spatial relationship between species  
97richness and precipitation across five grassland sites in the U.S., but no  
98temporal relationship between annual rainfall and species richness across  
99years at one site at the midpoint of their spatial precipitation gradient. In  
100contrast, in a Chihuahuan Desert grassland a positive temporal relationship  
101between rainfall and species richness was found (Xia et al. 2010), suggesting  
102that species richness may be more sensitive to interannual variation in  
103precipitation in more water-limited systems. To date there have been few  
104studies that have investigated how species richness varies with interannual  
105variation in precipitation (but see Tilman and El Haddi 1992, Peco et al.  
1061998), and no studies that have investigated how species composition varies  
107temporally versus spatially across multiple sites in relation to variability in  
108precipitation.

109       There may be important parallels between community composition and  
110primary production in their responses to precipitation variability, given that  
111both have been shown to respond to increasing variation in rainfall (Knapp et  
112al. 2002). For example, productivity has differing spatial compared to  
113temporal relationships with precipitation (Sala et al. 2012). Across the North  
114American grassland biome there is a strong positive relationship between net  
115primary production and mean annual precipitation (MAP) (Sala et al. 1988,

116Knapp and Smith 2001). Similar patterns are observed globally where  
117regions of higher precipitation support higher net primary production  
118(Huxman et al. 2004). In contrast, within a site over time primary production  
119is far less sensitive to interannual variation in precipitation (Lauenroth and  
120Sala 1992, Knapp and Smith 2001, Adler and Levine 2007, Hsu et al. 2012,  
121Sala et al. 2012). Differences in temporal versus spatial responsiveness in  
122production have been largely viewed as differences in short-term versus  
123longer-term dynamics, respectively, relating to turnover in species  
124composition.

125       Prior work aimed at understanding regional patterns of productivity  
126can also inform our expectations about compositional responsiveness across  
127spatial gradients of precipitation. Across the U.S., the maximum sensitivity of  
128production to interannual precipitation variability has been found at sites  
129with intermediate levels of precipitation (Knapp and Smith 2001, Hsu et al.  
1302012). In arid sites, the low temporal sensitivity of production has been  
131attributed to life history attributes of the dominant species that often exhibit  
132low responsiveness to resource pulses (Lauenroth and Sala 1992, Ladwig et  
133al. 2012). In mesic systems, the response of productivity to interannual  
134precipitation variability may be constrained by nutrient and/or light  
135limitation, or by storage mechanisms in the dominant species (Knapp and  
136Smith 2001). Grasslands with intermediate levels of precipitation tend to  
137have the highest sensitivity of production to interannual variation in  
138precipitation. These grasslands are dominated by species capable of fast

139growth from abundant dormant meristems (Knapp and Smith 2001, Dalgleish  
140and Hartnett 2006), pointing to the importance of the perennial bud bank  
141(*sensu* Harper 1977) in determining sensitivity to interannual climate  
142variation.

143       Sensitivity in species composition to interannual precipitation variation  
144might be expected to follow patterns similar to sensitivity in production  
145because ANPP represents an aggregate response of species in a community.  
146However, mechanisms that operate at the community level, such as  
147variation among species in their response to environmental fluctuations  
148(Houlahan et al. 2007) may cause these patterns to differ. For instance,  
149differences in species life history traits along bioclimatic gradients may  
150influence the sensitivity of species richness to environmental change  
151(Eriksson 1993, Gough et al. 1994, Zobel 1997). Species richness in mesic  
152grasslands may be buffered to interannual precipitation variability because  
153of dominance by long-lived, bud-banking species (Benson and Hartnett  
1542006), compared to arid systems that contain a higher proportion of seed  
155banking annual species (Aronson and Shmida 1992, Angert et al. 2009), with  
156the potential for high interannual variation in species composition due to the  
157appearance and disappearance of rare species. Alternatively, species that  
158dominate in less fertile sites are often found to be slow-growing, long-lived  
159and stress tolerant, leading to lower predicted turnover in the composition of  
160the dominant species in response to climate variation (Grime et al. 2000,  
161Grime et al. 2008).

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

174

## 175 Methods

### 176 Data set

177 To evaluate the relationship between interannual variation in species  
178 richness and precipitation, we identified data sets from 10 grassland sites  
179 (Figure 1, Table 1) where plant species composition had been documented in  
180 replicated plots for at least 10 consecutive years, and where both  
181 measurement techniques and management regimes had remained  
182 consistent over the period of data collection. We focused on North American  
183 grasslands where prior work has evaluated spatial and temporal patterns of  
184 primary production (Knapp and Smith 2001, Hsu et al. 2012). Data collection



185 techniques varied among studies; species composition for most sites was  
186 monitored on permanent plots, but destructive biomass harvests were  
187 performed for species composition measurements at Cedar Creek (CDR) and  
188 Kellogg Biological Station (KBS). Furthermore, the plot-size and replication  
189 for measurements of species composition varied among locations (Table 1).  
190 Because species-area relationships are non-linear, variation in plot-size and  
191 replication presents a major challenge for cross-site synthesis efforts (e.g.  
192 Gross et al. 2000). Six sites measured species composition at the 1 m<sup>2</sup> scale,  
193 but for those that used a different plot size we identified supplementary data  
194 from the same location in order to calculate a mean value for species  
195 richness at the 1 m<sup>2</sup> scale. For Konza (KNZ), Sevilleta (SEV) and Shortgrass  
196 Steppe (SGS) we utilized visually-estimated percent cover data collected  
197 using a common methodology (30, 1 m<sup>2</sup> plots sampled in 2007), as part of  
198 the Nutrient Network Research Collective (Adler et al. 2011). While there is a  
199 Nutrient Network site at CDR, it was not located in Field D where the long-  
200 term community composition data were collected. Hence, for CDR we used  
201 published richness values in 120, 1m<sup>2</sup> plots from Field D (Figure 2a in Tilman  
202 et al. 1996).

203 Annual precipitation for each site was obtained from the closest  
204 available weather station, and was calculated as the water-year that  
205 contributed to the growing season (October of the previous year to  
206 September of the calendar year). This calculation allowed a common water  
207 year across sites; all of these sites have a summer growing season except

208for Jasper Ridge (JRG) which has a Mediterranean-type climate and a winter  
209growing season cued by the onset of fall rains in October or November, with  
210almost no precipitation during summer months.

211 Data analysis

212 Unless otherwise indicated, all data analysis was performed in R v.  
2132.12 (R Core-Development Team 2011). We examined three aspects of  
214species composition: richness, temporal turnover, and Bray-Curtis  
215dissimilarity in community composition from one year to the next. The  
216spatial richness/precipitation relationship was evaluated using a linear model  
217to predict average species richness per 1 m<sup>2</sup> at each site based on MAP. Due  
218to variation among sites in plot size, number, and the methodology used to  
219collect species composition, we first calculated the number of unique species  
220(S) found across all plots within a site in a given year. To evaluate the  
221temporal richness/precipitation relationship we subsequently predicted  
222yearly site-level richness with annual precipitation at each site. Prior  
223analyses have identified time lags in community response to precipitation  
224(i.e. Adler and Levine 2007), so we performed these analyses using both  
225precipitation in the current and previous year. The slope of this relationship  
226was then compared across sites as an index of sensitivity to interannual  
227variation in precipitation (Knapp and Smith 2001).

228 Turnover in species composition from year to year can mask changes  
229in species composition as measured solely by species richness (Collins et al.  
2302008). To address this problem, we calculated the proportion of species

231turnover from one year to the next as: (Number of species gained + Number  
232of species lost) / Total number of species observed in both the focal year and  
233previous year combined (Rusch and van der Maarel 1992). This calculation is  
234based on the original formulation by MacArthur and Wilson (1963) for  
235evaluating species turnover on islands, as modified by Diamond (1969) to  
236express proportional turnover in order to compare sites that differ in starting  
237species richness. As for yearly site-level richness, turnover was calculated by  
238combining all plots in a location to minimize potential bias introduced by  
239variation in sampling area and method across sites.

240 To incorporate aspects of species composition associated with shifting  
241species abundances independent from species richness, we calculated Bray-  
242Curtis dissimilarity (Bray and Curtis 1957) in community composition  
243between years. Briefly, Bray-Curtis dissimilarity is the sum of the absolute  
244value of the difference in species abundances between year 1 and 2, divided  
245by the sum of the total number of species observed in each year; this metric  
246is most influenced by the dynamics of abundant species (McCune and Grace  
2472002). As with our other metrics of species composition, Bray-Curtis  
248dissimilarity was calculated using average species abundances across all  
249plots in a site in a given year (including zero values for plots where a species  
250was not found). To evaluate spatial relationships between annual  
251precipitation and turnover or Bray-Curtis dissimilarity, we utilized mean  
252values averaged across all years within a site.

253 To evaluate whether annual species played a disproportionate role in  
254 yearly species turnover as opposed to perennial species, we performed  
255 repeated-measures logistic regressions predicting the likelihood of individual  
256 species loss or gain in a given year at each site, on the basis of duration  
257 (annual or perennial), species relative abundance (in the prior year for loss,  
258 in the current year for gain), and their interaction (all fixed effects). Site was  
259 included as a random effect and species was the subject of repeated  
260 measures across year. These analyses were conducted using PROC GLIMMIX  
261 in SAS v.9.2, using the Laplace method for maximum likelihood estimation  
262 (Littell et al. 2006). To demonstrate the relative influence of annual versus  
263 perennial species for turnover across sites we calculated the proportion of  
264 annual species in the species pool at each location. We estimated the  
265 species pool as the number of unique species identified across all years and  
266 plots in a location, excluding species where the taxonomy was not resolved  
267 to the species level. The proportion of annuals was the number of those  
268 unique species with an annual life history divided by the total number of  
269 species in the species pool. Finally, to evaluate whether annual species were  
270 more likely than perennial species to be rare across our sites we calculated  
271 the mean relative abundance of annual and perennial species at each site,  
272 and performed a Wilcoxon signed-rank test (a non-parametric test to  
273 compare paired samples). Data from the Montana (MON) site were excluded  
274 from the Bray-Curtis dissimilarity analysis and the Wilcoxon signed-rank test

275because abundances were monitored using different methods for annual  
276versus perennial species (Anderson et al. 2011).

277

## 278Results

279 We found a positive relationship between species richness at the 1 m<sup>2</sup>  
280scale and MAP across sites (Figure 2A,  $P = 0.02$ ,  $R^2 = 0.46$ ). Within sites  
281there were few significant temporal relationships between mean site-level  
282richness and annual precipitation in the current year or with previous year's  
283precipitation (Figure 2B, statistics summary in Table 2). Two sites with low  
284MAP had significantly positive temporal richness-precipitation relationships  
285(Jornada Basin -JRN - and MON), while KBS with intermediate MAP displayed a  
286significant negative relationship between richness and precipitation the prior  
287year.

288 Across sites MAP was a significant negative predictor of species  
289turnover when one site with unusually low turnover was excluded (Figure 3A,  
290 $P = 0.05$ ,  $R^2 = 0.44$ , if Jasper Ridge is included the relationship is not  
291significant). Interannual precipitation variability (coefficient of variation of  
292MAP) did not predict mean turnover ( $P = 0.35$ , results not shown). Sites with  
293low MAP had a high proportion of annual species in their species pools  
294(Figure 3B,  $P = 0.04$ ,  $R^2 = 0.38$ ; if the outlier Jasper Ridge, which is an  
295annual-dominated grassland, is removed this relationship is highly  
296predictive:  $P = 0.006$ ,  $R^2 = 0.64$ ). The proportion of annual species in the  
297species pool positively predicted turnover across sites, but this relationship is

298only marginally significant (Figure 3C,  $P = 0.09$ ,  $R^2 = 0.26$ ). Annual species  
299tend to have lower relative abundances across these focal sites than  
300perennial species (Wilcoxon signed-rank test  $P=0.01$ ). Species were more  
301likely to contribute to turnover via loss if they were annual (duration,  $P=0.01$ ,  
302 $F_{1,4147}=6.01$ ) or had low abundance in the prior year ( $P<0.0001$ ,  $F_{1,4147}=23.1$ ).  
303In 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  
304perennial species. Similarly, rare species were more likely to contribute to  
305turnover via gains in a given year ( $P<0.0001$ ,  $F_{1,4183}=16.2$ ), and rare annuals  
306were more likely to be gained than rare perennial species (duration by  
307abundance interaction  $P<0.0001$ ,  $F_{1,4183}=17.5$ ). As with richness, there were  
308few significant temporal relationships between turnover and annual  
309precipitation within sites (Table 2), with the exception of CDR where annual  
310precipitation positively predicted turnover, and MON where there was a  
311positive relationship between turnover and precipitation in the previous year.

313       As the total area sampled at a site decreases, there is an increasing  
314chance of undersampling the species pool and introducing random sampling  
315error from year to year (Nilsson and Nilsson 1982). The area sampled at KNZ  
316was nearly 5 times greater than the site with the next greatest area  
317sampled, and was 130 times greater than the site with the least area  
318sampled. While KNZ did sample the largest number of species and had low  
319turnover, total area sampled was a poor predictor of turnover across sites ( $R^2$

320= 0.08,  $P = 0.43$ ), suggesting that differences in plot area across site did not  
321introduce a systematic bias to these results.

322 Mean Bray-Curtis dissimilarity between years was unrelated to MAP  
323across sites, and was also unrelated to the proportion of annuals in the  
324species pool across sites. Within sites, Bray-Curtis dissimilarity between  
325years had a positive temporal relationship with annual precipitation only at  
326JRN (Table 2).

327

### 328Discussion

329 We found that the relationship between species richness and  
330precipitation depended on whether we examined the relationship focusing on  
331temporal (within a site) or spatial variation (across sites). While plot-scale  
332species richness was positively related to mean annual precipitation across  
333our sites, site-scale species richness was not related to interannual variation  
334in precipitation in 8 of the 10 sites, consistent with the findings of Adler and  
335Levine (2007). However, we found a positive temporal richness-precipitation  
336relationship at two of the driest sites in our analysis. Turnover driven by the  
337appearance of more annual species in wet years may account for this  
338relationship (Polis et al. 1997). We did not find evidence that lag effects  
339were important in predicting richness-precipitation relationships, unlike  
340previous studies which focused on within site relationships (Adler and Levine  
3412007).

342 While most of our sites displayed little variation in species richness  
343 across years, there was remarkable species turnover across years. The four  
344 driest sites displayed the highest levels of species turnover, with an average  
345 of 35-53% of species turning over each year (Figure 3A). These sites  
346 generally had a high proportion of annual species in their species pools (35-  
347 75%, Figure 3B), consistent with the idea that annual species represent an  
348 important reservoir of temporally rare species that might be exceptionally  
349 sensitive to future climate change (Xia et al. 2010). Dominance by annual  
350 species, however, does not necessarily mean a site will have high turnover.  
351 For example, JRG had the lowest average species turnover (11%), but had  
352 the highest proportion of annual species (80%). Serpentine grasslands like  
353 those at JRG contain many endemic species adapted to the unusual  
354 chemistry of their soils, and they tend to occur in relatively small patches  
355 with large distances between patches. This may result in lower rates of  
356 dispersal from adjacent communities than other more continuous habitat  
357 types (Harrison 1997). Indeed, recent work has documented extremely low  
358 year to year variability in species composition in serpentine sites as  
359 compared with more fertile sandy soils in California (Fernandez-Going et al.  
360 2012).

361 Unlike the presence-absence metrics of richness and turnover, our  
362 abundance-weighted measure of species composition (Bray-Curtis  
363 dissimilarity between years) was unrelated to precipitation on both spatial  
364 and temporal scales, with the exception of JRN where there was a positive



365relationship between precipitation and dissimilarity from the previous year.  
366High interannual variation in community composition in relation to climate  
367has been documented at other Chihuahuan desert sites (Guo and Brown  
3681997). The general lack of a response of abundant species to interannual  
369variation in rainfall across our data sets, and the increased likelihood of  
370species loss for rare species, indicate that the dynamic nature of turnover we  
371observed in these communities is likely due to substitutions among rare  
372species (Benedetti-Cecchi et al. 2008). A temporal analysis of tallgrass  
373prairie communities at KNZ showed that a small number of dominant species  
374occurred in almost all years, but over half of the species were found only  
375once or a few times over the 15 year time period (Collins 2000). This high  
376level of turnover occurred despite the fact that the plots sampled were large  
377(10 m<sup>2</sup>) and there was high replication (20 plots per year), suggesting that  
378high turnover is common and is an important mechanism by which a large  
379regional species pool buffers site-level diversity from interannual variation in  
380climate. Although dominant species tend to have the greatest influence on  
381ecosystem functioning (i.e. the mass ratio hypothesis; Grime 1998), rare  
382species can nevertheless influence ecosystem functions such as invasion  
383resistance (Lyons and Schwartz 2001) and provide important resources for  
384specialist consumers (Ehrlich and Murphy 1987) and mutualists (Kearns et al.  
3851998), making it important to document both the temporal dynamics of rare  
386and abundant species in ecosystems.

387 While we have documented patterns relating species richness and  
388 composition to annual precipitation, it is possible that other factors that co-  
389 vary with precipitation ultimately drive this interannual variation in species  
390 composition. For instance, annual precipitation is highly correlated with  
391 annual rates of wet N deposition, an aspect of environmental change that  
392 can have a great influence over species composition in plant communities  
393 (Suding et al. 2005, Bobbink et al. 2010); however, species richness was not  
394 predicted by rates of N deposition across our focal sites (see Supplementary  
395 material). Other factors which likely vary across sites, and could play a large  
396 role in determining interannual species composition include the timing and  
397 temperature at the onset of the rainy season. In arid and semi-arid  
398 environments these are important cues to break dormancy for species in the  
399 seed bank and bud bank because of their combined effects on soil-moisture  
400 availability (Chesson et al. 2004). Seed banks can differ strikingly from the  
401 community composition of the surrounding vegetation (e.g. Rabinowitz and  
402 Rapp 1980), and are likely the source of the high interannual turnover in  
403 species composition we observed in our xeric sites. In contrast, bud banks  
404 are often reflective of the extant community (Lee 2004), potentially acting to  
405 stabilize community composition in response to interannual climate  
406 variation, similar to their role as a reservoir of potential vegetative regrowth,  
407 allowing communities to recover quickly following disturbance (reviewed in  
408 Klimešová and Klimeš 2007). It has been argued that species composition in  
409 North American tallgrass prairie, for instance, is determined largely by the

410 dynamics of vegetative growth from perennial species rather than by  
411 dynamics of seed production and dispersal (Benson & Hartnett 2006).  
412 Perennial meristems increase across a precipitation gradient that includes  
413 several of our focal sites (Dalglish and Hartnett 2006), consistent with our  
414 observations of lower interannual turnover in response to interannual  
415 precipitation variability in mesic compared with xeric sites.

416       Over the longer timescales necessary for species to disperse to new  
417 habitats, we expect that areas with consistent increases in precipitation will  
418 have increased local species richness while regions with prolonged  
419 decreases in precipitation will experience declining local species richness.  
420 Our analysis demonstrated that plant community structure in arid  
421 ecosystems showed the greatest responsiveness to inter-annual variability in  
422 precipitation, unlike primary productivity where ecosystems with  
423 intermediate levels of MAP were most responsive to inter-annual variation in  
424 precipitation (Knapp and Smith 2001). Based on our analysis we can  
425 conclude that among grassland ecosystems, arid grasslands are likely to  
426 demonstrate the greatest short-term response of species richness to  
427 changing precipitation regimes, due to the dynamics of short-lived annual  
428 species capable of responding on the same time-scale as year-to-year  
429 variation in precipitation. We also found that across our sites annual species  
430 were more likely to be rare compared to perennial species, and sites with a  
431 greater number of rare species are more likely to see richness declines with

432increasing environmental variation due to stochastic demographic events  
433(Oksanen 1996, Goldberg and Miller 1990).

434 Plant ecology has a strong tradition of documenting patterns in species  
435composition in relation to climatic factors (i.e. von Humboldt 1858, Schimper  
4361903, Whittaker 1975), but this work has primarily focused on spatial  
437variation. Few studies have monitored community composition and climatic  
438variables for long enough (10+ years) to be able to evaluate how  
439communities respond to temporal climate variation. Differences in the  
440methodology used to monitor species composition present a significant  
441hurdle for cross-site analyses due to the influence of scale, extent and grain  
442on patterns of species richness and turnover (Gross et al. 2000). Species  
443richness does not scale linearly with area, while primary production usually  
444does, and perhaps as a consequence our knowledge of spatial and temporal  
445variation in production-climate relationships has progressed further (e.g.  
446Knapp and Smith 2001, Hsu et al. 2012). The advent of consistent cross-site  
447sampling efforts at continental to global scales, such as NEON (Keller et al.  
4482008) and the Nutrient Network Research Collective (Adler et al. 2011), will  
449eventually provide invaluable datasets for identifying how species  
450composition changes both over space and over time in relation to climate  
451variability. Nevertheless, our cross-site analysis demonstrated that  
452interannual variation in species identity and richness is high in North  
453American 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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728Table 1. Summary of datasets included in this cross-site synthesis.

Abbreviation	Location	Years	plot size (m <sup>2</sup> )	# of plots sampled each year	Mean total area	Dataset 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. Dataset 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. Dataset 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 x 0.02 m segments. Dataset 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, Dataset ID: ARS #32 Grazing and Soil Texture experiment

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

Site	# years	S vs AP	S vs AP prior yr	T vs AP	T vs AP prior yr	BC vs AP	BC vs AP prior yr
CDR	22	ns	ns	p=0.03, pos, r <sup>2</sup> =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 <sup>2</sup> =0.41	ns	ns	ns	p=0.04, pos, r <sup>2</sup> =0.23	ns
KBS	11	ns	p=0.01, neg, r <sup>2</sup> =0.50	ns	ns	ns	ns
KNZ	24	ns	ns	ns	ns	ns	ns
MON	12	p=0.008, pos, r <sup>2</sup> =0.47	ns	ns	p=0.01, pos, r <sup>2</sup> =0.50	NA	NA
NWT	8	ns	ns	ns	ns	ns	ns
SEV	21	ns	ns	ns	ns	ns	ns
734 SGS	14	ns	ns	ns	ns	ns	ns

## 735 Figure Legends

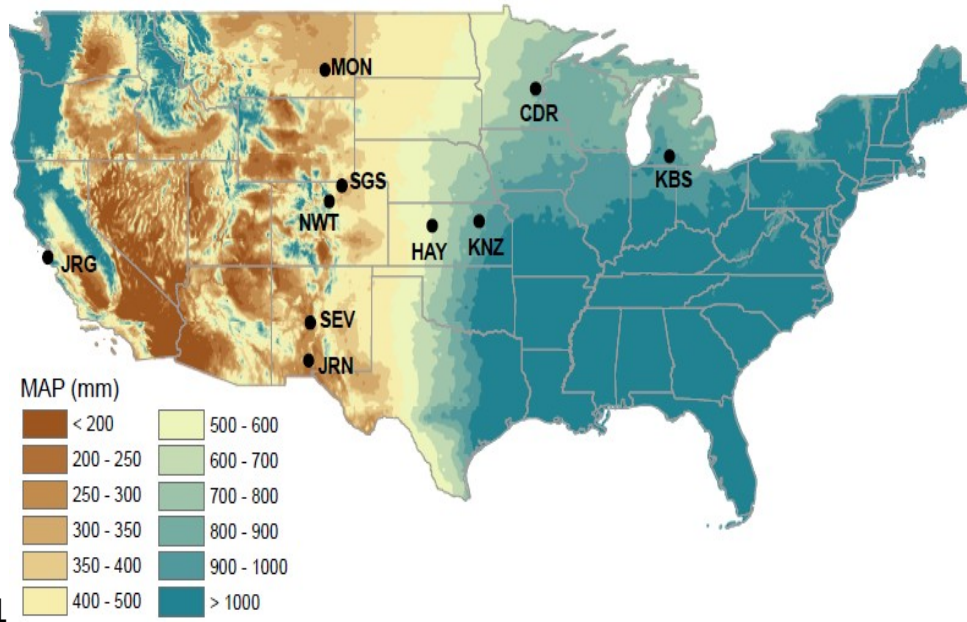
736

737 Figure 1. Map of the locations of the 10 sites superimposed on mean annual  
738 precipitation (MAP) in mm derived from the Prism dataset.

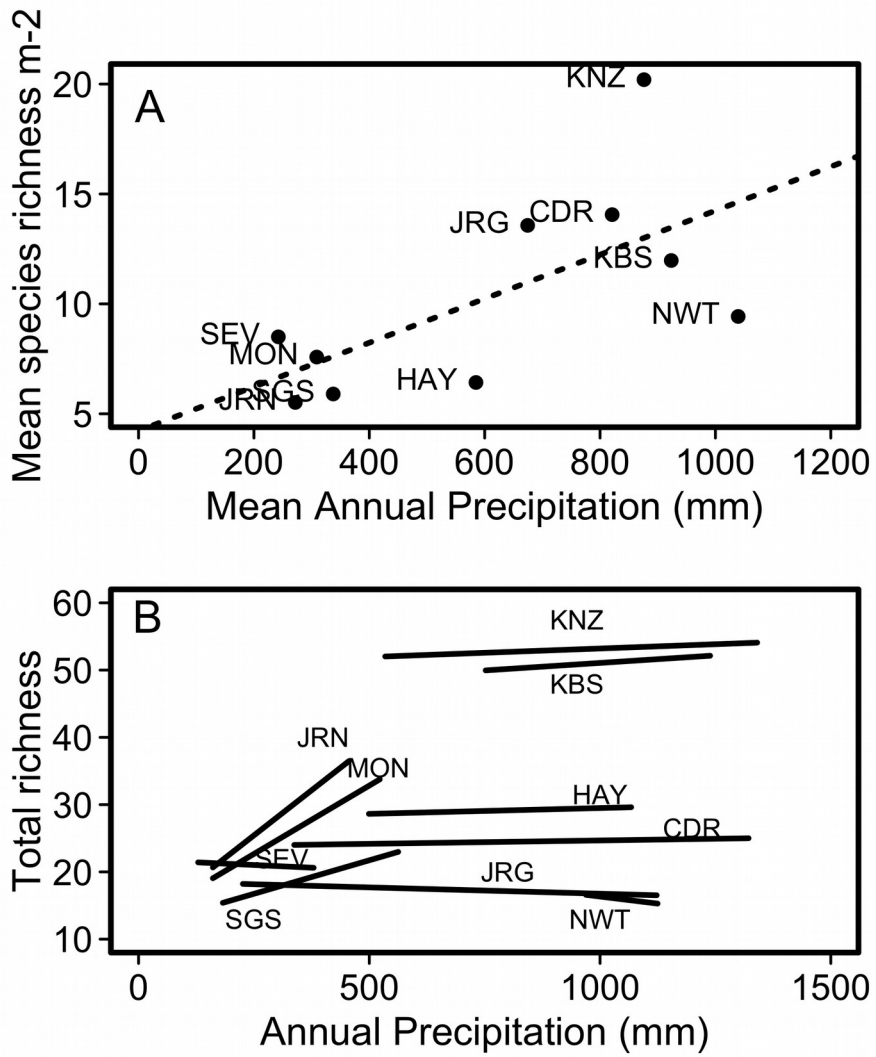
739 Figure 2. A) Species richness at the 1-m<sup>2</sup> scale is positively predicted by  
740 spatial variation in MAP ( $P = 0.02$ ,  $R^2 = 0.46$ ). B) Species richness is  
741 sensitive to temporal variation in annual precipitation only at the driest sites.

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

750Figure 1.



752Figure 2.



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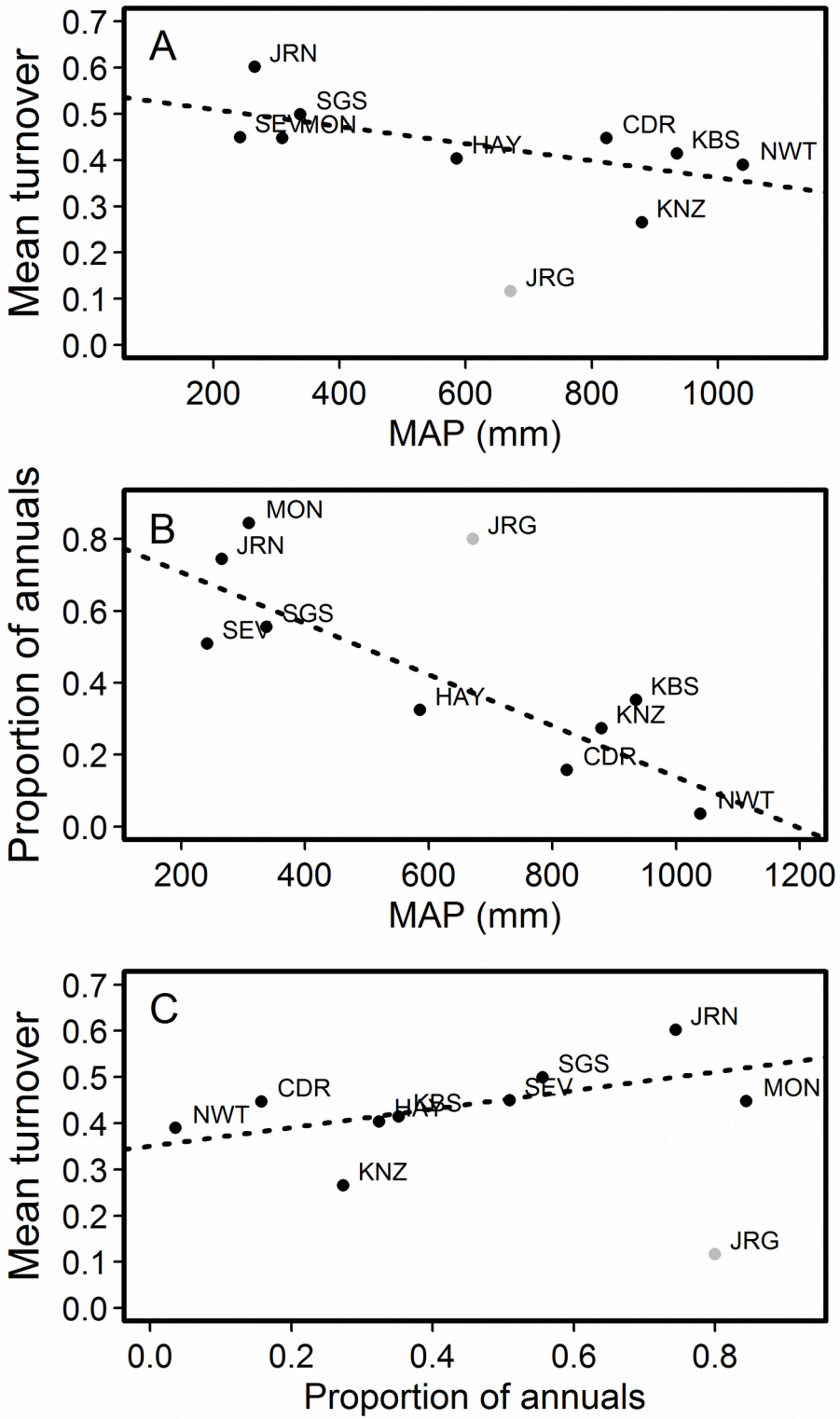
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759 Figure 3.



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