

1 **Running head:** Biotic mechanisms of stability

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3 **Biotic mechanisms of community stability shift along a precipitation**

4 **gradient**

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26**Keywords:** dominant species; compensatory dynamics; LTER; mean-

27variance scaling; negative covariance; portfolio effect; Taylor's power law

## 28**Abstract**

29Understanding how biotic mechanisms confer stability in variable  
30environments is a fundamental quest in ecology, and one that is becoming  
31increasingly urgent with global change. Several mechanisms, notably a  
32portfolio effect associated with species richness, compensatory dynamics  
33generated by negative species covariance and selection for stable dominant  
34species populations can increase the stability of the overall community.  
35While the importance of these mechanisms is debated, few studies have  
36contrasted their importance in an environmental context. We analyzed nine  
37long-term datasets of grassland species composition to investigate how two  
38key environmental factors – precipitation amount and variability – may  
39directly influence community stability and how they may indirectly influence  
40stability via biotic mechanisms. We found that the importance of stability  
41mechanisms varied along the environmental gradient: strong negative  
42species covariance occurred in sites characterized by high precipitation  
43variability, whereas portfolio effects increased in sites with high mean annual  
44precipitation. Instead of questioning whether compensatory dynamics are  
45important in nature, our findings suggest that debate should widen to  
46include several stability mechanisms and how these mechanisms vary in  
47importance across environmental gradients.

## 48**Introduction**

49Understanding the mechanisms that maintain community stability has been  
50a central goal in ecology for many decades (MacArthur 1955, May 1973,

51 Tilman 1996, Cottingham et al. 2001). Environmental variability can have a  
52 direct effect on the variability in community properties such as primary  
53 productivity if community properties track the environment over time (Knapp  
54 and Smith 2001, La Pierre et al. 2011, Craine et al. 2012). However, species  
55 dynamics within communities may moderate the direct effect of  
56 environmental forcing (Tilman and Downing 1994, Leary et al. 2012, Yang et  
57 al. 2012). Biotic stability mechanisms are species dynamics that result in the  
58 community being more stable than would be predicted based on variability in  
59 the environment (Lehman and Tilman 2000).

60 Biotic stability mechanisms have been the subject of much debate  
61 (Loreau et al. 2001, Hooper et al. 2005, Ives 2005). One of the most widely-  
62 focused on – and controversial – mechanisms is whether negative covariance  
63 in species populations creates “compensatory dynamics” in which trade-offs  
64 among species populations stabilize the overall community (Houlahan et al.  
65 2007, Gonzalez and Loreau 2009). Some studies confirm the presence of  
66 compensatory dynamics and its links to community stability (Descamps-  
67 Julien and Gonzalez 2005, Vasseur and Gaedke 2007, Downing et al. 2008,  
68 Leary and Petchey 2009), but recent syntheses have questioned the  
69 widespread existence of these dynamics in natural systems (Houlahan et al.  
70 2007, Mutshinda et al. 2009).

71 However, it has been long recognized that other biotic stability  
72 mechanisms can exist as well. For instance, species richness can create a  
73 “portfolio effect” if increased richness leads to a community property to be

74distributed among more species, causing the relative fluctuation of the  
75community to be less than the relative fluctuation of the constituent species  
76(Doak et al. 1998, Tilman et al. 1998, Lehman and Tilman 2000). The  
77portfolio effect depends on the relationship between the mean and variance  
78of species within a community; theoretical work has shown that community  
79stability should increase with diversity if the scaling function of the Taylor's  
80power law ( $z$ ) is greater than one (Doak et al. 1998). While the portfolio  
81effect should be particularly important for communities where biomass is  
82relatively evenly distributed among many species, population stability of  
83dominant species may be critical for communities with a more unbalanced  
84distribution of biomass. In these cases, dominance can create a "selection  
85effect" in which the population stability of the dominant species, because it  
86contributes much of the biomass of the overall community, strongly  
87influences community stability (Doak et al. 1998, Steiner et al. 2005,  
88Hillebrand et al. 2008).

89 Because environmental forcing can influence population as well as  
90community dynamics, and the cumulative effect can influence longer-term  
91adaptation and species pools, it is likely that the strength of these  
92mechanisms vary along environmental gradients (Grman et al. 2010, Thibaut  
93and Connolly 2013). Thus, contextualizing stability mechanisms in relation to  
94the environment may help to resolve debate about the importance of species  
95dynamics for community stability. Here, we focus on two well-documented  
96drivers of spatial and temporal dynamics in ecological communities:

97precipitation amount and variability (Tilman and Downing 1994, Knapp and  
98Smith 2001, Huxman et al. 2004). For example, across spatial gradients  
99mean annual aboveground net primary productivity (ANPP) in grasslands is  
100strongly related with mean annual precipitation (MAP) (Sala et al. 1988).  
101However, ANPP is typically far less sensitive to inter-annual variation within  
102grassland sites over time than it is to cross-site variation in precipitation  
103(Adler and Levine 2007, Hsu et al. 2012, Sala et al. 2012). Although it has not  
104been tested, differences in how communities respond to precipitation across  
105spatial versus temporal scales may be due to differences in biotic stability  
106mechanisms across sites.

107 We hypothesized that biotic mechanisms contribute to community  
108stability across grassland sites, but that the importance of different  
109mechanisms is associated with differences in long-term precipitation  
110patterns. For example, species richness commonly increases with MAP (Adler  
111and Levine 2007, Cleland et al. 2013), and so the portfolio effect may be a  
112particularly important stability mechanism in sites with high MAP. Negative  
113species covariance can enhance stability if trade-offs between species are  
114driven by differential responses to environmental conditions (Ives et al.  
1151999, Loreau and de Mazancourt 2013) and compensatory dynamics may  
116therefore be an important mechanism in sites characterized by highly  
117variable precipitation (Yachi and Loreau 1999, de Mazancourt et al. 2013).  
118The selection effect due to the buffering of variability by dominant species  
119would be more likely to be strong in sites with high dominance (or a very

120uneven distribution of species abundances) and perhaps operate in the  
121opposing direction as the portfolio effect (Polley et al. 2007).

122 To test our hypotheses we capitalized on a regional gradient in  
123precipitation and long-term plant community data at nine grassland sites in  
124North America (Table A1). We quantified species dynamics in relation to  
125three biotic mechanisms that could contribute to stability of ANPP (portfolio  
126effect, compensatory dynamics, dominant selection effect). We then used  
127structural equation modeling to test whether MAP and the CV of annual  
128precipitation related to community stability directly or indirectly via these  
129biotic mechanisms.

## 130**Methods**

### 131*Community stability*

132We analyzed community stability in nine grassland sites using long-term ( $\geq 9$   
133years) datasets of plant species composition that were either contributed by  
134coauthors or publicly available (Table A1, Fig. A1). All analyses were  
135conducted in R version 3.0.1 (R Core Team 2013). We restricted our analyses  
136to sites in which measurement techniques and management regimes had  
137remained constant over the collection period and in which data collection  
138methods were not relativized. For example, sites in which species  
139composition were measured as percent cover were included only if estimates  
140were not required to sum to 100. We aggregated species abundances within  
141replicate and year and used these values to calculate community stability

142( $\mu/\sigma$ ; Tilman 1999, Lehman and Tilman 2000) for each site. We paired the  
143community data with long-term data of ANPP and repeated this calculation  
144for ANPP (data from Hsu et al. (2012) and from Hobbs et al. (1988) for Jasper  
145Ridge; no biomass data were available for Vasco Caves). Because these two  
146measures were strongly correlated ( $r = 0.93$ ,  $df = 6$ ,  $p < 0.0001$ ) we  
147considered community stability (aggregated species abundance) a proxy for  
148productivity stability.

#### 149*Direct relationships between precipitation and community stability*

150We obtained long-term precipitation records for each site from the closest  
151available weather station to calculate MAP and the CV of annual  
152precipitation. We used multiple regression to directly relate community  
153stability (calculation described above) with MAP and the CV of annual  
154precipitation and used Pearson correlation to test the relationship between  
155the two precipitation metrics. Because many composition estimates in our  
156dataset were cover based, for these analyses we coupled our dataset with  
157measures of stability calculated using ANPP from 19 other sites in a  
158productivity dataset (data from Hsu et al. in revision).

#### 159*Relationships between precipitation and biotic mechanisms of community* 160*stability*

161We calculated metrics to characterize the three biotic mechanisms of  
162community stability: species richness and the scaling power  $z$  (the portfolio  
163effect), negative species covariance (compensatory dynamics), and



164 dominant species population stability and species evenness (dominant  
165 selection effect).

166 We calculated species richness as the mean number of species that  
167 occurred in a 1 m<sup>2</sup> replicate each year. Most sites measured species  
168 composition at the 1-m<sup>2</sup> scale, but for those that used a different plot size we  
169 used supplemental data from the same location that were collected at the 1-  
170 m<sup>2</sup> scale (datasets described in Cleland et al. 2013; no 1-m<sup>2</sup> scale data were  
171 available for Vasco Caves).

172 Species richness should generate a “portfolio effect” if the variances in  
173 species abundances increase more steeply than their mean abundances  
174 (Doak et al. 1998, Tilman 1999). We verified that increasing species richness  
175 should enhance the portfolio effect at our sites using Taylor’s power law such  
176 that  $\sigma^2 = c\mu^z \sigma^2 = c\mu^z$  where  $c$  and  $z$  are constants,  $\sigma^2$  is the variance in  
177 species abundance and  $\mu$  is mean species abundance. A portfolio effect  
178 occurs when  $z$  values are between one and two, whereas additional species  
179 can be destabilizing when  $z$  is less than one (i.e., when stability would  
180 instead be maximized by a single, low-variance species). Because  $z$  ranged  
181 from 1.4 to 1.8 across our sites (Fig. A2), we retained species richness as a  
182 measure of the portfolio effect in subsequent analyses.

183 We quantified negative covariance using the variance ratio, which  
184 compares the variance of the community ( $C$ ) as a whole relative to the sum  
185 of the individual population ( $P_i$ ) variances (Schluter 1984, Houlahan et al.  
186 2007):

187 
$$VR = \frac{\text{var}(C)}{\sum_{i=1}^n \text{var}(P_i)}$$

188 where:

189 
$$\text{var}(C) = \left[ \sum_{i=1}^n \text{var}(P_i) \right] + 2 \left[ \sum_{i=1}^n \sum_{j=1}^{i-1} \text{cov}(P_i, P_j) \right]$$

190 A variance ratio less than one would indicate predominately negative species  
191 covariance, signifying evidence for compensatory dynamics. To test whether  
192 variance ratios significantly differed from one we used a temporal  
193 modification of the torus-translation (Harms et al. 2001) in which we  
194 randomly selected different starting years for each species' time series. This  
195 generated a null community matrix in which species abundances varied  
196 independently but within-species autocorrelation was maintained. We  
197 repeated this randomization 10000 times to create a null distribution of  
198 variance ratios calculated from independently-varying populations and  
199 compared our observed variance ratio against this null distribution.

200 To quantify the role of dominant species for community stability we first  
201 identified the species in each replicate that had the highest mean relative  
202 abundance over time. We used the stability of this species ( $\mu/\sigma$ ) as a metric  
203 of dominant species stability. Because the relative abundance of the  
204 dominant species varied widely across sites (from 29% to 84%), we  
205 additionally calculated Pielou's evenness index within replicates and  
206 averaged across years (Pielou 1966). Pielou's evenness index was tightly  
207 negatively correlated with dominant species relative abundance ( $r = -0.97$ ,

208  $df = 7, p < 0.001$ ), reflecting the fact that an increase in evenness decreases  
209 the influence that a dominant species has on the overall community.

210 To test that these mechanisms are important for community stability we  
211 used multiple regression with species richness, the variance ratio, dominant  
212 species stability and Pielou's evenness index as explanatory variables. Prior  
213 to regression we used Pearson correlation to check for collinearity among  
214 variables. Because species richness and evenness were significantly  
215 correlated ( $r = 0.72, df = 6, p = 0.04$ ), we retained species richness as a  
216 proxy for both variables in the full model. No other biotic metrics were  
217 significantly correlated.

218 To relate these biotic mechanisms with precipitation we first regressed  
219 each term against MAP and the CV of annual rainfall. Second, to holistically  
220 characterize the relationships among precipitation, biotic stability  
221 mechanisms and community stability we employed a structural equation  
222 model in which MAP and the CV of precipitation were linked to community  
223 stability both directly and indirectly via species richness, the variance ratio,  
224 and the stability of dominant species (fit with maximum likelihood estimation  
225 using the lavaan package (Rosseel 2012)).

## 226 **Results**

227 Across sites MAP and the CV of annual precipitation were not correlated ( $r =$   
228  $-0.15, df = 26, p = 0.44$ ); nor were precipitation variables correlated within  
229 the focal sites ( $r = -0.38, df = 7, p = 0.31$ ). There was no direct relationship  
230 between community stability and either MAP ( $F_{2,25} = 0.14, p = 0.16, R^2 =$

2310.03; Fig. 1a) or the CV of annual precipitation ( $p = 0.57$ ; Fig. 1b) Within the  
232productivity dataset community stability was positively related with mean  
233ANPP ( $F_{1,35} = 31.2$ ,  $\beta = 0.007$ ,  $p < 0.001$ ,  $R^2 = 0.46$ ), indicating that in  
234general increasing mean biomass had a greater effect on community  
235stability than decreasing the standard deviation of biomass.

236 Species richness and the variance ratio, but not dominant species  
237stability, were significant predictors of community stability in the multiple  
238regression model ( $F_{3,4} = 15.8$ ,  $R^2 = 0.86$ ; Fig. 1c-e). Community stability  
239increased with mean species richness ( $\beta = 0.17 \pm 0.047$ ,  $p = 0.018$ ; Fig. 1c),  
240which ranged from 5.5 to 20.2 species/m<sup>2</sup>. Community stability decreased  
241with the variance ratio (i.e., increased with negative covariance,  $\beta = -3.55$   
242 $\pm 0.70$ ,  $p = 0.007$ ; Fig. 1d), and five of the nine sites had a variance ratio that  
243was significantly less than one. Species richness was significantly positively  
244related with MAP ( $F_{1,6} = 9.9$ ,  $\beta = 0.015 \pm 0.005$ ,  $p = 0.02$ ,  $R^2 = 0.56$ ; Fig. 2a)  
245but unrelated with the CV of annual precipitation (Fig. 2b). The variance ratio  
246was not related with MAP (Fig. 2c) but was significantly negatively related  
247with the CV of annual precipitation ( $F_{1,7} = 5.6$ ,  $\beta = -0.038 \pm 0.016$ ,  $p = 0.05$ ,  
248 $R^2 = 0.37$ ; Fig. 2d). Dominant stability was not directly related with either  
249MAP or the CV of annual rainfall (Fig. 2e,f).

250 All three biotic mechanisms were significantly related to community  
251stability in the structural equation model, whereas neither MAP nor the CV of  
252annual rainfall directly related to community stability (Fig. 3). However, both  
253precipitation variables related to community stability indirectly via their

254relationships with biotic stability mechanisms. Species richness showed a  
255significant positive relationship with MAP, whereas negative species  
256covariance increased with the CV of annual precipitation (Fig. 3, bivariate  
257relationships in Fig. 1a-e, Fig. 2a-f).

## 258**Discussion**

259Across spatial gradients precipitation is a primary control on grassland  
260composition and production, yet we found that the stability of grassland  
261communities was not directly related to either MAP or precipitation  
262variability. This remarkable finding was due to a shift in the biotic stability  
263mechanisms that operated along the precipitation gradient: the portfolio  
264effect (species richness) contributed to community stability in sites with high  
265MAP, whereas negative species covariance contributed to community  
266stability in sites with highly variable precipitation. Thus, instead of  
267questioning whether compensatory dynamics are important in nature, our  
268results suggest that the debate should shift to how compensatory dynamics  
269and other stability mechanisms may vary in importance across  
270environmental gradients.

271 The first pathway by which precipitation affected community stability was  
272via species richness, where sites with high MAP supported high numbers of  
273species, and high species richness was related to increased community  
274stability over time. We interpret this relationship as evidence of the portfolio  
275effect increasing in importance in sites that receive high amounts of MAP  
276(e.g., in the tallgrass prairie site in Kansas; Table A1). While species richness

277does not necessarily need to lead to a portfolio effect, all sites used in the  
278analysis had Taylor power law  $z$  values over one, indicating that species  
279diversity was stabilizing (species abundance variance increased more than  
280species mean abundance). Thus,  $z$  values  $> 1.0$  combined with the positive  
281influence of species richness on community stability are consistent with  
282expectations of the portfolio effect (Doak et al. 1998, Tilman 1999).

283 While the portfolio effect was strongest at sites with high MAP, negative  
284species covariance was greatest in sites characterized by high precipitation  
285variability. Previous synthesis studies that have calculated the variance ratio  
286at multiple sites for several taxa reported more positive than negative  
287covariance (Houlahan et al. 2007, Valone and Barber 2008). These patterns  
288contrast with experimental findings, which often provide evidence of  
289compensatory dynamics (Klug et al. 2000, Hector et al. 2010). Our findings  
290suggest that compensatory dynamics may occur in natural systems – over  
291half the sites we studied exhibited significant negative covariance – but that  
292the strength of compensatory dynamics in natural systems may be context-  
293dependent. These results indicate that in sites with strong environmental  
294fluctuations, such as the arid southwestern US and Mediterranean-climate  
295California sites, climate-driven variation in competitive hierarchies may  
296enforce patterns of negative species covariance while destabilizing individual  
297populations.

298 The frequency with which we observed negative species covariance is  
299particularly striking given that the null hypothesis for coexisting species

300dependent on the same resources is that they should positively co-vary in  
301response to resource availability (Loreau and de Mazancourt 2008).  
302Experimental manipulations within sites suggest that the observed negative  
303covariance is largely driven by dominant species interactions (Roscher et al.  
3042011), whereas rare species often respond synchronously to precipitation.  
305Sasaki and Lauenroth (2011), for example, manipulated dominance at the  
306Short Grass Steppe and found that the strength of negative species  
307covariance increased with the relative abundance of dominant species. In  
308contrast, sites in which dominants were removed tended to have more  
309positive covariance, with rare species flickering in and out synchronously  
310with high precipitation years. Similarly, Hobbs et al. (2007) observed highly  
311asynchronous dominant species populations at Jasper Ridge, but found that  
312the majority of species responded positively to increased precipitation.

313 Dominant species stability did not exhibit a direct relationship with  
314community stability, but it did emerge as a third significant stability  
315mechanism in the structural equation model. This result is aligned with  
316experimental work that has shown that dominant species are important for  
317maintaining stability in primary productivity over time for some systems  
318(Smith and Knapp 2003, Sasaki and Lauenroth 2011). However, the effect  
319size of dominant species stability was less than either the portfolio effect or  
320negative species covariance. This may be because the two components of a  
321dominant selection effect – high dominance and population stability – did not  
322occur in tandem along the precipitation gradient. Although dominant species

323comprised relatively more of the total community as total MAP decreased,  
324the stability of the dominant species did not significantly vary with  
325precipitation.

326 The alternating strength of different stability mechanisms with  
327precipitation may help explain why productivity is strongly governed by  
328precipitation over space but less so over time. Our findings suggest that  
329across spatial gradients, different precipitation patterns may shape different  
330population dynamics that moderate the direct effects of precipitation on  
331primary productivity. This understanding sheds light on the mechanisms  
332explaining patterns of primary productivity and will be relevant for predicting  
333ecosystem responses to the greater climate variability forecasted for coming  
334decades. For instance, our analyses suggest that compensatory dynamics  
335will become more important to the stability of sites that experience  
336increased precipitation variability. However, we suspect that rapid increases  
337in precipitation variability may outpace the colonization rates of species  
338adapted to variable conditions (Adler and Levine 2007). If specific trait  
339adaptations are required for communities to exhibit compensatory dynamics,  
340then patterns generated by long-term climate, as we analyzed here, may be  
341disconnected from community responses to more rapid precipitation change.

### 342**Acknowledgements**

343This effort was funded through a Cross-Site Synthesis grant from the Long-  
344Term Ecological Research Network. We are grateful to all the researchers



345who originally collected these data. We particularly wish to thank Peter Adler  
346and Claire Baldeck for providing advice on analyses, Andrew Gonzalez and  
347an anonymous reviewer for comments on an earlier version of this  
348manuscript, and Peter Adler, James Bartolome, Michele Hammond, Peter  
349Hopkinson and the East Bay Regional Park District for providing data.  
350Significant funding for the collection of these data was provided by the  
351National Science Foundation (NSF) through the LTER network grant numbers:  
352DEB-0080382 (CDR), DEB-0917668, DEB-1235828 & DEB-1242747 (JRN),  
353DEB-1027253, DEB-0423627 & DEB-9810220 (KBS), DEB-0620482 (SEV), and  
354DEB-0217631 (SGS). L. M. H. was supported by a UC Berkeley Chancellor's  
355Fellowship.

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## 508 **Supplemental material**

### 509 **Appendix**

510 Descriptive summaries of the datasets included in our analyses, including

511 source information and representative times series of species abundances

512 over time.



513

#### 514 **Figure Legends**

515 **Fig. 1.** Community stability in relation to precipitation and biotic  
516 mechanisms. **(a,b)** Community stability in relation to **(a)** mean annual  
517 precipitation (mm) (MAP) and **(b)** the CV of annual precipitation across 28  
518 grasslands sites. Focal sites with available community composition data are  
519 labeled (community stability is calculated on aggregated species  
520 abundances). Community stability for the remaining sites is calculated on  
521 annual net primary productivity; data from Hsu et al. in revision. **(c-e)**  
522 Community stability in relation to three biotic stability mechanisms. Lines  
523 indicate significant relationships in a multiple regression model relating  
524 these metrics with community stability, all biotic mechanisms were  
525 significantly related with stability in a structural equation model: **(c)** Species  
526 richness (species/m<sup>2</sup>), which is positively associated with the portfolio effect;  
527 **(d)** the variance ratio, which describes species covariance. A variance ratio  
528 less than one indicates predominantly negative covariance, reflective of  
529 compensatory dynamics; **(e)** the stability ( $\mu/\sigma$ ) of the most-abundant  
530 (dominant) species.

531

532 **Fig. 2** Biotic stability mechanisms in relation to precipitation across nine  
533 grassland sites; lines indicate significant bivariate relationships. **(a,b)**  
534 Species richness in relation to **(a)** mean annual precipitation (mm) (MAP) and

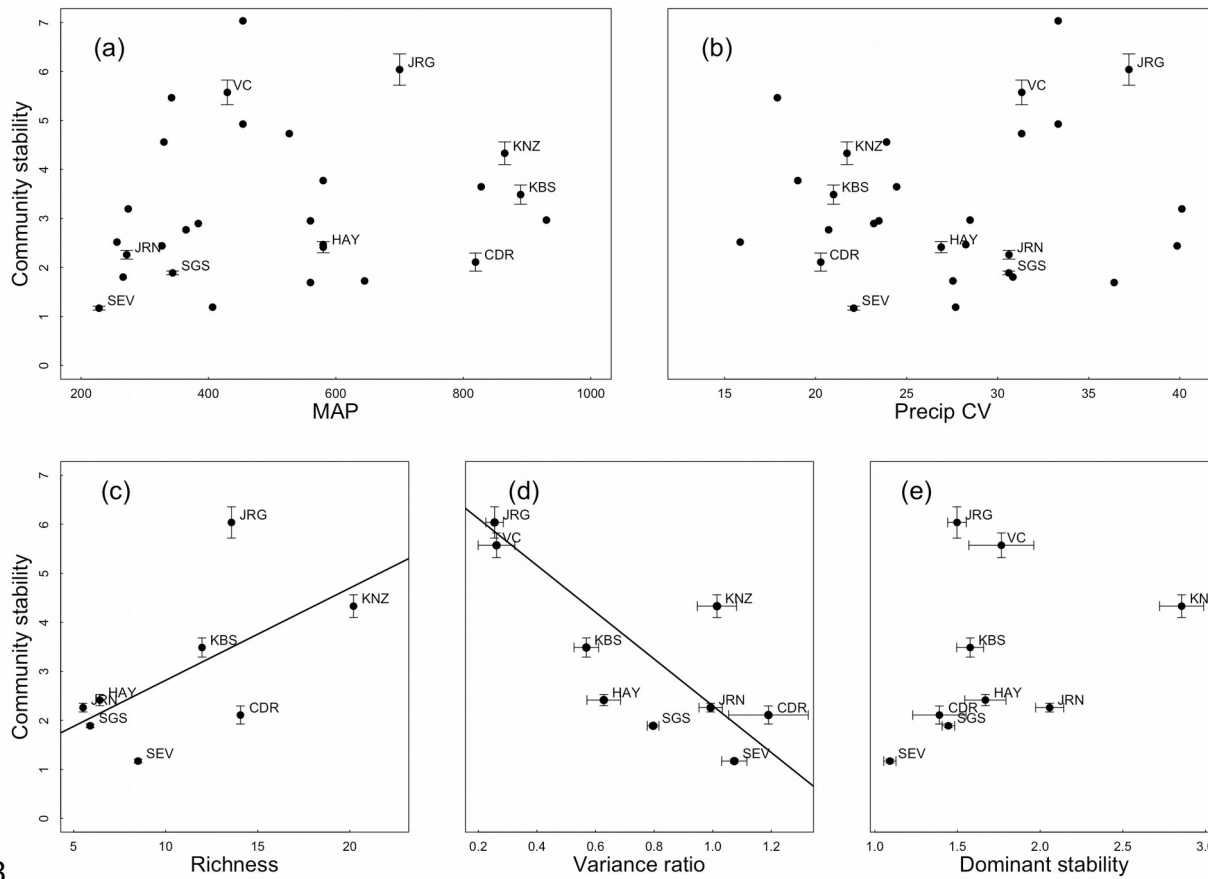
535**(b)** the CV of annual precipitation; **(c,d)** The variance ratio in relation to **(c)**  
536MAP and **(d)** the CV of annual precipitation. Small gray dots with error bars  
537indicate the mean and 95% confidence intervals of a null model (simulated  
538variance ratios with independently varying species); **(e,f)** The stability ( $\mu/\sigma$ )  
539of the most abundant (dominant) species in relation to **(e)** MAP and **(f)** the  
540CV of annual precipitation.

541

542**Fig. 3.** Structural equation model developed to relate precipitation, biotic  
543stability mechanisms and community stability across nine grassland sites.  
544Lines denote significant relationships and are scaled in relation to their effect  
545size.  $R^2$  values represent the proportion of variance explained for each  
546dependent variable. All three biotic mechanisms directly contribute to  
547community stability, whereas precipitation relates to community stability  
548indirectly via pathways between mean annual precipitation and the portfolio  
549effect (species richness) and between precipitation variability and  
550compensatory dynamics.

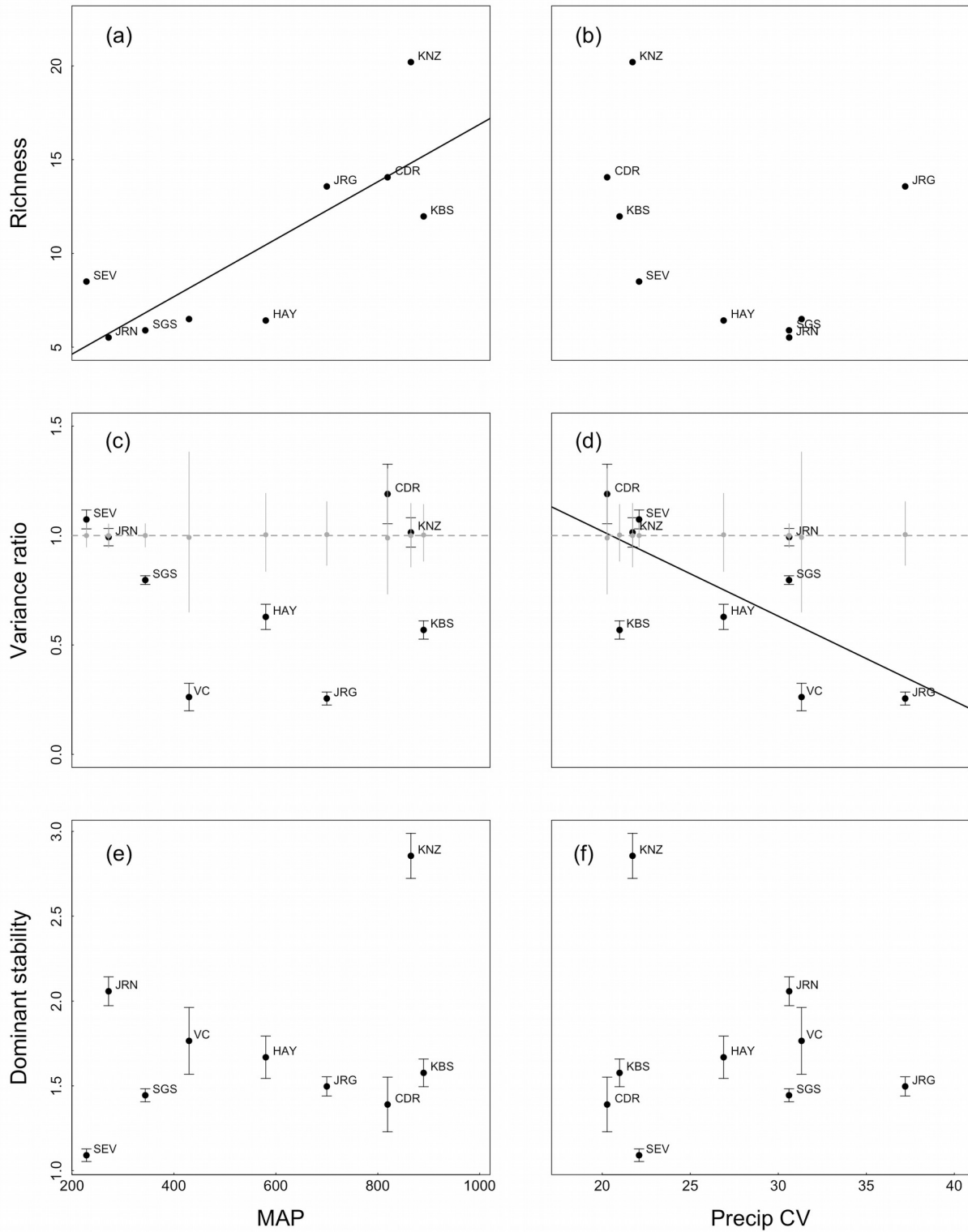
551 **Fig. 1.**

552



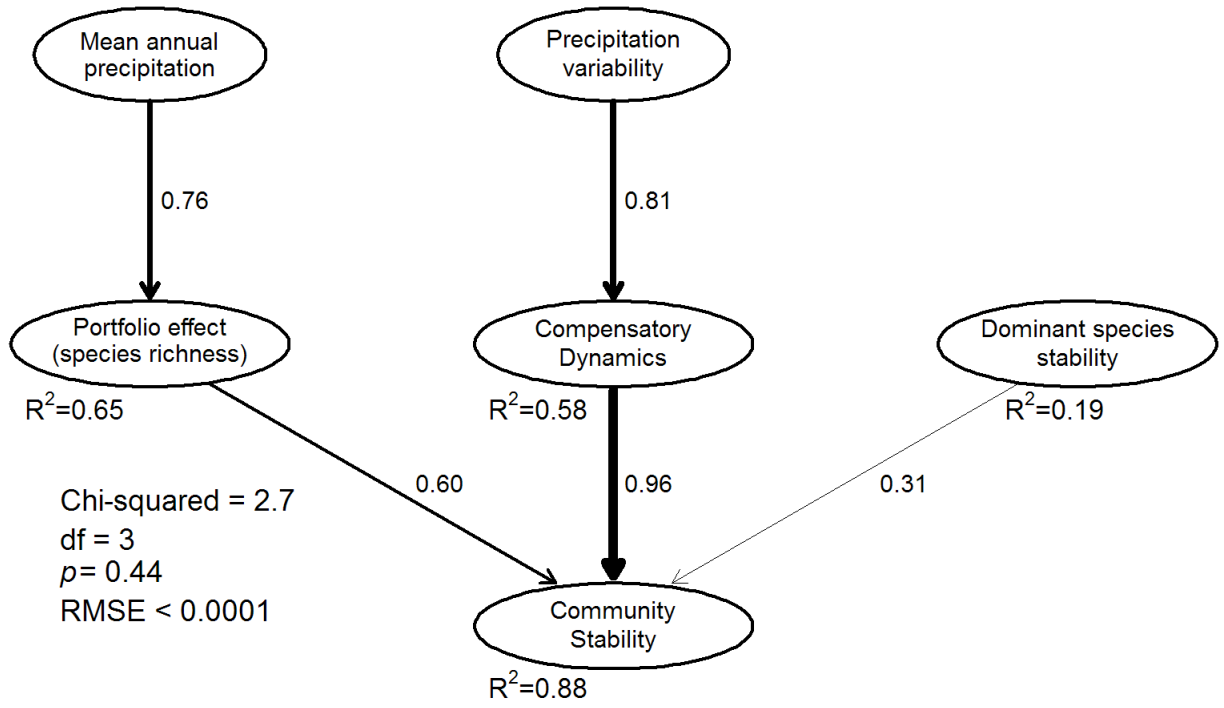
553

554 **Fig. 2.**



555

556 **Fig. 3.**



557