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Biotic mechanisms of community stability shift along a precipitation gradient

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Abstract

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

Introduction

Understanding the mechanisms that maintain community stability has been a central goal in ecology for many decades (Macarthur 1955, May 1973, Tilman 1996, Cottingham et al. 2001). Environmental variability can have a direct effect on the variability in community properties such as primary productivity if community properties track the environment over time (Knapp and Smith 2001, La Pierre et al. 2011, Craine et al. 2012). However, species dynamics within communities may moderate the direct effect of environmental forcing (Tilman and Downing

1994, Leary et al. 2012, Yang et al. 2012). Biotic stability mechanisms are species dynamics that result in the community being more stable than would be predicted based on variability in the environment (Lehman and Tilman 2000).

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

However, it has been long recognized that other biotic stability mechanisms can exist as well. For instance, species richness can create a “portfolio effect” if increased richness leads to a community property to be distributed among more species, causing the relative fluctuation of the community to be less than the relative fluctuation of the constituent species (Doak et al. 1998, Tilman et al. 1998, Lehman and Tilman 2000). The portfolio effect depends on the relationship between the mean and variance of species within a community; theoretical work has shown that community stability should increase with diversity if the scaling function of the Taylor’s power law (z) is greater than one (Doak et al. 1998). While the portfolio effect should be particularly important for communities where biomass is relatively evenly distributed among many species, population stability of dominant species may be critical for communities with a more unbalanced distribution of biomass. In these cases, dominance can create a “selection effect” in which the population stability of the dominant species, because it contributes much of the biomass of the overall community, strongly influences community stability (Doak et al. 1998, Steiner et al. 2005, Hillebrand et al. 2008).

Because environmental forcing can influence population as well as community dynamics, and the cumulative effect can influence longer-term adaptation and species pools, it is likely that the strength of these mechanisms vary along environmental gradients (Grman et al. 2010, Thibaut and Connolly 2013). Thus, contextualizing stability mechanisms in relation to the environment may help to resolve debate about the importance of species dynamics for community stability. Here, we focus on two well-documented drivers of spatial and temporal dynamics in ecological communities: precipitation amount and variability (Tilman and Downing 1994, Knapp and Smith 2001, Huxman et al. 2004). For example, across spatial gradients mean annual aboveground net primary productivity (ANPP) in grasslands is strongly related with mean annual precipitation (MAP) (Sala et al. 1988). However, ANPP is typically far less sensitive to inter-annual variation within grassland sites over time than it is to cross-site variation in precipitation (Adler and Levine 2007, Hsu et al. 2012, Sala et al. 2012). Although it has not been tested, differences in how communities respond to precipitation across spatial versus temporal scales may be due to differences in biotic stability mechanisms across sites.

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

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

Methods

Community stability

We analyzed community stability in nine grassland sites using long-term (≥ 9 years) datasets of plant species composition that were either contributed by coauthors or publicly available (Table A1, Fig. A1). All analyses were conducted in R version 3.0.1 (R Core Team 2013). We restricted our analyses to sites in which measurement techniques and management regimes had remained constant over the collection period and in which data collection methods were not relativized. For example, sites in which species composition were measured as percent cover were included only if estimates were not required to sum to 100. We aggregated species abundances within replicate and year and used these values to calculate community stability (μ/σ; Tilman 1999, Lehman and Tilman 2000) for each site. We paired the community data with long-term data of

ANPP and repeated this calculation for ANPP (data from Hsu et al. (2012) and from Hobbs et al. (1988) for Jasper Ridge; no biomass data were available for Vasco Caves). Because these two measures were strongly correlated ($r = 0.93$, df = 6, $p < 0.0001$) we considered community stability (aggregated species abundance) a proxy for productivity stability.

Direct relationships between precipitation and community stability

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

Relationships between precipitation and biotic mechanisms of community stability

We calculated metrics to characterize the three biotic mechanisms of community stability: species richness and the scaling power z (the portfolio effect), negative species covariance (compensatory dynamics), and dominant species population stability and species evenness (dominant selection effect).

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

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

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

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

where:

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

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

To quantify the role of dominant species for community stability we first identified the species in each replicate that had the highest mean relative abundance over time. We used the stability of this species (μ/σ) as a metric of dominant species stability. Because the relative abundance of the dominant species varied widely across sites (from 29% to 84%), we additionally calculated Pielou's evenness index within replicates and averaged across years (Pielou 1966). Pielou's evenness index was tightly negatively correlated with dominant species relative abundance (r = -0.97, df = 7, p < 0.001), reflecting the fact that an increase in evenness decreases the influence that a dominant species has on the overall community.

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

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

Results

Across sites MAP and the CV of annual precipitation were not correlated (r = -0.15, df = 26, p = 0.44); nor were precipitation variables correlated within the focal sites (r = -0.38, df = 7, p = 0.31). There was no direct relationship between community stability and either MAP ($F_{2,25}$ = 0.1.4, p = 0.16, R^2 = 0.03; Fig. 1a) or the CV of annual precipitation (p = 0.57; Fig. 1b) Within the productivity dataset community stability was positively related with mean ANPP ($F_{1,35}$ = 31.2, β = 0.007, $p < 0.001$, R^2 = 0.46), indicating that in general increasing mean biomass had a greater effect on community stability than decreasing the standard deviation of biomass.

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

All three biotic mechanisms were significantly related to community stability in the structural equation model, whereas neither MAP nor the CV of annual rainfall directly related to community stability (Fig. 3). However, both precipitation variables related to community stability indirectly via their relationships with biotic stability mechanisms. Species richness showed a significant positive relationship with MAP, whereas negative species covariance increased with the CV of annual precipitation (Fig. 3, bivariate relationships in Fig. 1a-e, Fig. 2a-f).

Discussion

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

The first pathway by which precipitation affected community stability was via species richness, where sites with high MAP supported high numbers of species, and high species richness was related to increased community stability over time. We interpret this relationship as evidence of the portfolio effect increasing in importance in sites that receive high amounts of MAP (e.g., in the tallgrass prairie site in Kansas; Table A1). While species richness does not necessarily need to lead to a portfolio effect, all sites used in the analysis had Taylor power law z values over one, indicating that species diversity was stabilizing (species abundance variance increased more than species mean abundance). Thus, z values > 1.0 combined with the positive influence of species richness on community stability are consistent with expectations of the portfolio effect (Doak et al. 1998, Tilman 1999).

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

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

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

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

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Supplemental material

Appendix

Descriptive summaries of the datasets included in our analyses, including source information and representative times series of species abundances over time.

Figure Legends

Fig. 1. Community stability in relation to precipitation and biotic mechanisms. **(a,b)** Community stability in relation to **(a)** mean annual precipitation (mm) (MAP) and **(b)** the CV of annual precipitation across 28 grasslands sites. Focal sites with available community composition data are labeled (community stability is calculated on aggregated species abundances). Community stability for the remaining sites is calculated on annual net primary productivity; data from Hsu et al. in revision. **(c-e)** Community stability in relation to three biotic stability mechanisms. Lines indicate significant relationships in a multiple regression model relating these metrics with community stability, all biotic mechanisms were significantly related with stability in a structural equation model: **(c)** Species richness (species/m^2), which is positively associated with the portfolio effect; **(d)** the variance ratio, which describes species covariance. A variance ratio less than one indicates predominantly negative covariance, reflective of compensatory dynamics; **(e)** the stability (μ/σ) of the most-abundant (dominant) species.

Fig. 2 Biotic stability mechanisms in relation to precipitation across nine grassland sites; lines indicate significant bivariate relationships. **(a,b)** Species richness in relation to **(a)** mean annual precipitation (mm) (MAP) and **(b)** the CV of annual precipitation; **(c,d)** The variance ratio in relation to **(c)** MAP and **(d)** the CV of annual precipitation. Small gray dots with error bars indicate the mean and 95% confidence intervals of a null model (simulated variance ratios with independently varying species); **(e,f)** The stability (μ/σ) of the most abundant (dominant) species in relation to **(e)** MAP and **(f)** the CV of annual precipitation.

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

Fig. 1.

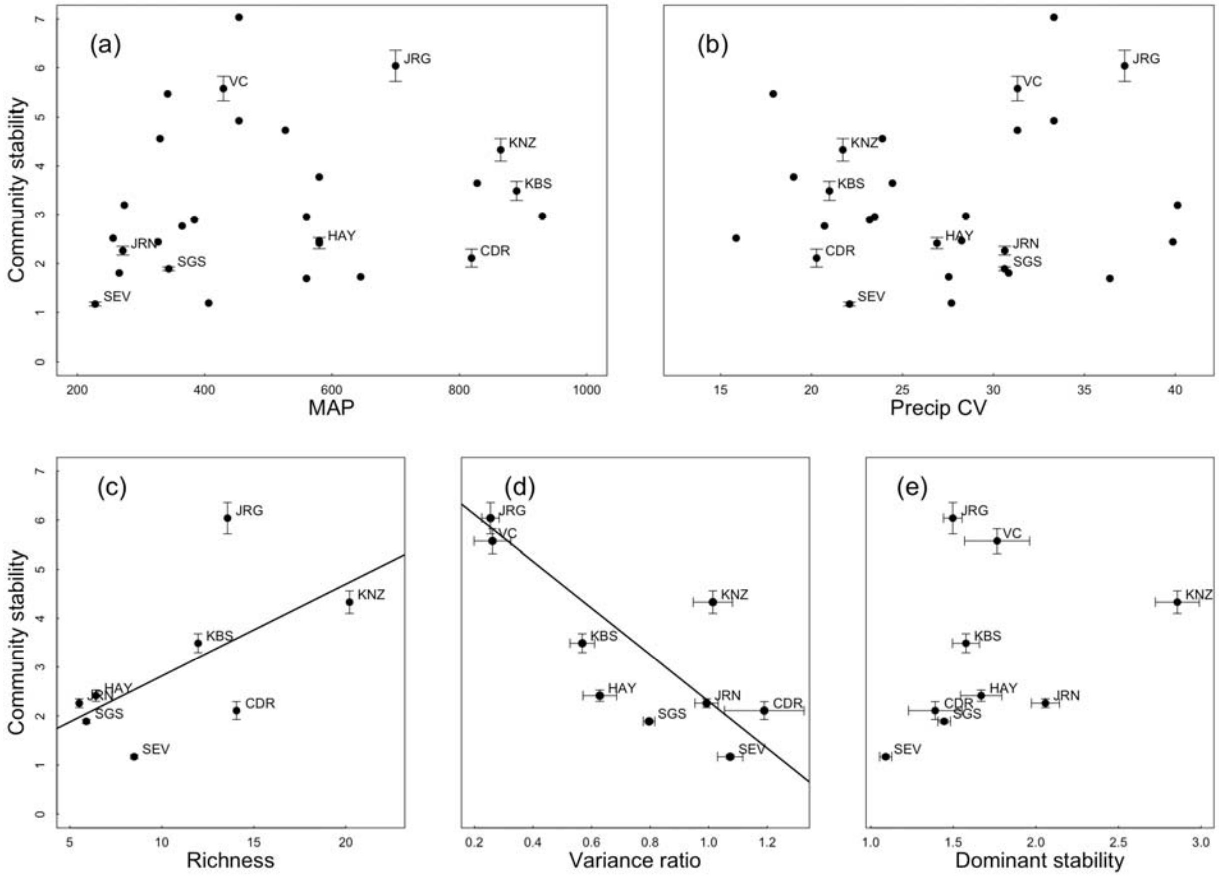

(a)
(b)
(c)
(d)
(e)
Community stability
MAP
Precip CV
Richness
Variance ratio
Dominant stability
JRG
VC
KNZ
KBS
HAY
CDR
JRN
SGS
SEV
0
1
2
3
4
5
6
7
200
400
600
800
1000
15
20
25
30
35
40
5
10
15
20
0.2
0.4
0.6
0.8
1.0
1.2
1.0
1.5
2.0
2.5
3.0

Fig. 2.

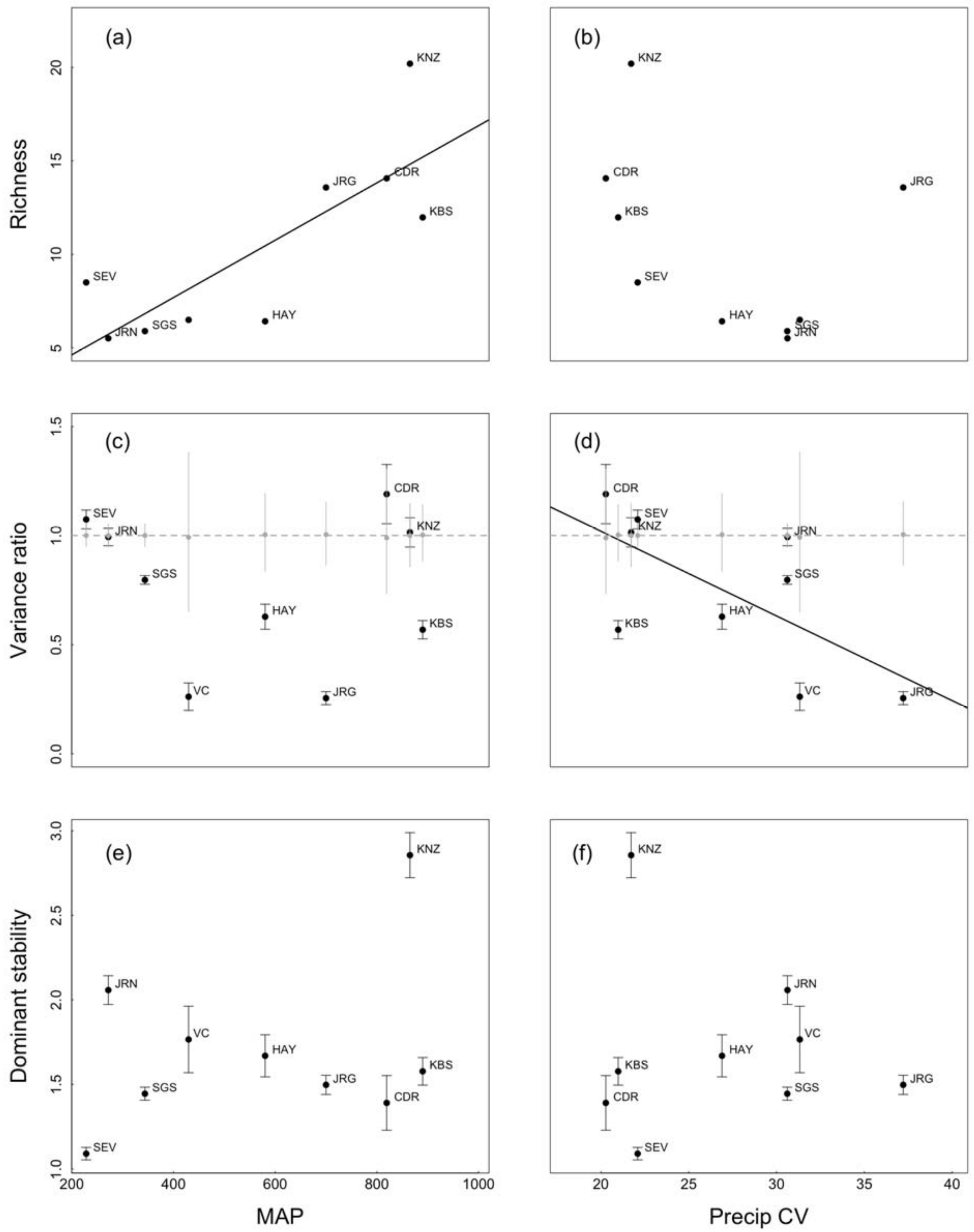
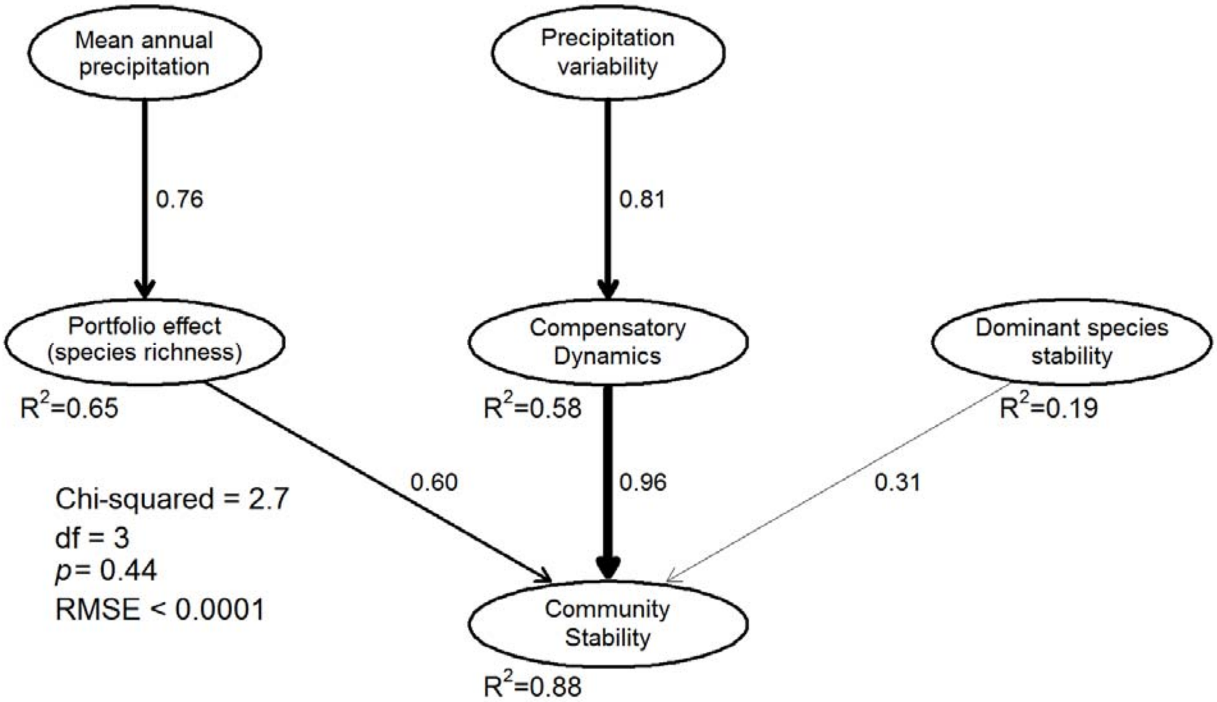

(a)
(b)
(c)
(d)
(e)
(f)
Richness
Variance ratio
Dominant stability
MAP
Precip CV
KNZ
CDR
JRG
KBS
SEV
HAY
SGS
JRN
VC
5
10
15
20
0.0
0.5
1.0
1.5
1.0
1.5
2.0
2.5
3.0
200
400
600
800
1000
20
25
30
35
40

Fig. 3.


Mean annual precipitation
Precipitation variability
0.76
0.81
Portfolio effect (species richness)
Compensatory Dynamics
Dominant species stability
R2=0.65
R2=0.58
R2=0.19
0.60
0.96
0.31
Chi-squared = 2.7
df = 3
p= 0.44
RMSE < 0.0001
Community Stability
R2=0.88