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

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

3

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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 m² 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 m² 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 m² 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, 1m² 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 m² 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 m²
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 m²) 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 ²)	# 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 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
734 SGS	14	ns	ns	ns	ns	ns	ns

735 Figure Legends

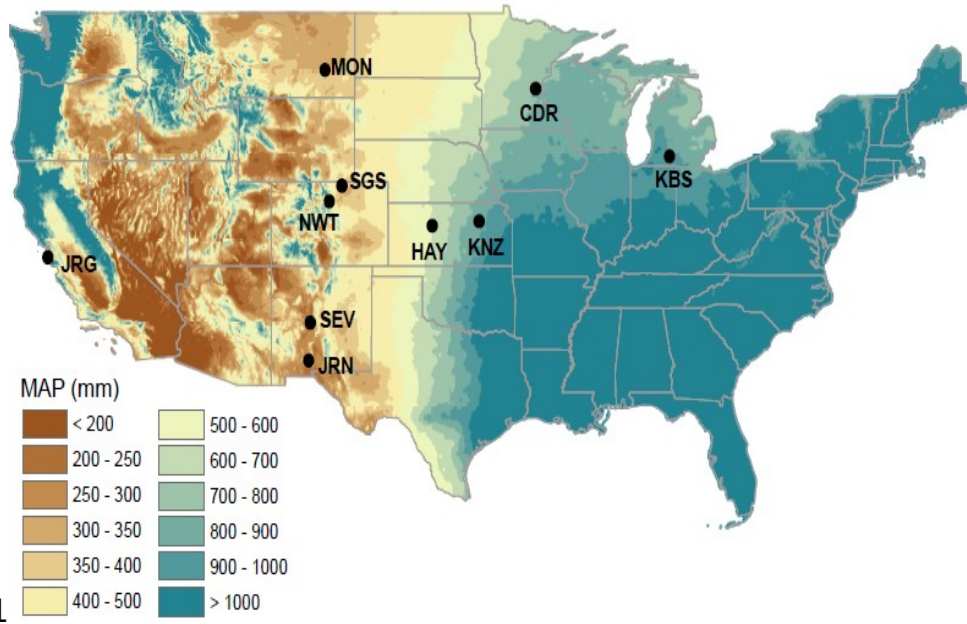
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737 Figure 1. Map of the locations of the 10 sites superimposed on mean annual
738 precipitation (MAP) in mm derived from the Prism dataset.

739 Figure 2. A) Species richness at the 1-m² 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.

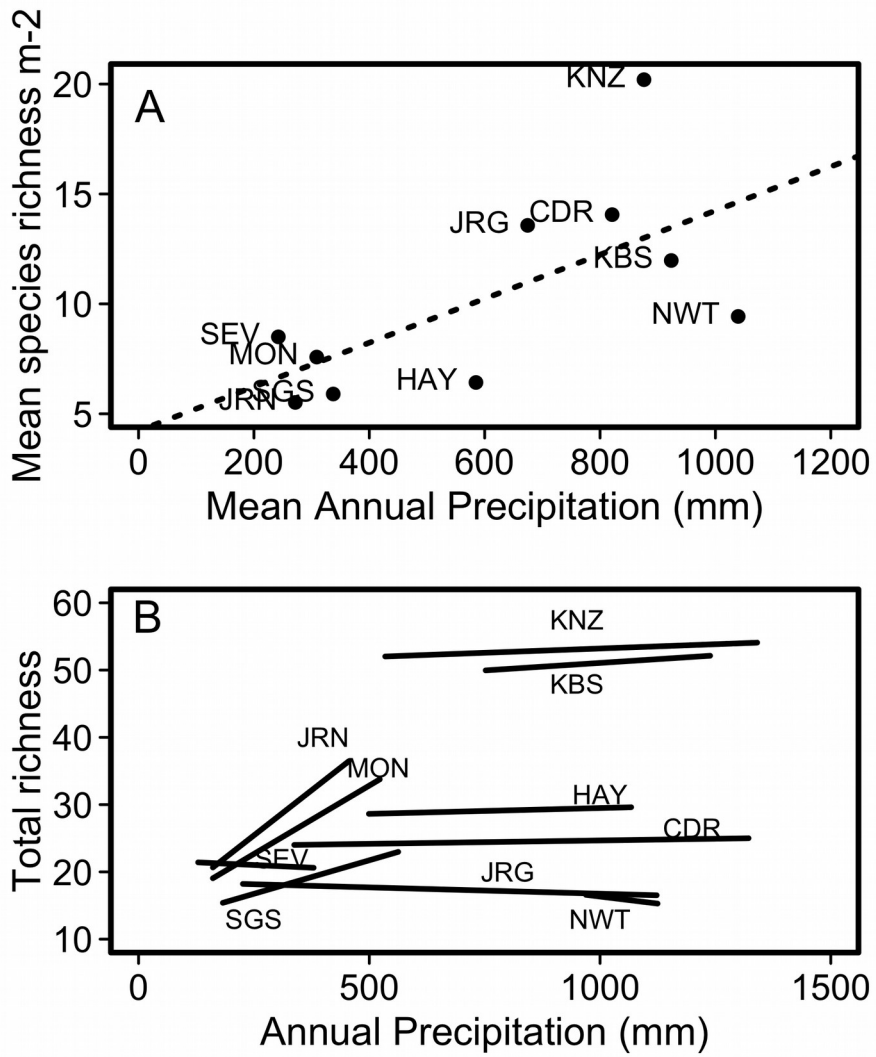
742 Figure 3. A) Interannual turnover in species composition (see Methods for
743 definition) is lower for sites with higher MAP ($P = 0.05$, $R^2 = 0.44$). B) Sites
744 with low MAP have a higher proportion of annual species in the local species
745 pool ($P = 0.006$, $R^2 = 0.64$). C) Sites with high 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.



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752Figure 2.



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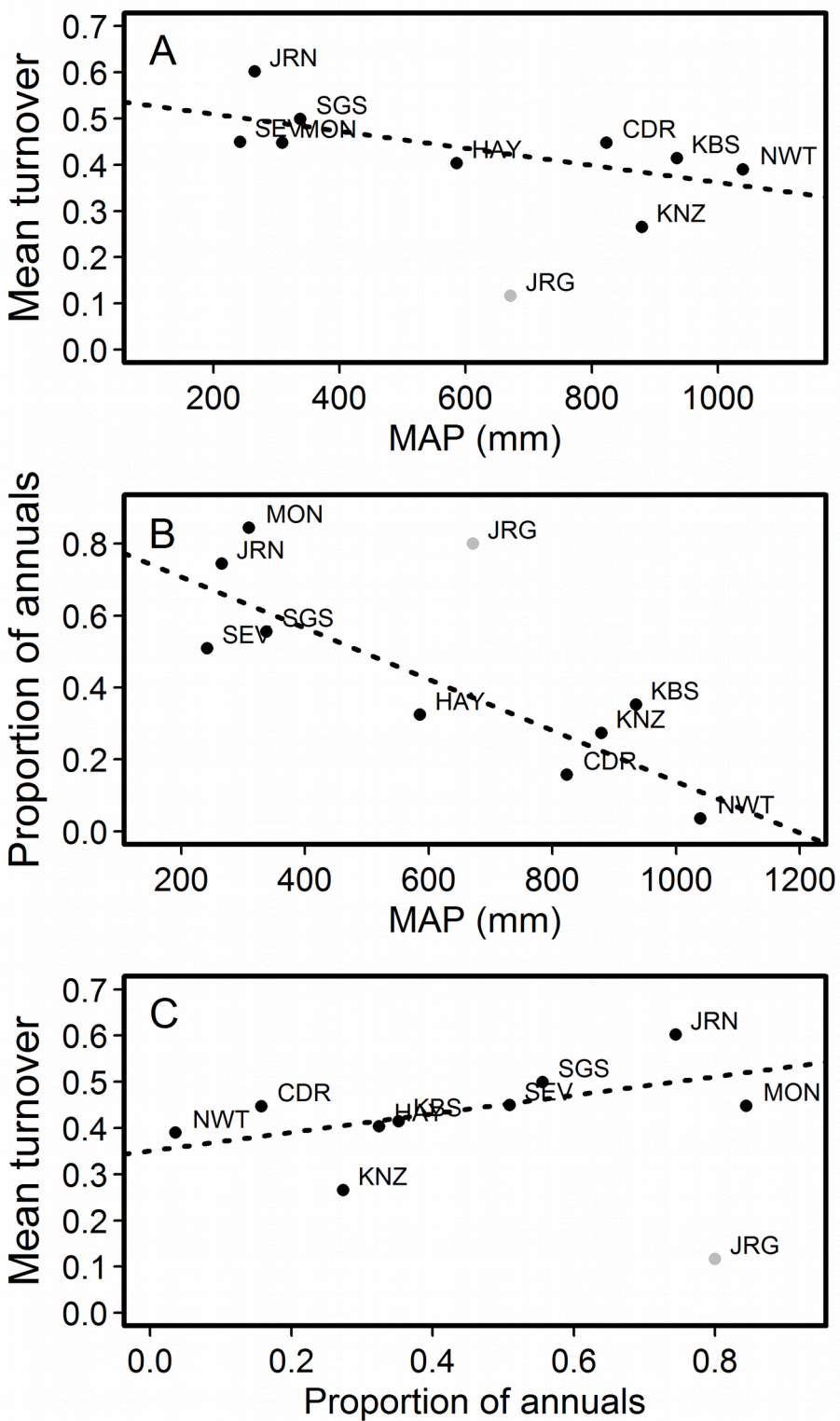
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759 Figure 3.



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