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Causes and Consequences of Grass versus Forb Years in California Rangelands

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by

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Abstract

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Global circulation models consistently forecast an increase in the frequency of extreme events such as severe storms and droughts. These changes will alter species interactions and ecosystem functions shaped by precipitation, such as productivity. Ecosystem management will need to anticipate, and where possible, mitigate the effects of increased climate variability in order to maintain ecosystem services and biodiversity. This is a pressing issue for California rangelands, which host a high percentage of California's endemic plants and support a large ranching industry that depends on reliable forage production. My dissertation uses observational and experimental approaches to understand the implications of increased precipitation variability for the stability of forage production (i.e. aboveground productivity) and the persistence of rare species in California rangelands.

Chapter 1 explores how species interactions affect the stability of aboveground productivity and whether these patterns change along precipitation gradients. I compiled and analyzed nine long-term datasets of plant species composition and aboveground productivity from grassland sites across the United States. I found that productivity in mesic grasslands was stabilized by species richness, whereas productivity in climatically variable grasslands was stabilized by species asynchrony over time. The latter pattern was exemplified by California rangelands, which experienced the most variable precipitation as well as exhibited the most species asynchrony.

Chapters 2 and 3 experimentally test the relationship between precipitation variability and species asynchrony in California rangelands and its implications for the stability of cover and aboveground productivity over time. In Chapter 2, I used rainout shelters and irrigation to experimentally create dry and wet conditions, which I replicated across areas with both low and moderate grazing histories. In moderately grazed areas, my rainfall treatments generated a classic pattern of "grass years" in wet conditions and "forb years" in dry. This pattern helped to stabilize cover across rainfall treatments and is a likely reason for the relationship

between precipitation variability and species asynchrony that I observed in Chapter 1. In low grazed areas, however, my treatments essentially generated “grass years” in wet conditions and “no-grass years” in dry; forb cover was both low and unresponsive to rainfall in these areas. This suggests that moderate grazing may be an important management tool to maintain the functional responsiveness of California rangelands to precipitation variability.

Chapter 3 tests whether competitive and functional differences between grasses and forbs affect the degree to which asynchrony stabilizes total biomass production. Within wet and dry plots I manipulated species interactions to create monocultures of *Avena barbata* (the most abundant grass), *Erodium botrys* (the most abundant forb) and a mixture of *Avena* and *Erodium*. I found that *Avena* exerted a stronger competitive effect on *Erodium* under wet conditions relative to dry, which should help stabilize community productivity. However, this effect was overwhelmed by highly unequal production capacity between the two species; *Erodium* productivity was much lower than *Avena* and, consequently, tradeoffs between the species did not increase the stability of the mixture relative to either monoculture.

Chapter 4 further investigates tradeoffs between grass and forb years, but in the context of species population dynamics in a ecosystem of conservation concern. Serpentine grassland patches in California host a unique, predominately native flora that is threatened by non-native grass invasion. I focused on a serpentine site that over the past 32 years has exhibited high fluctuations in native forb abundances, and has experienced a series of invasions and subsequent recessions by a non-native annual grass, *Bromus hordeaceus*. Effective native species conservation and invasive species management require an understanding of what drives such variation in species abundances. I applied a population model to the six most-abundant species at the site – four native annual forbs, a native annual grass and *Bromus* – to test factors affecting their population size and stability. I found that species could have large population sizes (measured as mean abundance over time) for different reasons – three species had high intrinsic growth rates, whereas the other three, including *Bromus* and the native grass, had minimal self-limitation. Population stability was highly affected by these differences: species with both low intrinsic growth rates and minimal self-limitation had less stable populations and were more sensitive to rainfall. These findings suggest a framework to describe population stability and to identify which species are likely to be sensitive to environmental change.

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Chapter 1

Biotic mechanisms of community stability shift along a precipitation gradient

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 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, I 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.

I 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 my hypotheses I capitalized on a regional gradient in precipitation and long-term plant community data at nine grassland sites in North America (Appendix 1). I quantified species dynamics in relation to three biotic mechanisms that could contribute to stability of ANPP (portfolio effect, compensatory dynamics, dominant selection effect). I 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

I analyzed community stability in nine grassland sites using long-term (≥ 9 years) datasets of plant species composition that were either contributed by colleagues or publicly available (Appendices 1 and 2). All analyses were conducted in R version 3.0.1 (R Core Team 2013). I restricted my 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. I 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. I 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, $p < 0.0001$) I considered community stability (aggregated species abundance) a proxy for productivity stability.

Direct relationships between precipitation and community stability

I obtained long-term precipitation records for each site from the closest available weather station to calculate MAP and the CV of annual precipitation. I 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 my dataset were cover based, for these analyses I coupled my dataset with measures of stability calculated using ANPP from 19 other sites in a productivity dataset (data from Hsu and Adler 2014).

Relationships between precipitation and biotic mechanisms of community stability

I 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).

I 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 I 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). I verified that increasing species richness should enhance the portfolio effect at my 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 my sites (Appendix 3), I retained species richness as a measure of the portfolio effect in subsequent analyses.

I 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 I used a temporal modification of the torus-translation (Harms et al. 2001) in which I 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. I repeated this randomization 10000 times to create a null distribution of variance ratios calculated from independently-varying populations and compared my observed variance ratio against this null distribution.

To quantify the role of dominant species for community stability I first identified the species in each replicate that had the highest mean relative abundance over time. I 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%), I 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 I used multiple regression with species richness, the variance ratio, dominant species stability and Pielou's evenness index as explanatory variables. Prior to regression I used Pearson correlation to check for collinearity among variables. Because species richness and evenness were significantly correlated ($r = 0.72$, df = 6, $p = 0.04$), I 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 I 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 I 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 ($F_{2,25} = 0.1.4$, $p = 0.16$, $R^2 = 0.03$; Figure 1a) or the CV of annual precipitation ($p = 0.57$; Figure 1b) Within the productivity dataset community stability was positively related with mean ANPP ($F_{1,35} = 31.2$, $\beta = 0.007$, $p < 0.001$, $R^2 = 0.46$), 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 ($F_{3,4} = 15.8$, $R^2 = 0.86$; Figure 1c-e). Community stability increased with mean species richness ($\beta = 0.17 \pm 0.047$, $p = 0.018$; Figure 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, $\beta = -3.55 \pm 0.70$, $p = 0.007$; Figure 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 ($F_{1,6} = 9.9$, $\beta = 0.015 \pm 0.005$, $p = 0.02$, $R^2 = 0.56$; Figure 2a) but unrelated with the CV of annual precipitation (Figure 2b). The variance ratio was not related with MAP (Figure 2c) but was significantly negatively related with the CV of annual precipitation ($F_{1,7} = 5.6$, $\beta = -0.038 \pm 0.016$, $p = 0.05$, $R^2 = 0.37$; Figure 2d). Dominant stability was not directly related with either MAP or the CV of annual rainfall (Figure 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 (Figure 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 (Figure 3, bivariate relationships in Figure 1a-e, Figure 2a-f).

Discussion

Across spatial gradients precipitation is a primary control on grassland composition and production, yet I 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, my 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. I 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; Appendix 1). 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). My findings suggest that compensatory dynamics may occur in natural systems – over half the sites I 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 I 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. My 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, my analyses suggest that compensatory dynamics will become more important to the stability of sites that experience increased precipitation variability. However, I 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 I analyzed here, may be disconnected from community responses to more rapid precipitation change.

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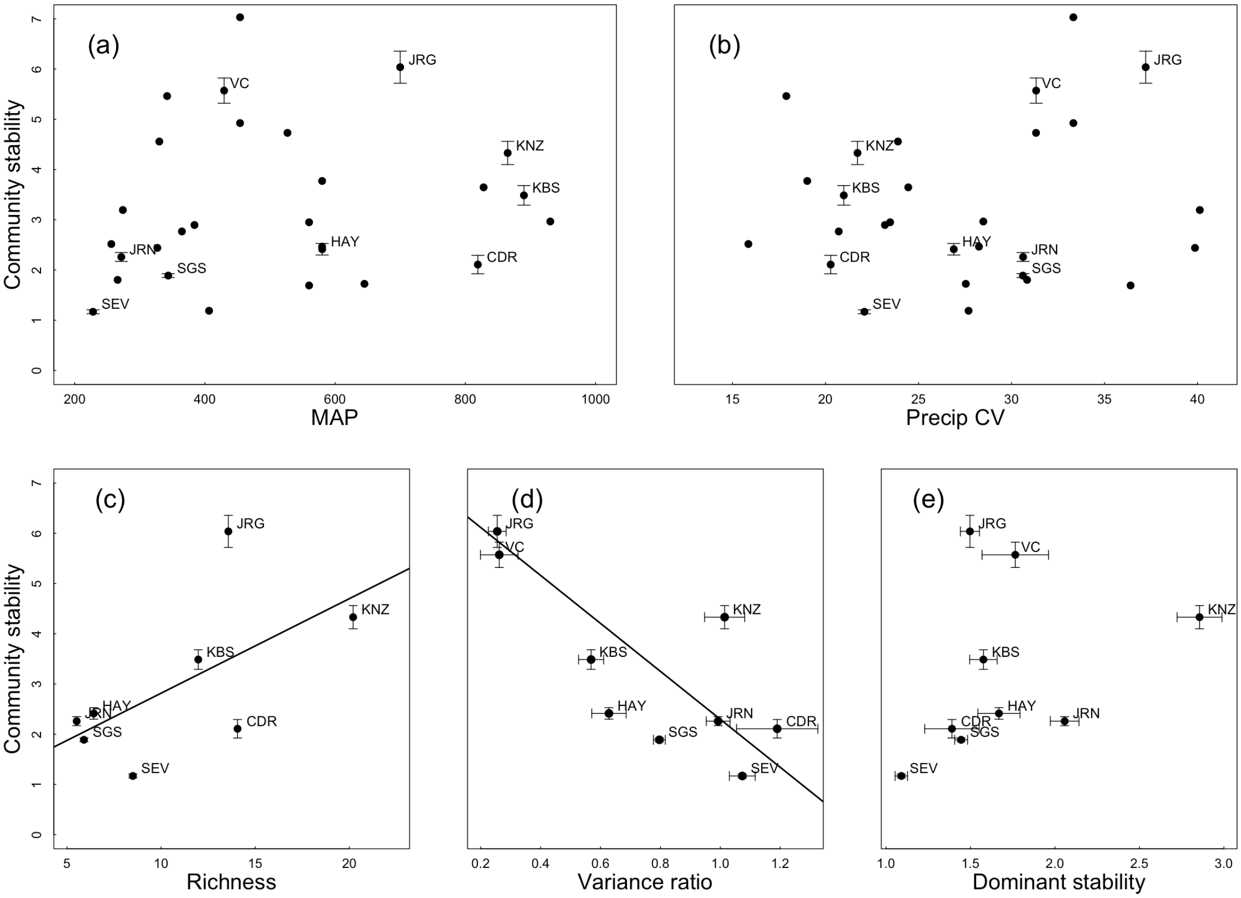

Figure 1. Community stability in relation to precipitation and biotic mechanisms. (a,b) Community stability in relation to (a) mean annual precipitation (mm) (MAP) and (b) the CV of annual precipitation across 28 grasslands sites. Focal sites with available community composition data are labeled (community stability is calculated on aggregated species abundances). Community stability for the remaining sites is calculated on annual net primary productivity; data from Hsu and Adler (2014). (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.

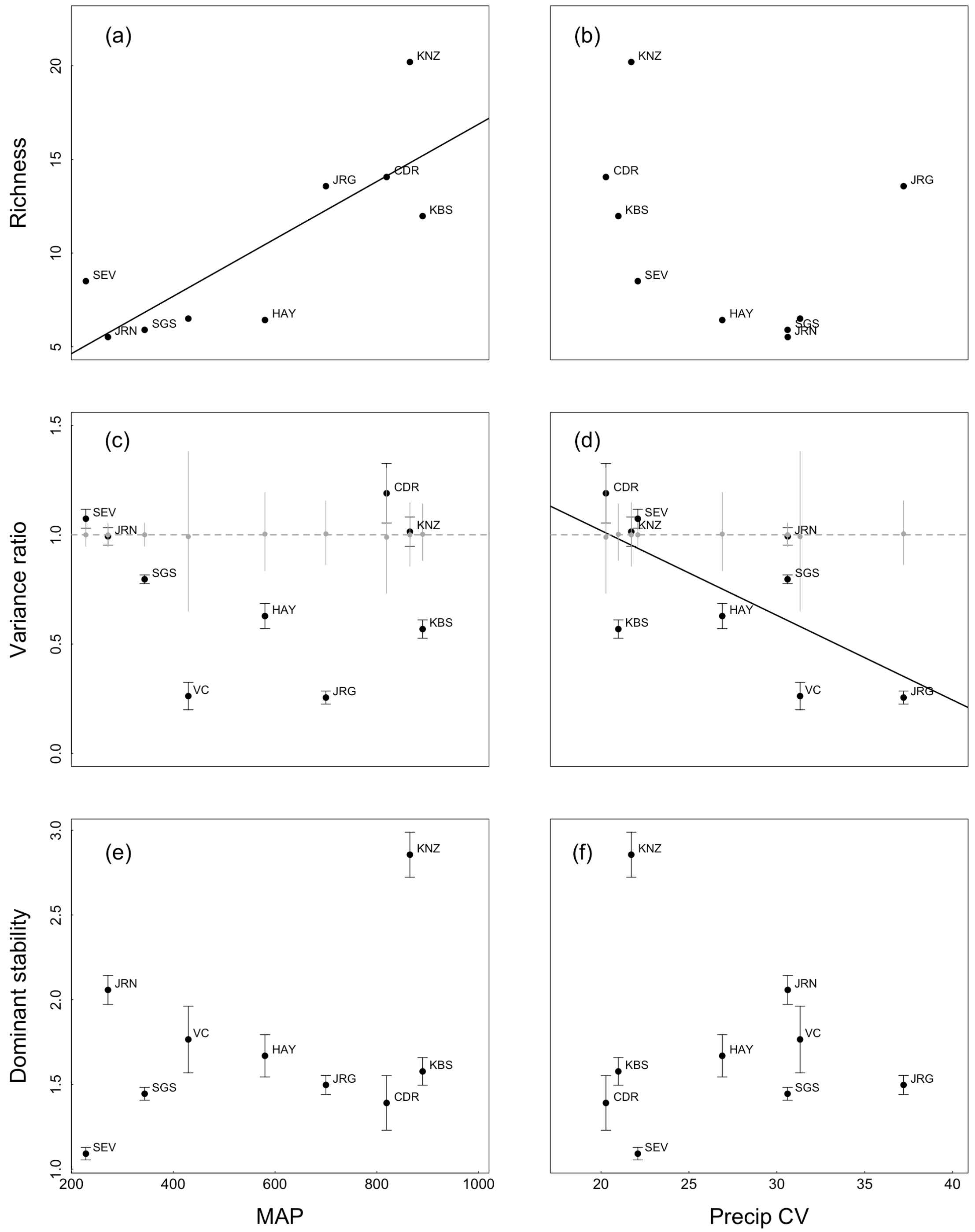

Figure 2. Biotic stability mechanisms in relation to precipitation across nine grassland sites; lines indicate significant bivariate relationships. (a,b) Species richness in relation to (a) mean annual precipitation (mm) (MAP) and (b) the CV of annual precipitation; (c,d) The variance ratio in relation 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.

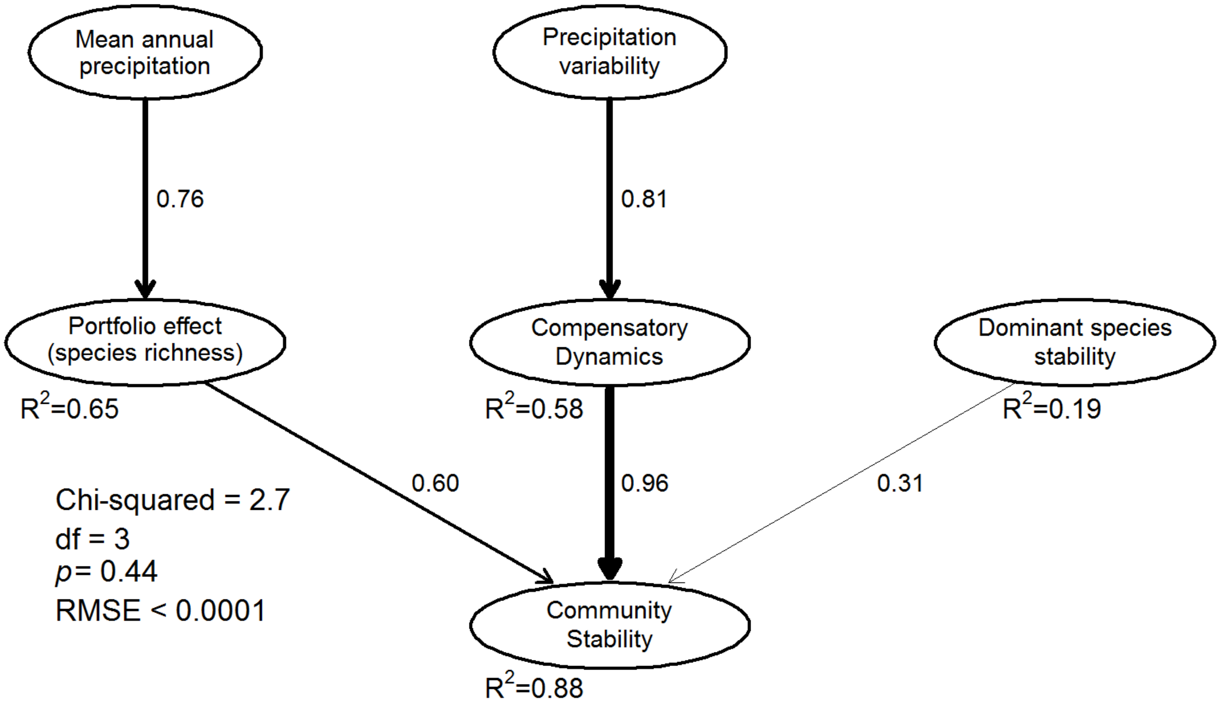

Figure 3. Structural equation model developed to relate precipitation, biotic stability mechanisms and community stability across nine grassland sites. Lines denote significant relationships and are scaled in relation to their effect size. R^2 values represent the proportion of variance explained for 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.

Chapter 2

"Grass" vs. "no-grass" years: An experimental test of functional group responses to rainfall and grazing in California

Introduction

Rangeland systems, particularly those in arid and semiarid regions such as California, are highly responsive to short-term environmental fluctuations, especially in water availability. Consequently, these systems are often dubbed "non-equilibrium" because climate variability can overwhelm the effect of grazing and other biotic interactions on community composition (George et al. 1992, Jackson and Bartolome 2002). Many rangeland ecologists account for these complex dynamics by using state and transition models as opposed to successional models of community composition. State and transition models split rangeland ecosystems into discrete states and describe processes that drive transitions between states (Westoby et al. 1989, Jackson and Bartolome 2002, Briske et al. 2003). Importantly, a given state may support a dynamic set of cover types that appear over time, often in relation to climate (Jackson and Bartolome 2002, Spiegal et al. 2014). Consequently, a key question for management is to differentiate factors that cause fluctuations in cover type within a state from factors that drive transitions between states (Spiegal et al. 2014).

A common set of cover classifications divides California rangelands into "grass", "filaree" (*Erodium* sp.) and "clover" (*Trifolium* sp.) years. Shifts between cover types are associated with rainfall: grass years are associated with consistently high rainfall, *Erodium* years occur under low rainfall, and *Trifolium* years occur when early-season drought is followed by high rainfall (Talbot et al. 1939, Pitt and Heady 1978). This pattern has been established through a series of long-term observational studies as well as through range manager experience (Talbot et al. 1939, Pitt and Heady 1978). However, the generality of the pattern has been challenged (Duncan and Woodmansee 1975), largely on the basis that observed correlations between species responses and climate may be confounded by site-level effects and grazing practices. For example, high residual dry matter (RDM) from the previous year (due either to high production or low grazing intensity) can also favor grasses over forbs (Heady 1956, Bartolome et al. 1980, 2007). Further, the accumulated effect of RDM or of successive years with similar weather conditions may change seed bank composition. This could drive a transition between states if a depleted seed bank no longer supports the same set of cover types.

Experiments can help differentiate the effect of different drivers on cover type. I present an experimental manipulation of rainfall availability and grazing legacy (quantified as RDM) in a California rangeland to better understand variation in grass, *Erodium* and *Trifolium* cover. I have two goals: 1) To verify observationally-established relationships between rainfall and cover response; 2) To test whether grazing histories impact a system's functional responsiveness, for example, by altering RDM and seed bank composition in ways that reduce the potential set of cover types it supports.

Methods

Site description

I conducted the experiment in a valley grassland at the University of California Sierra Foothills Research Extension Center, Browns Valley, California, USA (39º 15' N, 121º 17' W). The site is characterized by a Mediterranean climate with cool, wet winters and hot, dry summers. Average annual rainfall is 730 mm, most of which falls during the growing season from October through April. The site was previously grazed by cattle, but it was fenced to enable controlled grazing manipulations during the study.

Grazing

In May 2008, a grazing gradient was established using a combination of trampling by cattle and mechanical mowing. The full grazing gradient included six levels, ranging from non-grazed to highly grazed (described by Stein et al. 2014); here I focus on two grazing levels. The "low" level was trampled twice per year, once in late March when plants started flowering and a second time in June/July after most plants were senesced. The "moderate" level was both mowed and trampled in March and June/July. Both grazing levels were replicated in four 10 m x 3 m blocks. Grazing treatments were maintained through September 2012.

The grazing gradient was characterized using residual dry matter (RDM), which is the plant material that remains just before the start of a new growing season and is a standard measure of grazing intensity in rangeland management (Bartolome et al. 2007). RDM was harvested in early October each year by clipping a 0.25 m × 0.25 m subplot within each block, drying the biomass (60°C for 72 h) and weighing it. To avoid re-harvesting the same area, the subplot position was shifted each year. I verified that the grazing treatments were reflected in RDM using ANOVA with RDM as the response variable, grazing level as a fixed effect and year and block as error terms.

To test the legacy effect of the grazing gradient on seed bank composition I collected five quantitative soil cores (5 cm depth, 5.08 cm diameter) in each grazing block for a total of 40 cores. I collected these cores in September 2012, shortly prior to the first germinating rains; thus, they reflect seeds available for the growing season following 4 years of experimental grazing. I spread each soil core over Sunshine Mix 1 in a half-flat and grew its contents in the greenhouse for 3 months (February-April 2014). I took a census of emerging seedlings weekly over that time and counted the total number of individuals that emerged for each species. I focused on three genera, *Avena* (the most abundant grass), *Erodium* (filaree) and *Trifolium* (clover). I analyzed the effect of grazing on the seed bank of each genus using three separate ANOVA with grazing treatment as a fixed effect and block as an error term.

Rainfall

In October 2012, I implemented a rainfall manipulation using rainout shelters and irrigation to create dry and wet conditions over the course of the growing season. Each grazing block included two shelters for a total of 16 paired dry and wet plots (i.e., 8 dry/wet pairs per grazing level). The rainout shelters were constructed with removable, solid, clear polyethylene roofs that fit over a 1.3 m × 2.6 m area. After the first germinating rains of the season, I erected the roofs shortly before rainfall events and removed them afterward; the roofs were only erect for approximately 10 percent of the growing season.

Shelter runoff was collected and used to irrigate the wet treatments. I maintained rainfall treatments over the course of two growing seasons (October 2012-May 2014). Due to extreme drought in the 2013-2014 growing season, I periodically irrigated the wet plots using (non-chlorinated) well water. Because I could not maintain the grazing treatments with the shelters in place, I instead hand-mowed the plots to comparable RDM levels. I monitored the effect on soil moisture using two 15-cm deep time domain reflectometer (TDR) probes in each plot and a 5-cm deep continuous data-loggers in half of the plots (Decagon Devices, Pullman, WA).

I measured species cover in a 0.5 m × 0.5 m subplot within each dry and wet plot in mid-April each year. I did not force cover estimates to equal 100 percent – total species cover could be greater than 100 owing to canopy overlap or less than 100 owing to bare ground. To test the combined effect of grazing legacies and rainfall conditions on species composition I summed cover estimates within genus (*Avena, Erodium,* and *Trifolium*) and conducted three separate ANOVA assessing the cover of each genus in response to grazing legacy, rainfall and a grazing × rainfall interaction, with year and block as error terms.

Results

Grazing and residual dry matter

Manipulations that simulated grazing resulted in significant differences in RDM ($F_{1,19}$ = 14.5, P = 0.0012), with on average 1426±414 g/m^2 in the low grazing and 511±152 g/m^2 in the moderate grazing treatment.

Seed bank

Overall *Avena* comprised a much higher percentage of the seed bank than *Erodium* or *Trifolium* (Figure 1). Grazing legacy only significantly affected the seed bank of *Avena* ($F_{1,37}$ = 5.4, P = 0.026) with fewer *Avena* seeds in the moderately grazed than low grazed areas. The seed bank of both *Erodium* ($F_{1,37}$ = 0.034, P = 0.86) and *Trifolium* ($F_{1,37}$ = 2.5, P = 0.12) did not differ between grazing treatments (Figure 1).

Rainfall and soil moisture

Both years experienced below-average rainfall, with 510 mm falling in the 2013 growing season and 398 mm in the 2014 growing season (Figure 2). The rainfall treatments resulted in significant differences in soil moisture throughout the growing season ($F_{1,152}$ = 185.6, P < 0.0001), with on average 28.1 ±0.75 percent soil moisture in the wet plots over the growing season compared to 21.3 ±0.81 in the dry (Figure 2).

Cover

Avena cover was significantly higher in the wet than dry plots ($F_{1,173}$ = 307.6, P < 0.0001), and the strength of this effect did not vary with grazing level (Figure 3). There was also a slight but significant main effect in which *Avena* cover was greater in the low than moderately grazed areas ($F_{1,173}$ = 8.34, P = 0.0043). In contrast, *Erodium* cover was significantly greater in the dry than wet plots ($F_{1,173}$ = 115.5, P < 0.0001) and in the moderately grazed areas ($F_{1,173}$ = 188.5, P < 0.0001; Figure 3). *Erodium* cover was disproportionately greater in the dry, moderately grazed plots (rain × grazing interaction, $F_{1,173}$ = 54.9, P < 0.0001). Like *Erodium*, *Trifolium* cover was greater in the moderately grazed areas ($F_{1,173}$ = 100.6, P < 0.0001). Unlike *Erodium*, however, *Trifolium* cover was greater in wet than dry plots ($F_{1,173}$ = 25.8, $P < 0.0001$), and there was an interaction effect in which *Trifolium* cover was disproportionally greater in the wet, moderately grazed plots ($F_{1,173}$ = 54.9, P = 0.0012; Figure 3).

Discussion

My experiment found that rainfall effectively drove shifts between "grass" and "no-grass" cover types; whether forbs were responsive to "no-grass" conditions depended on grazing legacy. Cover of the dominant grass *Avena* was higher under wet than dry conditions regardless of grazing history. Following moderate grazing, *Erodium* and *Trifolium* were highly responsive to rainfall treatment. Under moderately-grazed conditions, *Trifolium* (clover) cover was higher under wet than dry conditions, whereas *Erodium* (filaree) cover was greater under dry. In areas with a legacy of low grazing, however, *Erodium* and *Trifolium* cover was low regardless of rainfall treatment. These effects persisted across years, suggesting that grazing may drive a state-transition between grasslands with frequent and infrequent forb cover. This finding provides context for why observational research has often, but not always, observed rainfall-driven shifts between grass, *Erodium* and *Trifolium* years in California rangelands.

Grazing legacies may have affected the responsiveness of *Erodium* and *Trifolium* to rainfall in two ways. First, increased RDM following low grazing can directly suppress germination rates of forbs such as *Erodium* (Rice 1985, Stamp 1989). This may explain the minimal cover of forbs in the low grazing treatment, and also the comparable seed bank of forbs across the grazing treatments – low cover (and correspondingly low seed production) may be balanced by low germination under high RDM levels, whereas higher cover (and presumably higher seed production) may be countered by greater seed bank depletion under low RDM levels. Second, although grazing did not significantly affect the forb seed bank, increased grazing did decrease the *Avena* seed bank. Although this did not affect *Avena* cover responses – while smaller, the *Avena* seed supply was still substantial under moderate grazing – it may have altered competition dynamics between grasses and forbs, allowing for greater forb cover following periods of moderate grazing.

I found that moderate and low grazing histories had lasting effects on cover type fluctuations. It is likely that these differences were due to accumulating effects of grazing over time. For example, I found that forb cover was higher in areas with lower RDM. In contrast, an early seminal study by Heady (1956) found that some forbs, and in particular *Erodium*, were not highly affected by differences in RDM. This discrepancy may be because, in my experiment, shifts in RDM were the result of several years of grazing practices. This generated a seed bank that was overwhelmingly dominated by *Avena* in areas with high RDM. Thus, it may be changes in the seed bank more than RDM *per se* that led to an increase of *Erodium* in areas characterized by low RDM in my study. Another explanation may be that an *Erodium* response to RDM depended on rainfall; *Erodium* exhibited an interactive effect in which cover was greatest under low RDM conditions that were also dry. Both early (Talbot et al. 1939, Heady 1956, Pitt and Heady 1978) and recent (Vaughn and Young 2010) papers have highlighted the importance of replicate observations and experiments over multiple years to capture these dynamics. I suggest that factorial experiments, particularly ones that manipulate rainfall, may be an additional important tool to understand and model states and transitions in arid and semiarid rangeland systems.

Implications

Experimental studies can improve our understanding of non-equilibrium dynamics by parsing the effects of environmental and management drivers. My experiment corroborated observational studies that rainfall drives transitions between grass, *Erodium* and *Trifolium* cover types. It further highlighted that grazing legacy can affect the functional capacity of the system to respond to rainfall: forbs were unable to respond to a decline in rainfall under a low-grazed state (i.e., high RDM levels), whereas they were highly responsive to rainfall in a moderately-grazed state (i.e., lower RDM levels). Maintaining high cover is important in erosion control, especially in drought-prone systems such as California grasslands (Busby and Cox 1994, Allen-Diaz and Jackson 2000). Consequently, managing for intermediate levels of RDM may enable forbs to replace grasses under low-rainfall conditions and maintain greater total cover even in low-rainfall years.

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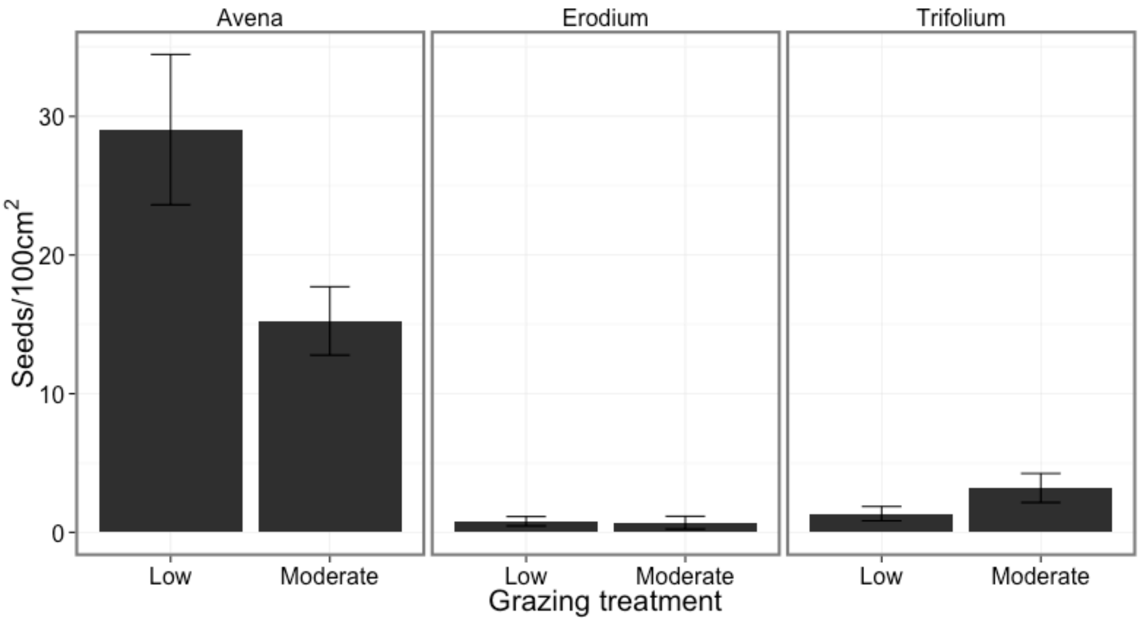

Figure 1. Effect of four years of experimental grazing on the seed bank of *Avena*, *Erodium*, and *Trifolium* species.

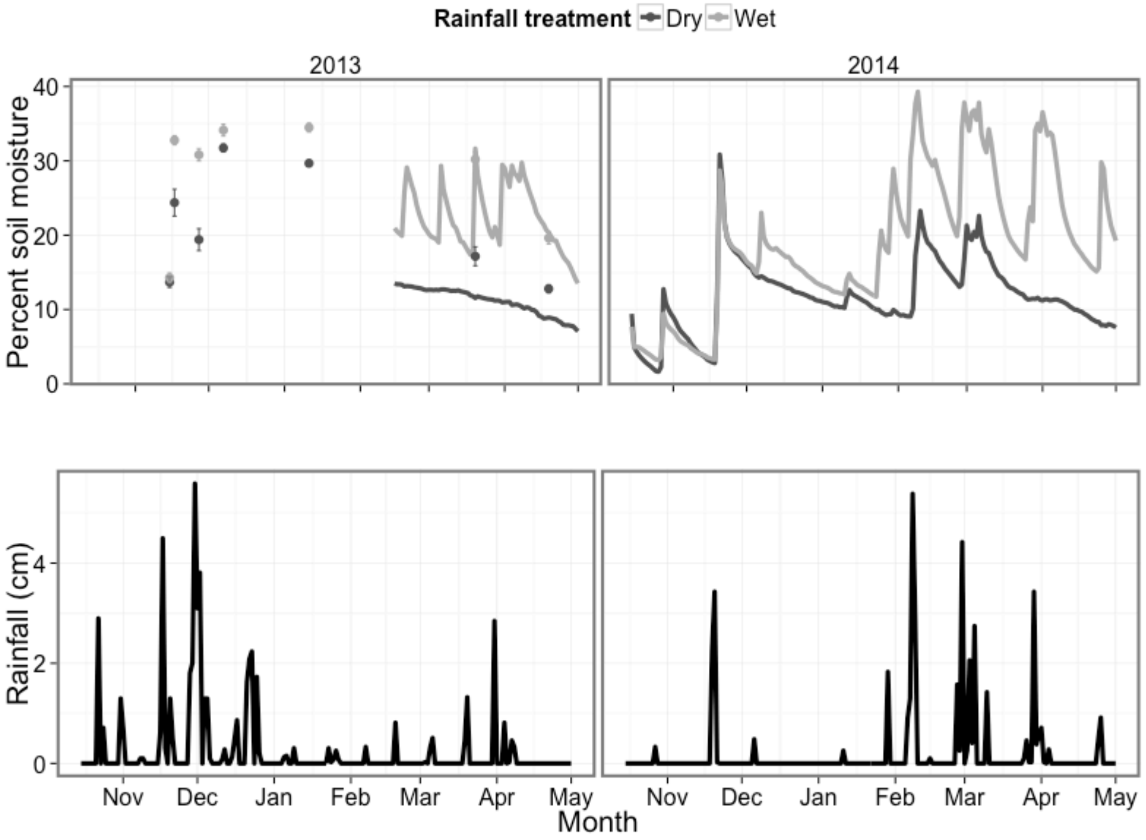

Figure 2. Percent soil moisture by experimental treatment and actual rainfall in the 2013 and 2014 growing season at the Sierra Foothills Research and Extension Center. Continuous soil moisture measurements were collected with Decagon Em50 soil moisture probes; point measurements were collected with a handheld TDR.

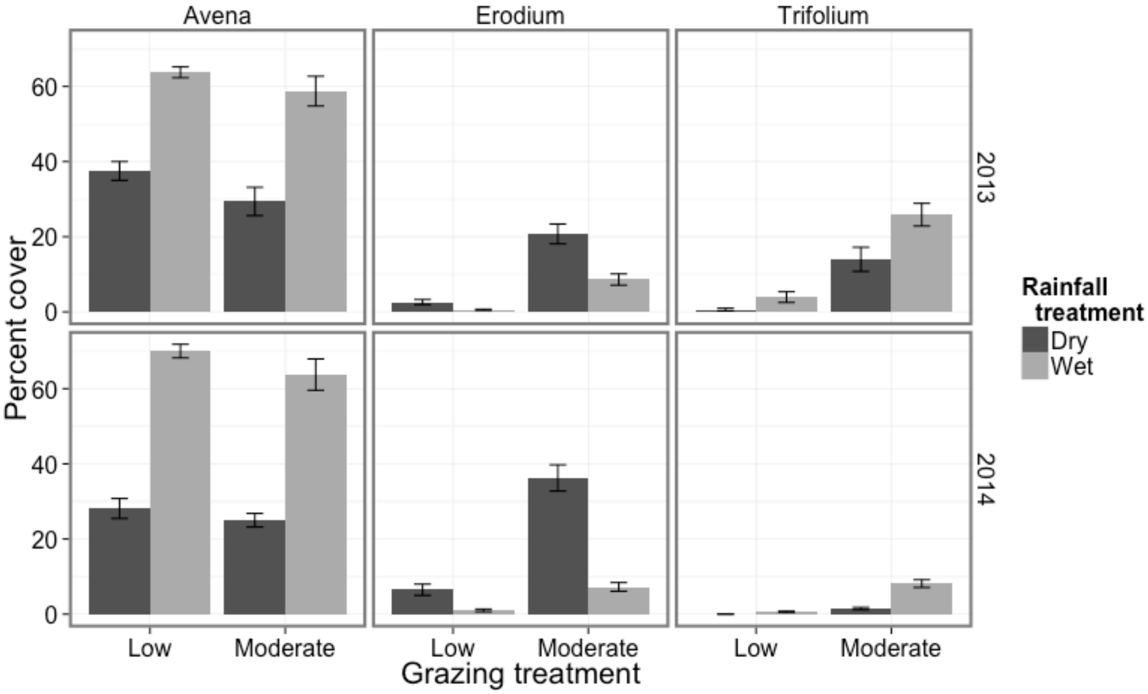

Figure 3. Cover responses of *Avena*, *Erodium*, and *Trifolium* to experimental grazing legacies and rainfall treatments over two years.

Chapter 3

Compensatory dynamics in variable precipitation environments: do real communities match theoretical predictions?

Introduction

Precipitation variability characterizes many ecosystems worldwide, and global circulation models consistently forecast increases in the frequency of extreme events such as severe storms and droughts (IPCC 2013). In arid and semiarid systems, increased precipitation variability is expected to lead to increased variability in primary production (Huxman et al. 2004). In 1972, MacArthur introduced the idea of compensatory dynamics, which has been evoked to argue that tradeoffs among species could reduce this destabilizing effect: production may be more stable than expected in a variable environment if some species do well in dry years while others do better in wetter years (MacArthur et al. 1972, Yachi and Loreau 1999, Gonzalez and Loreau 2009). Although intuitively appealing, compensatory dynamics have been the subject of great theoretical debate (Gonzalez and Loreau 2009, Loreau and de Mazancourt 2013).

Theory tackling this question – if and when species tradeoffs (asynchrony) stabilize community properties over time – has focused largely on whether the cause of species asynchrony determines its stabilizing effect (Ives et al. 1999, de Mazancourt et al. 2013, Loreau and de Mazancourt 2013). For instance, consider an asynchrony in which one species does better in wet conditions and another in dry. This asynchrony may be driven solely by the environment – occurring regardless of whether the species interact with one another – or it could be driven by one species responding to the environment and the other responding to changed competitive interactions with the first species (Gonzalez and Loreau 2009). Theoretical work on this front generally concludes that only the first scenario – tradeoffs caused by different responses to the environment – would stabilize functions of the entire system, for instance, net primary production (Ives et al. 1999, de Mazancourt et al. 2013, Loreau and de Mazancourt 2013).

Empirical tests have lagged behind theoretical work (Ives 2007, Gonzalez and Loreau 2009). Phenomenological studies have linked diversity to increased stability, particularly across variable precipitation conditions (McNaughton 1977, Tilman and Downing 1994, Tilman et al. 1996, Bai et al. 2004, Polley et al. 2013). Empirical investigations of compensatory dynamics as a mechanism for this relationship, however, have primarily focused on whether species asynchrony exists (Houlahan et al. 2007, Mutshinda et al. 2009, de Mazancourt et al. 2013, Hallett et al. 2014, Gross et al. 2014). Few studies have tested the conditions under which species asynchrony may be stabilizing (Gonzalez and Loreau 2009, but see Descamps-Julien and Gonzalez 2005).

A key stumbling block in integrating theory and experimental work may be that the patterns of species asynchrony considered by theory do not parallel commonly observed species tradeoffs in nature. Variability in resource-supply rates, as exemplified by precipitation variability, often drive a tradeoff between species with resource acquisitive and resource conservation traits (Grime 1998, Angert et al. 2009, Pérez-Ramos et al. 2013). Species with resource acquisitive traits capitalize on high-resource conditions, exerting a strong competitive effect on other species during these periods. However, traits that allow resource acquisition often come at the cost of the ability to conserve resources at times of low resource availability. When the environment has limited resources, species that use resources efficiently and reduce resource loss are favored (Grime 1998, McGill et al. 2006, Angert et al. 2009).

Current models of compensatory dynamics have not captured two important aspects of asynchrony arising from acquisitive-conservative resource tradeoffs. First, the focus on asynchrony caused by directionally different responses to the environment excludes most species asynchrony generated by variable resource availability. In these environments, species would be expected to share environmental responses in the absence of competitive interactions (e.g., all species would show a positive response to wetter conditions) (Loreau and de Mazancourt 2008). Species tradeoffs instead occur because acquisitive species capture a disproportionate share in wet conditions and conservative species experience a release from interspecific competition in dry, unfavorable, conditions (Levins 1979, Chesson 2000, McGill et al. 2006). This suggests that stability models should consider the implications of both differential species environmental responses and differential interspecific competitive effects in relation to environmental variability.

A second essential aspect for species asynchrony to stabilize community properties is that the species in their "good" times are functionally equivalent (e.g., in the case of production, species produce comparable biomass)(Yachi and Loreau 1999). In the general case of a tradeoff between resource acquisition and conservatism, slower-growing resource conservative species invariably have a lower production capacity (i.e., produce less biomass per unit time) than resource acquisitive species (Lavorel and Garnier 2002, Roscher et al. 2011). However, most modeling efforts assume that species capacity to produce biomass is random (Ives et al. 1999) or constant (Loreau and de Mazancourt 2008) among species.

Here, I tackle these challenges by integrating theory and experimental work to better understand the role of compensatory dynamics in natural systems. I focus on the degree to which acquisitive-conservative species tradeoffs can buffer production responses to precipitation variability. I first develop a model that varies both species asynchrony and species production capacity to explore their joint influence on community stability. Second, I examine a classic pattern in California rangelands of "grass years" in wet conditions and "forb years" in dry conditions using an experimental approach in which I manipulated rainfall and competitive interactions for a resource acquisitive grass and resource conservative forb. I separate the mechanisms that determine asynchrony and production capacity – namely, interspecific competition and differential environmental responses – to understand if and when this common pattern of species asynchrony generates compensatory dynamics.

Methods

Modeling the effect of functional tradeoffs on community stability

I developed a simple model for a two-species annual plant community that contains one resource acquisitive (RA) and one conservative (C) species and experiences two precipitation conditions, low resource (dry) and high resource (wet). I characterized stability as the coefficient of variation (CV; σ/μ) of aggregate species biomass across precipitation conditions – the lower the CV, the higher the stability (Tilman 1999).

The *RA* species produces maximum biomass under wet conditions ($P_{RA,wet}$), produces minimum biomass under dry conditions ($P_{RA,dry}$), and is unaffected by the *C* species. The degree of difference in the *RA* species' production between precipitation conditions reflects the difference in resource availability: altering it should affect absolute CV but not the relative effect of the *C* species on CV.

Biomass production of the *C* species varies in relation to the *RA* species along two axes: 1) Production capacity (Figure 1, y axis). Production capacity of the *C* species varies as a proportion (ranging from 0 to 1) such that:

$$Prop = \frac{\left(P_{C,dry} + P_{C,wet}\right)}{\left(P_{RA,dry} + P_{RA,wet}\right)}$$

2) Asynchrony in response to precipitation conditions (Figure 1, x axis). Asynchrony between the *C* and *RA* species varies from perfectly synchronous to perfectly asynchronous (0 to 1) such that:

$$Asynch = \frac{P_{C,dry}}{Prop * P_{RA,wet}}$$

For my model two-species community with standardized biomass, this is equivalent to:

$$Asynch = \frac{2 - VR}{2}$$

where *VR* is the variance ratio, a common metric used to characterize the degree of species asynchrony in time series data (Schluter 1984, Houlahan et al. 2007). The variance ratio compares the variance of the community (*C*) as a whole relative to the sum of the individual population (P_i) variances:

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

where:

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

My model assumes that both species share the same rate of response to the environment – a reasonable assumption for annual communities and an important one to note because different rates of response may also affect stability. For example, a lagged response in a "slow" species may compensate for a quick, environmentally-driven decline in a "fast" species (Loreau and de Mazancourt 2013).

I recognize that variation along both axes of my model could be due either to differential interspecific competitive effects or environmental responses between the two species. Indeed, these variables may be hard to separate if the species traits that affect community properties are linked to traits that structure interspecific competition and species tradeoffs (Lavorel and Garnier 2002, Suding et al. 2008). My intent for the model was to illustrate how stability changes with each parameter; in the subsequent field experiment I isolated each mechanism in an example system.

Field-testing the effect of functional tradeoffs on community stability

System and site

Contemporary California grasslands are comprised predominantly by exotic annual species, which germinate with the fall rains but grow primarily during the spring. Four-fold variation in total precipitation among years is correlated with major shifts in species composition, with high grass cover in wet years and high forb cover in dry years (Murphy 1970, Duncan and Woodmansee 1975, Pitt and Heady 1978, Young et al. 1981). I conducted the experiment for two years (September 2012 to May 2014) in a valley grassland system at the Sierra Foothills Research Extension Center, Browns Valley, California, USA (39º 15' N, 121º 17' W). The site experiences a Mediterranean climate with hot, dry summers and cool, wet winters. Annual precipitation at the site averages 730 mm/year and occurs primarily as rainfall between October and May. I focused on the most abundant annual resource-acquisitive grass and conservative forb, *Avena fatua* and *Erodium botrys*, respectively, which together compose the majority of the plant cover at the site (Chapter 2, Stein et al. 2014).

Rainfall manipulations

I paired dry and wet plots for a total of eight blocks. The rainout shelters were constructed with removable, solid, clear polyethylene roofs that fit over a 1.3 m × 2.6 m area. After the first germinating rains of the season, I erected the roofs shortly before rainfall events and removed them afterward; the roofs were only in place for approximately 10 percent of the growing season. I maintained this treatment over the course of the growing season (October-May). Shelter runoff was collected and used to irrigate the wet treatments. Due to extreme drought in the 2013-2014 growing season I periodically irrigated the wet plots using (non-chlorinated) well water. I monitored the effect on soil moisture using two 15-cm deep time domain reflectometer probes in all of the plots, and, starting in February 2013, 5-cm deep continuously-logged Em50 sensors in six of the plots (Decagon Devices, Pullman, WA).

Species treatments

I nested subplots of four composition treatments (*Avena* monoculture, *Erodium* monoculture*, Avena* and *Erodium* mixture and un-manipulated control) in a random-block design within the rainfall manipulation main plots for a total of 64 subplots. Each manipulated subplot was 0.25 m × 0.25 m and the un-manipulated control was 0.5 m × 0.5 m and was blocked separately. I maintained treatments through species removal throughout the fall and early winter (October-February).

I visually measured species percent cover in the 0.5 m × 0.5 m control subplots in April each year. To characterize species and total productivity I destructively harvested aboveground biomass in the manipulated subplots, sorted it to species, dried it for 48 h at 60^{o} C and weighed it. To account for differences in *Erodium* and *Avena* phenology I conducted this harvest twice each year, harvesting a randomly-selected half of each subplot in early April and the remaining half in early May. In all analyses I used the peak biomass produced by each species (i.e., the April harvest for *Erodium*, the May harvest for *Avena*).

Statistical analyses

Verifying field experiment matched model assumptions

I conducted three analyses to verify that field responses matched model assumptions. First, to confirm that rainfall manipulations generated two distinct environmental conditions, I used repeated measures ANOVA with soil moisture as the response variable, treatment as a fixed factor, time as a repeated measure and block as a random effect. Second, to confirm that rainfall drove shifts between grasses and forbs, I analyzed species cover in the un-manipulated control subplots using ANOVA, with rainfall treatment (dry, wet), species (*Avena, Erodium*) and their interaction and year as fixed factors and block as a random effect. Third, to confirm that grass-forb shifts matched the expected pattern of functional tradeoffs, I analyzed biomass production in the manipulated subplots using ANOVA, with rainfall treatment (dry, wet), species (*Avena, Erodium*), competition (monoculture, mixed) and year as main effects, species × treatment and species × competition as interaction terms, and block as a random effect. I paired this analysis with four planned comparisons to isolate the strength of the competition response of each species within rainfall treatments – four ANOVA comparing biomass production by competition (monoculture, mixture) and year within species and rainfall treatment, corrected with a Bonferroni adjustment.

Functional tradeoffs and community stability

To test if grass-forb tradeoffs increased stability I first analyzed the CV of biomass production across paired wet and dry plots and years using ANOVA with species treatment (*Erodium*, *Avena* or mixed) as fixed factors and block as a random factor.

Second, to characterize which model axes determined the stabilizing effect of grass-forb tradeoffs I calculated: 1) The production capacity of *Erodium* relative to *Avena* in mixture across treatments (dry, wet) within each block. 2) The asynchrony between *Erodium* in mixture and *Avena* in mixture across treatments within each block, calculated using the variance ratio.

Finally, to determine how differential environmental responses versus interspecific competition affected stability and model axes, I assumed that in an idealized community without interspecific competition, each species would produce its monoculture biomass. I summed monoculture biomass within each treatment and block and calculated CV across years and paired wet and dry plots. I compared the CV of the mixture biomass (i.e., actual competitive environment) and summed monoculture biomass (i.e., idealized, competition-free environment) using ANOVA with competition (yes or no) as an explanatory variable and block as a random effect. I used a similar ANOVA with mean and standard deviation as response variables to determine if these communities differed in the components that affect CV. Second, I recalculated each axis of my model using the summed monoculture biomass. I compared each model axis (*Prop*, *Asynch*) using ANOVA with competition (yes or no) as the explanatory variable and block a random effect. All analyses were conducted in R version 3.0.1 (R Core Team 2013), with ANOVA models tested using aov in the stats library.

Results

Model results

My model highlighted the joint importance of species production capacity and species asynchrony for a stabilizing effect of diversity on community productivity. Low proportional production capacity resulted in low stability regardless of the degree of asynchrony between species (as illustrated by the comparable community CVs in Figure 1 for all panels in which *Prop* = 0.1). An increase in proportional production capacity increased stability even when populations were highly synchronous, reflecting the fact that stability is enhanced by increasing the mean of community productivity as well as reducing its standard deviation (as illustrated by decreasing CV with increasing *Prop* but equal *Asynch* values, Figure 1). The CV of community productivity decreased most rapidly when species asynchrony and production capacity increased in tandem, because when species were asynchronous, equal production capacity both increased the mean and reduced the standard deviation of community productivity (Figure 1).

Experiment results

Field patterns matched model conditions

Both years experienced below-average rainfall, with 510 mm falling in the 2013 growing season and 398 mm in the 2014 growing season. The rainfall treatments resulted in significant differences in soil moisture throughout the growing season ($F_{1,108}$ = 1119, $P <$ 0.0001), with on average 28.9 ±0.48 percent soil moisture in the wet plots over the growing season compared to 22.5 ±1.2 in the dry (Figure 2). Mirroring observational studies, my rainfall treatments successfully created “grass” versus “forb” conditions in the control subplots (Figure 2). I found a significant species × rainfall interaction in which *Avena* cover was greater in the wet than dry and *Erodium* cover was greater in the dry than wet treatment ($F_{1,45}$ = 58.3, $P < 0.0001$, Figure 2). There was also a main effect in which *Avena* had greater cover overall ($F_{1,45}$ = 52.8, $P < 0.0001$).

Patterns of biomass production paralleled expectations of a tradeoff between resource acquisitive and conservative growth strategies (Figure 3). Across competitive environments biomass was consistently greater in the wet than dry plots ($F_{1,7}$ = 44, P=0.0003), but the strength of this response differed by species, with *Avena* biomass highly and *Erodium* biomass slightly greater in the wet treatment ($F_{1,92}$ = 22.8, P <0.0001; Figure 3). Species also differed in their overall biomass production, with *Avena* producing more than *Erodium* ($F_{1,92}$ = 82.9, $P < 0.0001$). Competition consistently reduced biomass production ($F_{1,15}$ = 6.7, P = 0.01). This effect was largely due to a strong negative response of *Erodium* to competition under wet conditions ($F_{1,14}$ = 24.6, P = 0.0006, Figure 3); biomass did not significantly differ by competitive environment for the other three planned comparisons.

Functional tradeoffs did not increase community stability

The CV of biomass production across treatments did not vary between mixed and monoculture subplots ($F_{2,14}$ = 1.3, P = 0.30). Although species in mixture were significantly asynchronous (*Asynch* = 0.59 ±0.07), *Erodium* production did not match that of *Avena*, with *Erodium* producing on average 0.35 ±0.06 that produced by *Avena.* Interspecific competition altered model axes but not overall stability. There was not a significant difference in the CV of the competitive environment and the idealized, competition-free environment (values of 0.52 ±0.09 and 0.49 ±0.06, respectively) (Figure 4). However, similar CV values were reached in different ways: the idealized, competition-free environment had a significantly larger mean ($F_{1,7}$ = 44.3, P = 0.0003) while the competitive environment trended toward a lower standard deviation ($F_{1,7}$ = 3.55, P = 0.10). This was because interspecific competition further decreased species proportional production capacity ($F_{1,7}$ = 5.22, P = 0.056) but increased species asynchrony ($F_{1,7}$ = 6.6, P = 0.037). In the absence of competition *Erodium* production increased to 0.49 ±0.07 that of *Avena* but the two species became synchronous (*Asynch* = 0.41 ±0.06).

Discussion

Whether and why species asynchrony increases the stability of community properties such as productivity has been the subject of great debate. This question has become particularly relevant for predicting the effect of increased precipitation variability on the stability of ecological communities. Here, I explore whether mismatches between theoretical models and realistic scenarios of species tradeoffs have encumbered our understanding of compensatory dynamics in natural systems. To bridge this gap I examined a well-documented pattern of species asynchrony – acquisitive-conservative tradeoffs in relation to variable precipitation – to explore the mechanisms that regulate compensatory species responses in nature.

In contrast to theoretical models, my field experiment highlights that species asynchrony driven by competition can be stabilizing if there is greater interspecific competition under high resource conditions. However, the stabilizing effect of species asynchrony was highly constrained by unequal production capacity between conservative and acquisitive growth patterns, resulting in no significant differences between the stability of the mixed and monoculture communities. The importance of unequal production capacity has been largely ignored by theoretical literature, but my findings suggest it may be an overwhelming factor that controls whether species asynchrony stabilizes community properties in nature. Because shifts in competition and functional traits are essential features of resource-driven tradeoffs, I expect my findings are highly general. My results also suggest a framework with which to predict stronger or weaker compensatory dynamics in nature.

Species asynchrony and interspecific competition

Understanding what controls community stability in the face of environmental resource variability has long motivated interest in the diversity-stability relationship (Hooper et al. 2005). Much of this research has centered on grassland responses to precipitation variability (McNaughton 1977, Tilman and Downing 1994, Tilman et al. 1996, Bai et al. 2004, Polley et al. 2013). Precipitation is a primary control on both production (Knapp and Smith 2001, Huxman et al. 2004) and diversity (Adler and Levine 2007, Cleland et al. 2013) in grasslands, and across grassland sites species asynchrony is correlated with greater precipitation variability (Hallett et al. 2014). Within sites this relationship is often the result of acquisitive-conservation tradeoffs in response to precipitation (Pitt and Heady 1978, Angert et al. 2009). Because species asynchrony driven by precipitation variability is a common scenario in grassland systems, I expect that my assumptions and findings are relevant for interpreting other grassland biodiversity-stability studies and important for understanding related ecosystem services (e.g., forage production).

While I focused on resource variability, there are plausible scenarios in which species asynchrony in response to precipitation is non-resource based. In grasslands, this scenario may occur when early-season precipitation variability differentially affects species' germination rates (as opposed to affecting resource competition; Bartolome 1979, Levine et al. 2008). Non-resource environmental variability is assumed in most theoretical models (Ives et al. 1999, Loreau and de Mazancourt 2013) and experimental tests of compensatory dynamics, which often vary pH or temperature (Klug et al. 2000, Descamps-Julien and Gonzalez 2005). Critically, the directional effect of interspecific competition on community stability hinges on whether or not the primary environmental driver is a limiting resource. My findings suggest that when resources vary, greater interspecific competition under high resource conditions should increase stability. In contrast, in the absence of resource variability, shifting degrees of interspecific competition over time should decrease stability (Hughes and Roughgarden 1998).

The context-dependent effect of interspecific competition on community stability – specifically, that its stabilizing effect depends on the whether competition co-varies with resource availability – poses a challenge for observational studies of compensatory dynamics. Should observational studies assume that asynchrony is driven by resource variation, or should they assume asynchrony is driven by other factors? Different answers to this question may lead to different analytical choices and observational findings. For example, two studies analyzed the same grassland biodiversity experiments under different assumptions, and reached different conclusions about the stabilizing role of species asynchrony (de Mazancourt et al. 2013, Gross et al. 2014). De Mazancourt et al. (2013) modeled species asynchrony based solely on species' performances in monoculture – an approach in line with the assumption that species are responding to non-resource environmental variability, and that interspecific competition is therefore destabilizing. Indeed, de Mazancourt et al. (2013) found that species were largely synchronous, and that diversity stabilized community productivity solely by increasing the temporal mean of community biomass. In contrast, Gross et al. (2014) measured species asynchrony based on species' performances in mixtures, and found that species asynchrony owing to interspecific competition reduced the variability of community biomass production.

All of the datasets analyzed by de Mazancourt et al. (2013) and Gross et al. (2014) experimentally varied species interactions but not environmental conditions. As such, it is difficult to determine the degree to which they were affected by resource variability, and therefore to weigh which modeling approach is more appropriate. Experimental studies such as ours can help resolve this problem by varying both species interactions and environmental conditions. The conclusion of de Mazancourt et al. (2013) – that diversity increased stability by elevating mean biomass – mirrored the effect of diversity in my idealized, competition-free scenario. In contrast, the conclusion of Gross et al. (2014) – that diversity increased stability via asynchrony that reduced the standard deviation in biomass – was in line with my actual two-species scenario that experienced interspecific competition.

Species production capacity

I found that, in addition to a direct effect on production, precipitation variability further curtailed the stabilizing effect of species asynchrony because it differentially favored a conservative species with limited production capacity under low resource conditions.

Acquisitive-conservative tradeoffs characterize many species interactions, and therefore I expect this is a common constraint for compensatory dynamics driven by variable environmental resources.

Under what conditions would compensatory dynamics driven by variable resource availability not be subject to this constraint? Although the focus of the diversity-stability debate has centered on stabilizing community productivity, a growing ecosystem service literature has emphasized other community properties and ecosystem functions (Lavorel and Grigulis 2012). The stabilizing effect of resource-driven functional tradeoffs may be much greater for community properties other than biomass production. Specifically, greater stability should occur if the functional traits that structure species tradeoffs are not tied to those that structure their ecosystem effects. For example, I observed high overall vegetation cover as well as pronounced asynchrony in species cover across treatments. Consistently high cover is important in erosion control, especially in drought-prone systems such as California grasslands (Busby and Cox 1994, Allen-Diaz and Jackson 2000). Similarly, conservative species have high below-ground investment, and asynchrony between acquisitive and conservative species could stabilize belowground processes (Butterfield and Suding 2013).

Conclusion

Linking models with field experiments is critical to determine whether the assumptions that guide theory are realistic for natural systems. This is a pressing issue for understanding whether biotic mechanisms, such as compensatory dynamics, will help to buffer communities to the effects of climate change. I modeled the phenomenological consequences of differing degrees of species asynchrony and production capacity in response to precipitation variability. This exercise highlighted the often-overlooked role of species production capacity for community stability. I then recreated the model in the field by growing a resource acquisitive and conservative species under different precipitation and competitive environments. Field results underscored the importance of including species production capacity in theoretical models; low production of the conservative species across precipitation conditions meant that it could not compensate for variation in the production of the acquisitive species between conditions. Further, my field test highlighted that interspecific competition – commonly assumed to be destabilizing in theoretical models - can be stabilizing if competition is stronger in high-resource conditions. Placing production capacity and interspecific competition in an environmental context provides a framework to guide further studies testing the extent and effect of compensatory dynamics.

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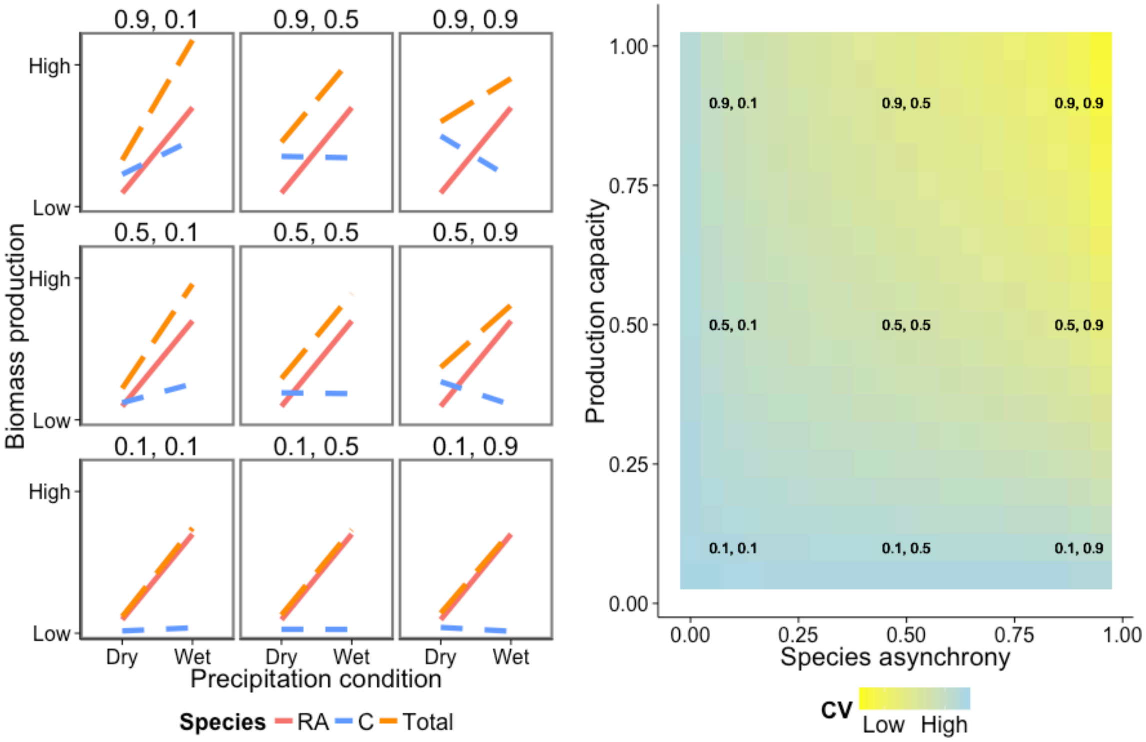

Figure 1. a) Model scenarios for a two species annual plant community that contains one resource acquisitive (*RA*) and one conservative (*C*) species and in which the conservative species varies in its production capacity and asynchrony relative to the resource acquisitive species under dry and wet conditions b) the corresponding coefficient of variation (CV) of total biomass production for each scenario.

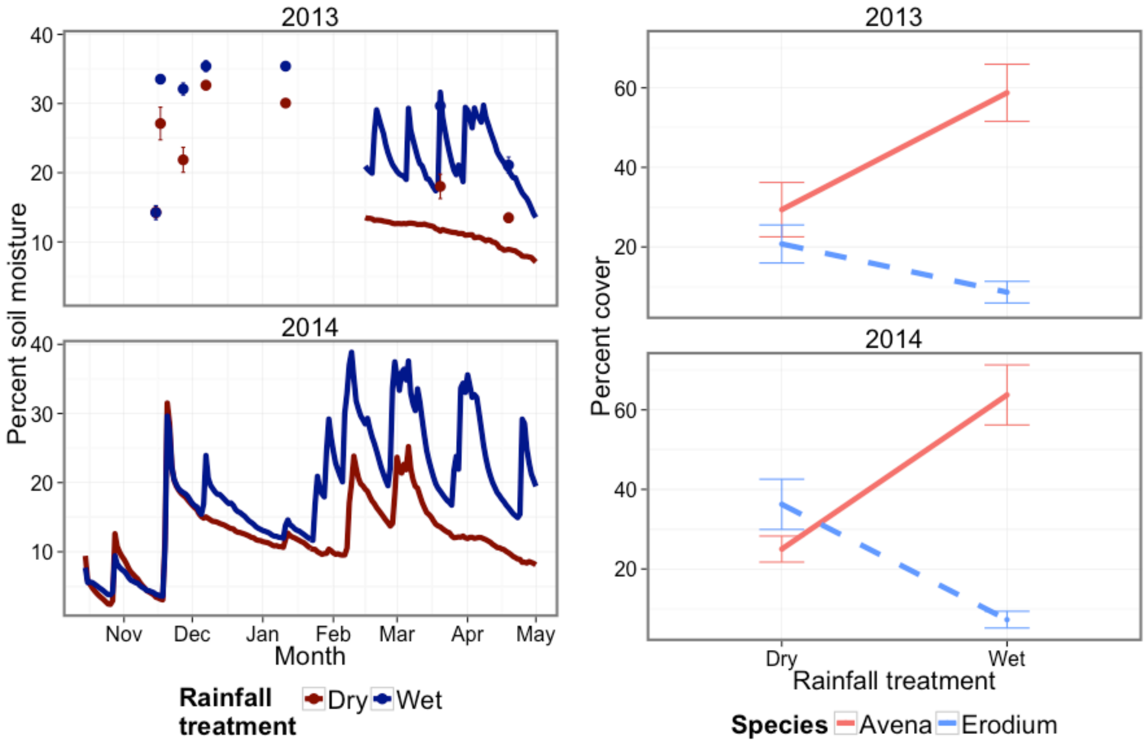

Figure 2. Percent soil moisture over time in the dry versus wet treatments by year, and the corresponding species cover response to rainfall treatments by year.

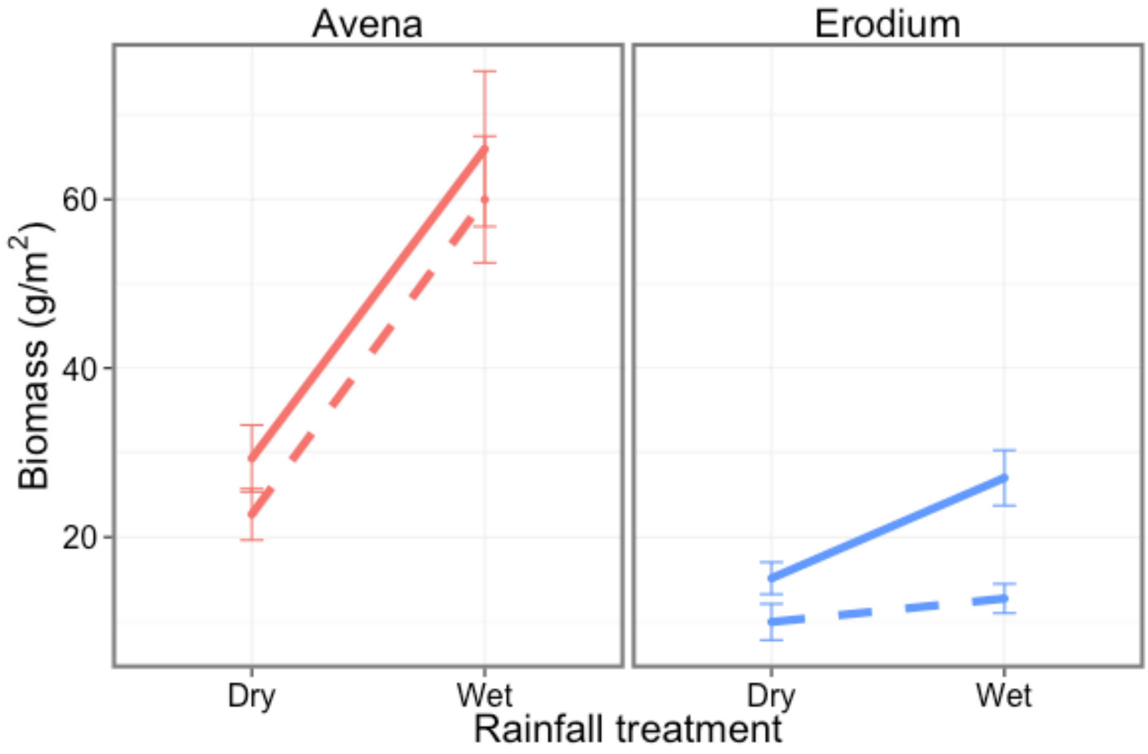

Figure 3. Biomass production by species and competitive environment averaged across years. Straight line = monoculture (without competition), dashed line = mixture (with competition).

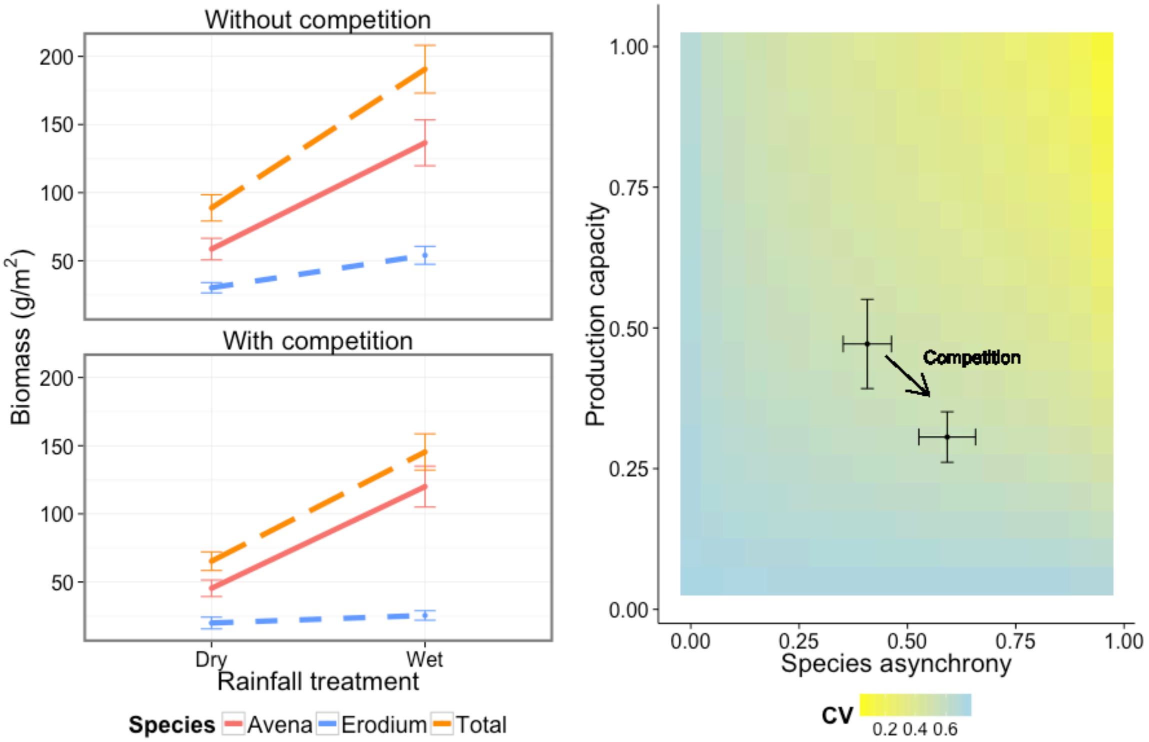

Figure 4. Biomass produced in monoculture (without competition) and mixture (with competition) by species and treatment and associated coefficient of variation (CV) for total biomass across treatments.

Chapter 4

Asymmetries in intrinsic growth rate and density dependence explain patterns of species population size versus stability

Introduction

Understanding why some species are common and others rare is a central question in ecology (Preston 1948, Whittaker 1965, Silvertown and Dale 1991) and essential to developing strategies for species conservation (Schemske et al. 1994, Espeland and Emam 2011). Long-term datasets increasingly highlight that, within a given spatial scale, species can be described as common versus rare in two different ways: 1) Mean population size and 2) Population stability over time (Magurran 2007, McGill et al. 2007). Importantly, these two classifications can vary independently; some species with high average abundances vary greatly over time, whereas many persistent species are never abundant (Thibault et al. 2004, Collins et al. 2008). Identifying the species characteristics that underscore these patterns may explain why some species are more sensitive than others to environmental variability and help predict the consequences of future environmental change.

Population size is a function of a species' intrinsic growth rate and density dependence (i.e., intraspecific and interspecific competition) (Figure 1; Chesson 2000). Species with high intrinsic growth rates are generally able to extract or use a limiting resource more efficiently than species with low intrinsic growth rates (Tilman 1982). As a result, empirical studies have observed a positive relationship between species' abundances and intrinsic growth rates (Figure 1a; Harpole and Tilman 2005, Fargione and Tilman 2006). A species' abundance is also affected by its intraspecific density dependence, or the rate at which the species' per capita growth rate declines with increasing abundance. Species that are less self-limited are also associated empirically with greater abundances (Figure 1b; Comita et al. 2010, Johnson et al. 2012). Thus, two species may be equally abundant despite highly unequal intrinsic growth rates if they also differ in the degree to which they experience density dependence (Figure 1c; Chisholm and Muller-Landau 2011).

In contrast to population size, tradeoffs between intrinsic growth rate and intraspecific density dependence may lead to large differences in population stability (Henderson and Magurran 2014). In the scenario of two species with equal population sizes described above, the species population with a higher intrinsic growth rate but stronger intraspecific density dependence will be more stable over time: it will be more likely to both recover when rare and return quickly to equilibrium population size when abundant (Figure 1d,e). High intrinsic growth rates balanced by strong density dependence have been invoked in theoretical explanations of rare but persistent species (Yenni et al. 2012). However, this mechanism has not yet been tested in natural systems (but see Henderson and Magurran 2014).

Population stability is also influenced by extrinsic drivers, such as rainfall variability, that can alter species' growth rates and carrying capacities over time (Adler et al. 2006, Angert et al. 2009). Consequently, high environmental variability generally results in less stable populations (Ives et al. 1999, Tilman 2004). A critical question, particularly in light of predicted increases in climate variability (IPCC 2013), is to what degree species characteristics moderate the destabilizing effect of environmental variability (Mueller and Huynh 1994, Brook and Bradshaw 2006). For example, theory suggests that for two species with equal population sizes but unequal intrinsic growth rates and density dependence, the species less affected by density dependence should experience larger shifts in their predicted abundance following an equal, environmentally-driven shift in intrinsic growth rate (Figure 1d,e). However, empirical tests have proven elusive, in part due to the confounding effect of age structure in perennial systems (Gurney and Nisbet 1980, Drake 2005).

Here I test the role of asymmetry in species' intrinsic growth rates and density dependence in explaining tradeoffs in species population size versus stability. I utilized a 32-year demographic dataset of annual plant populations in serpentine grassland that experienced five-fold variation in growing season rainfall over time (Figure 2). Previous research has focused mainly on the effects of rainfall variability and disturbance on plant community dynamics without explicitly considering the underlying species interactions (Hobbs and Mooney 1985, Hobbs et al. 2007). I apply a classic species population model to test the hypothesis that population size is jointly determined by species intrinsic growth rates and density dependence, while population stability is primarily determined by intrinsic growth rate. Second, I test the hypothesis that rainfall variability has a greater destabilizing effect on species with relatively low intrinsic growth rates and intraspecific density dependence.

Methods

Study system and sampling design

Data were collected from 1983-2015 at the Jasper Ridge Biological Preserve in San Mateo County, California, USA (122°12' W, 36°25' N). The study site is a serpentine outcrop that bisects the ridge (Area C). Soils at the site are characteristically shallow (<40 cm deep), with low nutrient concentrations, high Ni and Mn concentrations and a low Ca:Mg ratio. The climate is Mediterranean, with wet, mild winters and hot, dry summers. Mean growing season rainfall (September-April) over the study period was 604 mm but varied greatly across that time period, from 228 mm to 1155 mm. The site is dominated by annual plants (primarily annual forbs and a few annual grasses) that germinate in autumn and set seed in spring and summer. Previous research indicates that species at the site have minimal multi-year seed bank carryover (Hobbs and Mooney 1985).

Stem counts were censused by species each April from 1984-2015 in permanently marked 10 cm × 10 cm plots. This plot size was selected on the basis of the small stature of the annual plants and the high plant densities common at the site (several thousand plants per m^2; Hobbs and Mooney 1985). Periodic gopher disturbance is common at the site. An initial set of 30 plots was set up in 1983 to compare plant establishment on gopher mounds and in undisturbed areas (Hobbs and Mooney 1985). To ensure that post-gopher successional trajectories were stratified across years, at least 10 additional plots on fresh gopher mounds were added every year between 1987 and 1996. Fresh gopher disturbance was also recorded in the plots. This resulted in a total of 150 replicate plots whose time series ranged from 20 to 32 years.

Because my model requires that species reach high enough abundance values to calculate density dependence, I restricted subsequent analyses to species with a mean population density of ≥ 1 individual/10 cm^2. This resulted in a focal set of six species: four native annual forbs (*Calycadenia multiglandulosa, Lasthenia californica, Microseris douglasii, Plantago erecta*), one native annual grass (*Vulpia microstachys*) and one non-native annual grass (*Bromus hordeaceus*).

Analyses

I first characterized variation in species population size and stability. I described population size for each species as the temporal mean number of individuals, calculated within a plot and then averaged across plots. Second, I described population stability for each species as the temporal mean divided by standard deviation (μ/σ; Tilman 1999), calculated within a plot and then averaged across plots.

To assess the effects of intrinsic growth rate and density dependence on patterns of species abundance, I modified a simple competition model of annual plant species (Watkinson 1980, Rees and Westoby 1997, Harpole and Suding 2007, Levine and HilleRisLambers 2009, Yenni et al. 2012) such that:

$$N_{i,t+1} = \frac{(\lambda_i + \beta_i Rain_t)N_{i,t}}{1 + \alpha_{ii}N_{i,t} + \sum_1^j \alpha_{ij}N_{j,t}}$$

where N_i is the population size of species *i* and is a function of λ_i, the intrinsic rate of increase of species *i,* divided by total competition (i.e., the summed intra (α_{ii}) and interspecific (α_{ij}) competition terms). Because growing season rainfall varies widely at the site and may differentially affect species' carry capacities and growth rates, I include β_i to moderate λ_i based on total growing season rainfall (standardized around 0).

Localized gopher disturbance periodically reset populations at the site. To account for this, I restarted each time series when a plot experienced gopher disturbance. I then fit a logistic growth model for each species' population over the time series using maximum likelihood (nlsLM in the R package minepack.lm). Based on these models, I determined the number of years it took for a species' predicted abundance to reach carry capacity following disturbance. I truncated each time series to the years at which species were expected to have recovered from disturbance (for most species, post-disturbance population recovery took two years; Appendix 4).

I used these data to parameterize the population model for each species using maximum likelihood (nlsLM in the R package minepack.lm). I used the fitted parameters to test my prediction that population size is jointly determined by species' intrinsic growth rates and intraspecific density dependence, whereas population stability is related to intrinsic growth rate. To reflect the combined effect of intrinsic growth rate and intraspecific density dependence on population size I calculated each single-species equilibrium population size as $(\lambda_i - 1)/\propto_{ii}$ (i.e., I set $N_{i,t+1}$ equal to $N_{1,t}$ and $N_{j,t}$ equal to 0; Adler et al. 2007). I then regressed the species' observed population size (log-transformed) by predicted population size. I expected that these values would be positively related but that observed population size would be lower, reflecting the additional effect of interspecific competition. To test whether there were consistent tradeoffs I correlated intrinsic growth rate λ_i and intraspecific density dependence $\propto_{ii}$. Finally, I used a regression to relate observed species population stability with intrinsic growth rate λ_i. For this analysis I removed the effect of environmental variability by setting $Rain_t$= 0, reflecting an "average" rainfall year.

I assessed species sensitivity to rainfall by calculating these analyses across a range of observed rainfall values. I compared the slope of λ_i+$\beta_i Rain$ in response to rainfall between species to characterize the direct effect of rainfall on species' intrinsic growth rates. I compared the slope of the predicted population size $(\lambda_i+\beta_i Rain - 1)/\propto_{ii}$ by rainfall to characterize whether less self-limited species were more responsive to rainfall.

Results

Population size was a function of both species intrinsic growth rates λ_i and self-limitation $\propto_{ii}$; observed population size increased with predicted population size ($F_{1,4}$ = 9.45, P = 0.037, R^2 = 0.62; Figure 3). Species with high intrinsic growth rates λ_i also tended to experience greater intraspecific density dependence α_{ii} (Pearson's correlation coefficient = 0.82 $t_{1,4}$ = 2.79, P = 0.049). Observed population stability was significantly positively related with λ_i ($F_{1,4}$ = 12.92, P = 0.023, R^2 = 0.70; Figure 3).

Plantago and *Lasthenia*, two abundant and stable species, had the highest intrinsic growth rates and among the highest density dependence. *Calycadenia*, a less-abundant but stable species, had a lower intrinsic growth rate and comparable density dependence. In contrast, *Bromus* and *Microseris,* two abundant but unstable species, had low intrinsic growth rates and low density dependence. Finally, *Vulpia*, the least abundant and least stable species, had a growth rate < 1 and low density dependence (Table 1).

Rainfall had a strong, significant negative effect on the intrinsic growth rate λ_i of the two most-fit species, *Plantago* and *Lasthenia*, as well as a slight, significant negative effect on *Vulpia* (Figure 4b). The remaining three species, *Bromus*, *Calycadenia*, and *Microseris*, exhibited moderate, significant positive intrinsic growth rate λ_i responses to rainfall (Figure 4b). Although *Plantago* and *Lasthenia* had the highest absolute response to rainfall in terms of λ_i, *Bromus* and *Vulpia* had the largest magnitude of response to rainfall in terms of population size due to their minimal self-limitation (Figure 4c).

Discussion

I utilized a unique 32-year dataset of annual plant populations to test the implications of asymmetry in species intrinsic growth rates and density dependence for species population size versus stability. I found that several species had large population sizes, but for different reasons – some had high intrinsic growth rates and others minimal self-limitation. Population stability was highly affected by these differences: species with low intrinsic growth rates had less stable populations and were more sensitive to rainfall. My results suggest a framework to describe patterns of commonness and rarity, and to identify which species are likely to be sensitive to environmental change.

Across species, I observed a tradeoff in which higher intrinsic growth rates were associated with stronger intraspecific density dependence. Due to this asymmetry, the four most-abundant species obtained large populations in very different ways. Two native forbs, *Plantago* and *Lasthenia*, were abundant due to high intrinsic growth rates, but were constrained by strong intraspecific density dependence. In contrast, a native forb, *Microseris*, and a non-native grass, *Bromus*, reached high population sizes due to minimal intraspecific density dependence, despite low intrinsic growth rates. Although theory predicts that asymmetrical strategies should result in similar population sizes (Chisholm and Muller-Landau 2011), most empirical tests have failed to identify this pattern, as studies have focused on either only intrinsic growth rate (Harpole and Tilman 2005, Fargione and Tilman 2006) or only density dependent processes (Comita et al. 2010, Johnson et al. 2012, 2014).

Population stability varied widely among the four-most abundant species and increased with intrinsic growth rate. Determinants of population stability have been the subject of great debate (Tilman 1996, Ives et al. 1999, Ives and Carpenter 2007), but many studies have highlighted that that population stability is a function of species differences (Mutshinda et al. 2009, Magurran and Henderson 2012, Majeková et al. 2014, Henderson and Magurran 2014). For example, Henderson and Magurran (2012) observed two abundance patterns in fish communities: highly abundant species with strong density dependence and rare species with transient dynamics. In this community, the abundant, density-dependent species were the most stable. Because I observed abundant species with asymmetric intrinsic growth rate and density dependent terms, I can parse the relationship between population size and density dependence. In my system, stability was determined more by the asymmetry in intrinsic growth rate versus density-dependence strategy than by population size.

Environmental variability typically destabilizes populations (Ives et al. 1999), but species characteristics may moderate this relationship (Mueller and Huynh 1994). I found that the degree to which rainfall altered predicted population size was determined more by species characteristics than by the direct effect of rainfall on intrinsic growth rate. The two species with highest intrinsic growth rates both exhibited large, negative responses to rainfall in terms of growth rate. However, the greatest magnitude of response in terms of population size was experienced by species with lower intrinsic growth rates and also lower density dependence. This suggests that a combination of high intrinsic growth rate and high density dependence may have a dual stabilizing effect: species populations can recover quickly due to high intrinsic growth rates and their predicted populations are less variable due to strong density dependence.

Species with small populations are commonly assumed to be at greater risk of stochastic extinction (Schemske et al. 1994). Recent theoretical models, however, highlight that species may be rare due to strong self-limitation in conjunction with moderate or high intrinsic growth rates (Yenni et al. 2012). This tradeoff provides an explanation for species that are persistent but at low abundances. In my dataset, this phenomenon was exemplified by *Calycadenia*, which had a higher intrinsic growth rate than the more-abundant *Bromus* and *Microseris* but much stronger intraspecific density dependence. Consequently, *Calycadenia* maintained a small but stable population. Counter-intuitively, *Calycadenia* may therefore be at lower risk of stochastic extinction than species like *Microseris*, which are more abundant but have a lower intrinsic growth rates. I focused my analysis on the six most-abundant species, but an additional 20 species were observed continuously but at lower abundances across the 32 years. A similar pattern of high intrinsic growth rate and strong self-limitation may explain the continued persistence of these species in the system.

Conclusion and conservation implications

I found that two underlying species characteristics – intrinsic growth rate and density dependence – provided predictive, mechanistic explanations for patterns of species population size versus stability. Although theory predicts a dual effect of intrinsic growth rate and density dependence on species population size, my study was among the first to integrate these predictions empirically. I found that species exhibited strong trade-offs in their intrinsic growth rate and density dependence. This asymmetry led to consistent differences in population stability and provided a reason why some rare species may be more stable than some common species. My framework may be helpful in differentiating species for conservation focus. For example, my results indicate that it may take more effort to maintain rare species like *Vulpia,* which was rare due to a low intrinsic growth rate and therefore highly susceptible to environmental variation. In contrast, species like *Calycadenia*, whose high intrinsic growth rate allowed it to recover when rare, may be able to persist with minimal conservation effort. Similarly, my framework suggests that opportunities for invasive species management may vary with time. For example, the *Bromus* population fluctuated greatly as a result of low density dependence and high rainfall sensitivity. This suggests that eradication efforts may be most successful during the end of a consistently dry period, at which time *Bromus* abundance and growth rate are both likely to be low.

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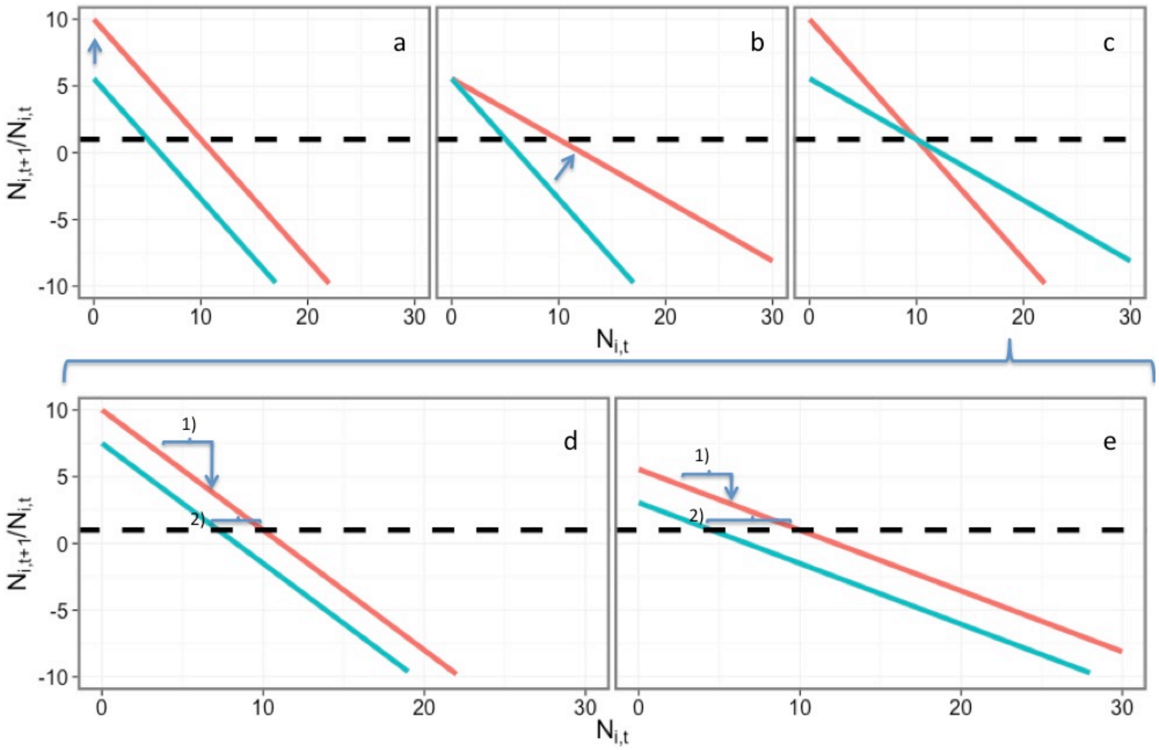

Figure 1. Per capita growth rate in relation to abundance under different of intrinsic growth rate and intraspecific density dependence scenarios. Assuming minimal interspecific competition, population size is reached when $N_{i,t+1}/N_{i,t}$ = 1 and is denoted by the dashed line. Top row (a-c): Red and blue lines denote two species. An increase in intrinsic growth rate (a) or a decrease in intraspecific density dependence (b) will both increase the population size; asymmetry in intrinsic growth rate and intraspecific density-dependence can result in two species with the same population size (c). Bottom row: (d) A species with high intrinsic growth rate and high density dependence under two environmental conditions (red versus blue lines) and (e) A species with low intrinsic growth rate and low density dependence under two environmental conditions (red versus blue lines). Comparing (d) and (e) highlights two points: 1) An equal shift in species' abundance yields a faster rate of return to equilibrium for the species with higher intrinsic growth rates and greater intraspecific density dependence (i.e., steep versus shallow slope marked by 1) for the species in panel d versus e) and 2) An equal, environmentally driven shift in intrinsic growth rate has a larger effect on the population size of the less density-dependent species (i.e., the difference in length of lines marked by 2) for species in panel e versus d, denoted the differenced in where lines cross $N_{i,t+1}/N_{i,t}$ = 1).

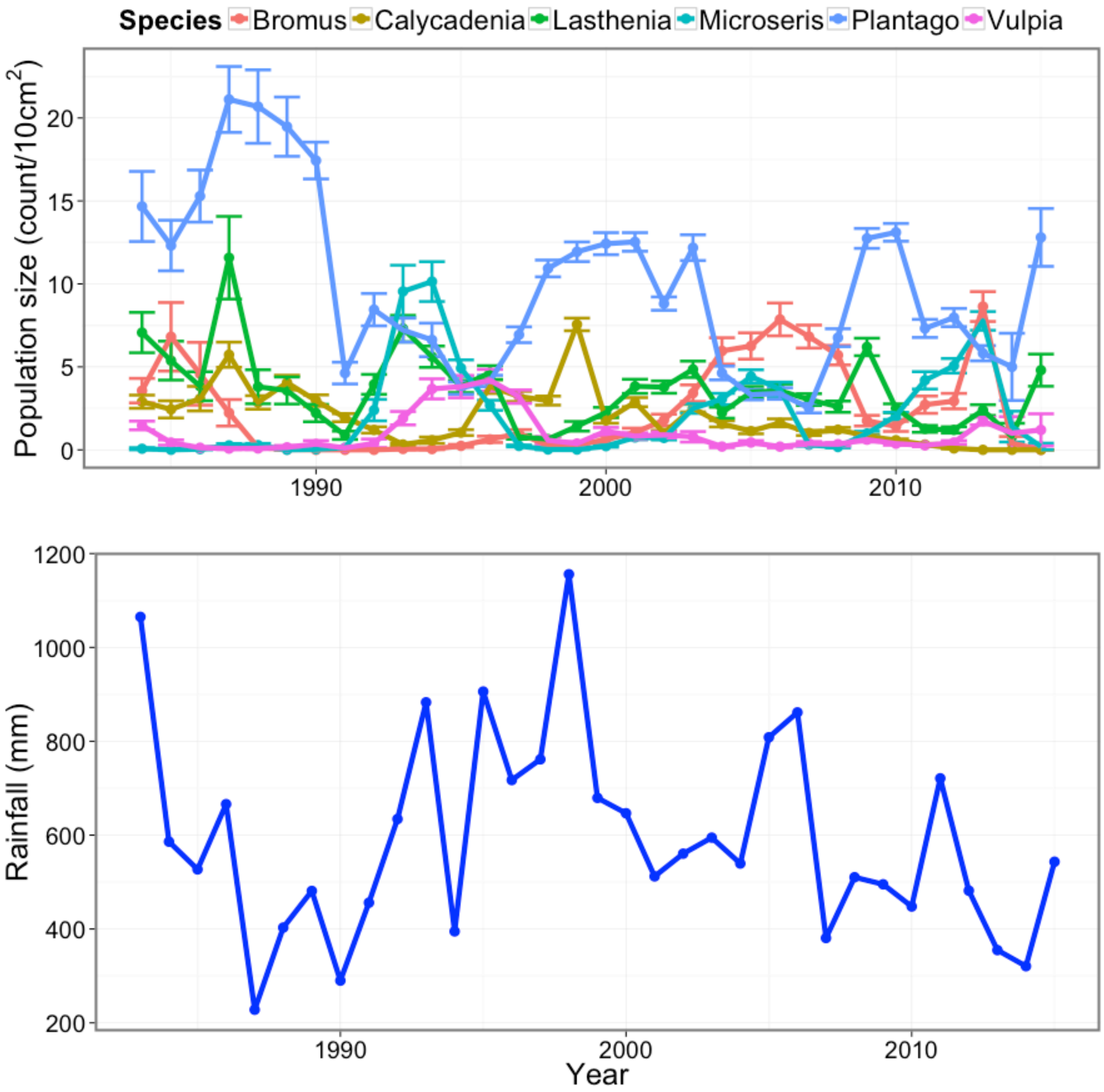

Figure 2. a) Abundance over time for six annual serpentine plants and b) growing season rainfall (September-April) over the same time.

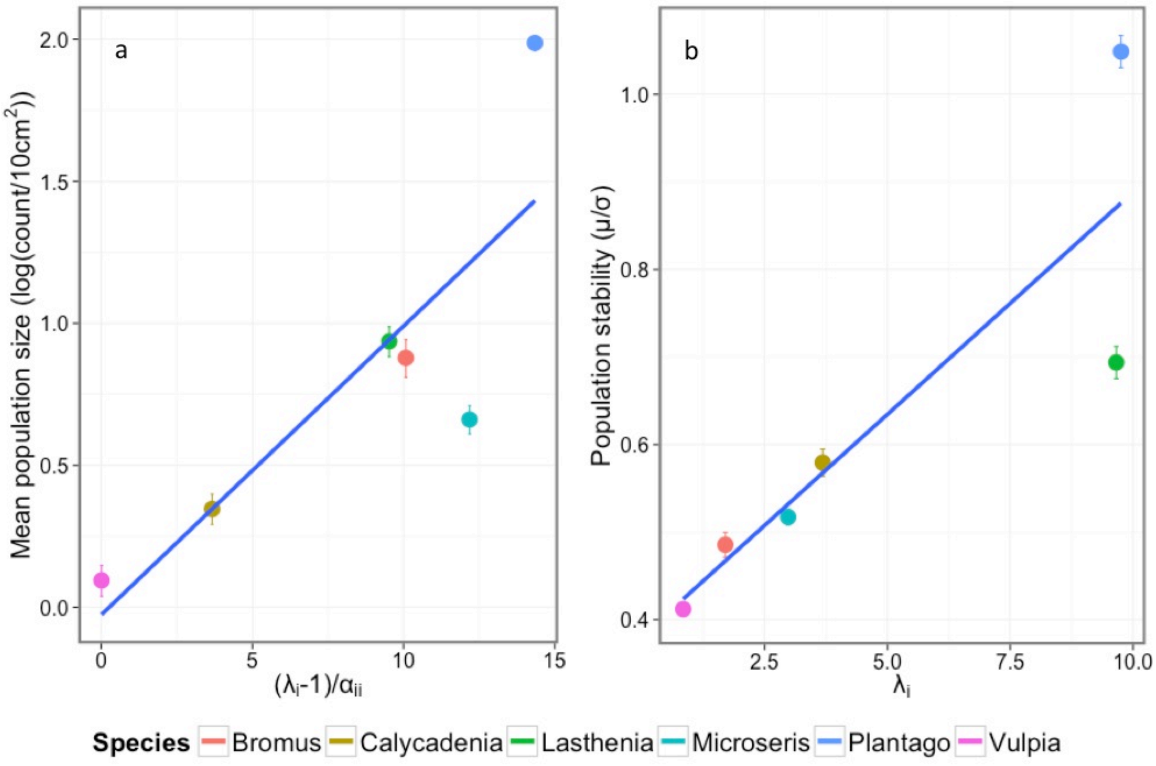

Figure 3. a) Population size, measured as mean abundance over time, in relation to predicted population size $(\lambda_i - 1)/\propto_{ii}$ and b) population stability, measured as μ/σ over time, in relation to predicted intrinsic rate of growth λ_i for six annual plants (±SE).

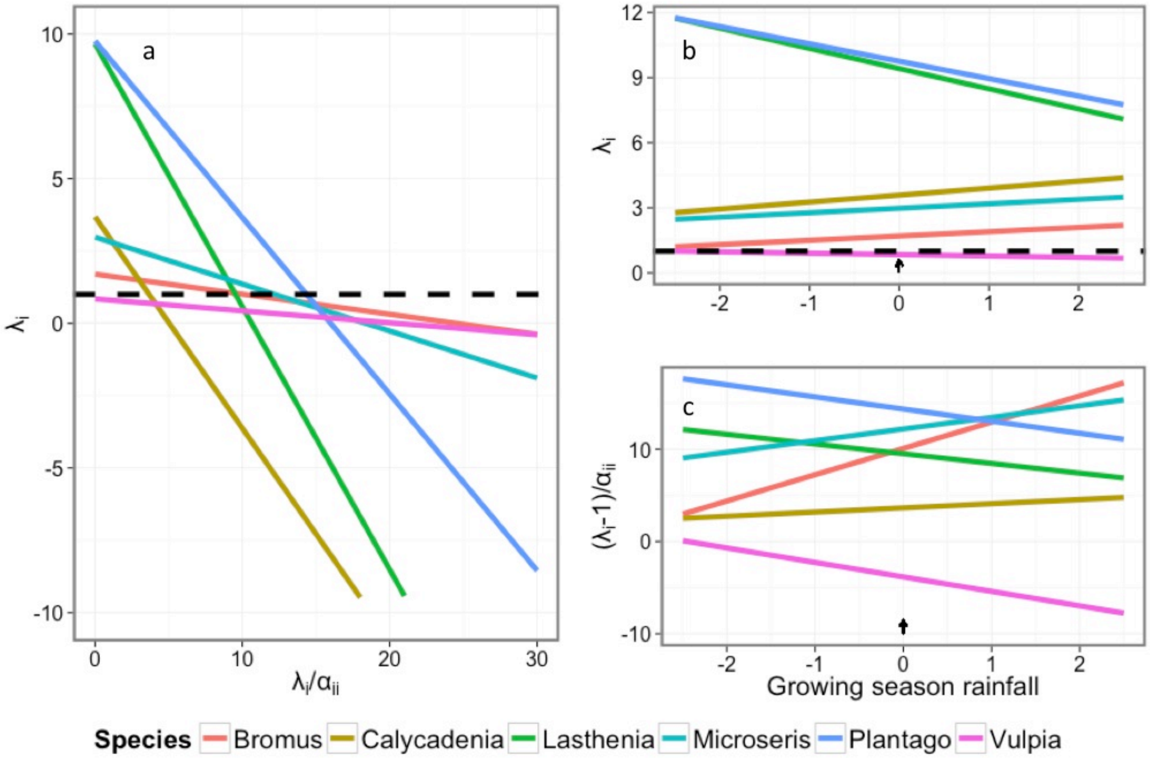

Figure 4. a) Relationship between intrinsic growth rate λ_i and population size $(\lambda_i)/\propto_{ii}$ for six annual plants when their competitors are rare. Dashed line indicates λ_i = 1; species' lines intersect this line when populations are at equilibrium $(\lambda_i - 1)/\propto_{ii}$ b) effect of rainfall on the intrinsic rate of growth λ_i for each species; dashed line indicates λ_i = 1 and c) the resultant effect of rainfall on the predicted population size $(\lambda_i - 1)/\propto_{ii}$ of each species. Growing season rainfall is presented as deviation from an average year; arrows at 0 indicate results for the average year.

Table 1. Parameter estimates for population models of six annual serpentine species, including intrinsic growth rate λ, the effect of rainfall on intrinsic growth rate β, intraspecific density dependence $\propto_{ii}$ (indicated by the species in competition with itself) and interspecific competition $\propto_{ij}$ (indicated by the species in competition with others). Values significant

Species	λ	β	*Bromus*	*Calycadenia*	*Lasthenia*	*Microseris*	*Plantago*	*Vulpia*
Bromus	**1.7**	**0.2**	**0.069**	**0.084**	0.01	**-0.027**	**-0.021**	-0.0067
Calycadenia	**3.7**	**0.33**	**0.43**	**0.73**	0.031	**-0.037**	0.014	-0.026
Lasthenia	**9.7**	**-0.95**	**0.56**	**0.31**	**0.91**	**0.51**	**0.22**	**0.63**
Microseris	**3.0**	**0.2**	**0.68**	**0.57**	**0.13**	**0.16**	-0.00079	**0.74**
Plantago	**9.8**	**-0.8**	**0.17**	0.011	**0.073**	**0.74**	**0.61**	**0.097**
Vulpia	**0.84**	**-0.065**	0.024	**0.092**	**-0.02**	**-0.035**	-0.002	**0.041**

Appendix 1. Summary of datasets used in Chapter 1. Percent cover datasets were only included if their abundance values were not forced to sum to 100. Species composition was measured annually on permanent plots with the exception of CDR and KBS, where species composition was measured via destructive biomass harvests and consequently plot location varied slightly each year.

Abbreviation	Site	Sampling interval	Number of replicate plots	Plot size	Data collection method	Description
CDR	Cedar Creek LTER	1982-2004	5	0.3 m^2	Biomass (g/m^2)	*Annually burned old-field.* Field D, no nutrients added plots (Tilman 1993)
HAY	Hayes, Kansas	1943-1972	13	1 m^2	Percent cover	*Tallgrass prairie.* Continuously-sampled plots (Adler et al. 2007)
JRG	Jasper Ridge Biological Preserve	1983-2010	18	1 m^2	Percent cover	*Serpentine grassland.* Control plots, (Hobbs et al. 2007)
JRN	Jornada Basin LTER	1989-2008	48	1 m^2	Allometric biomass (g/m^2)	*Desert grassland.* Grassland Basin site (Huenneke et al. 2002)
KBS	Kellogg Biological Station LTER	1999-2009	30	1 m^2	Biomass (g/m^2)	*Old-field.* Dataset ID: KBS019, T7 plots (Huberty et al. 1998)
KNZ	Konza Prairie LTER	1983-2006	20	10 m^2	Percent cover	*Annually burned tallgrass prairie*. Dataset ID: PVC02, watershed 1D (Collins 2000)
SEV	Sevilleta LTER	1999-2011	22	1.0 m^2	Biomass (g/m^2)	*Desert grassland.* Dataset ID: SEV187
SGS	Short Grass Steppe LTER	1995-2008	100	0.1 m^2	Percent cover	*Ungrazed shortgrass steppe.* Dataset ID: ARS #32 Grazing and Soil Texture experiment
VC	Vasco Cave Regional Park	2002-2010	6	17 m^2	Percent cover (transects)	*Valley Grassland.* Courtesy of James Bartolome.

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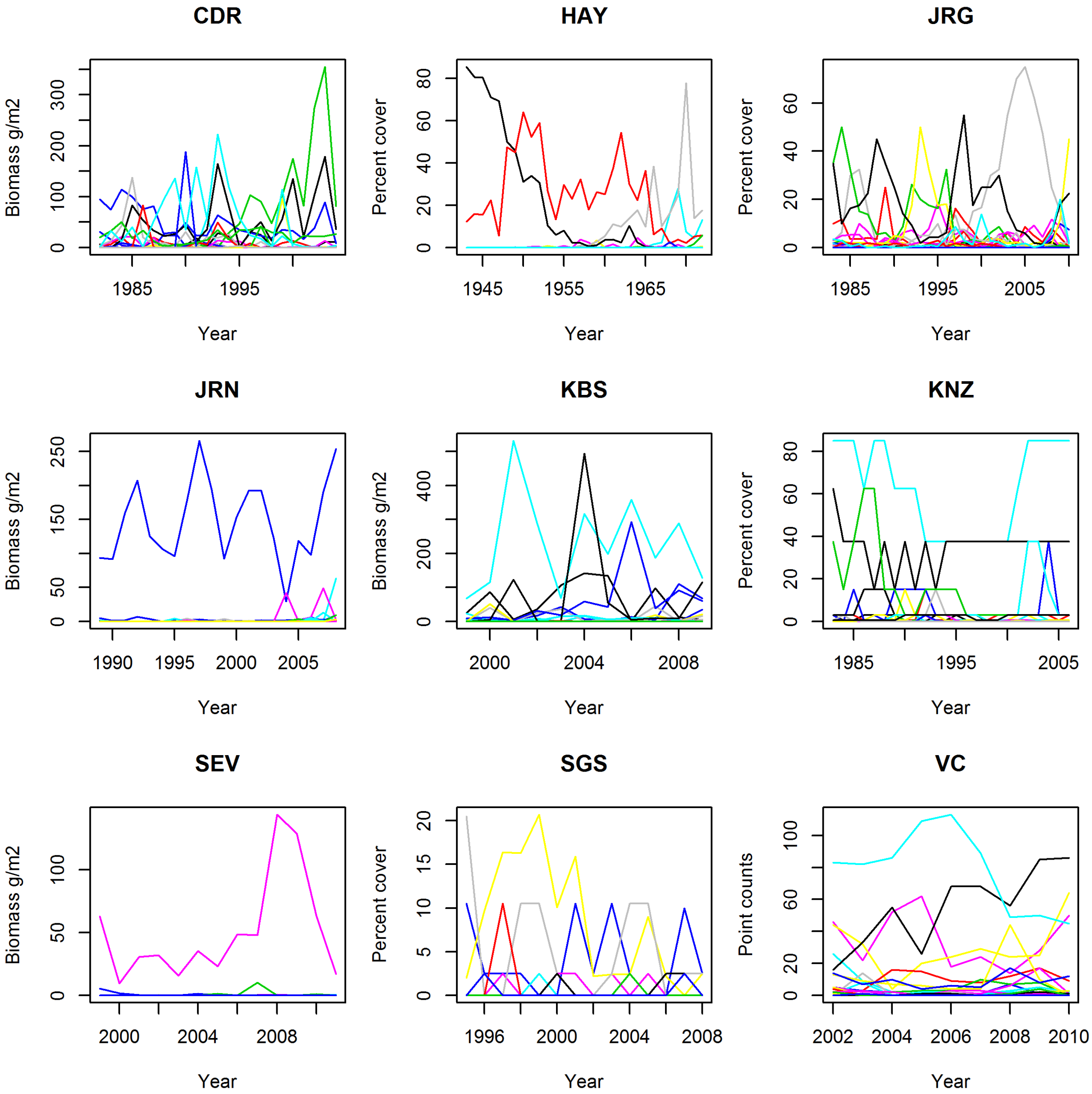
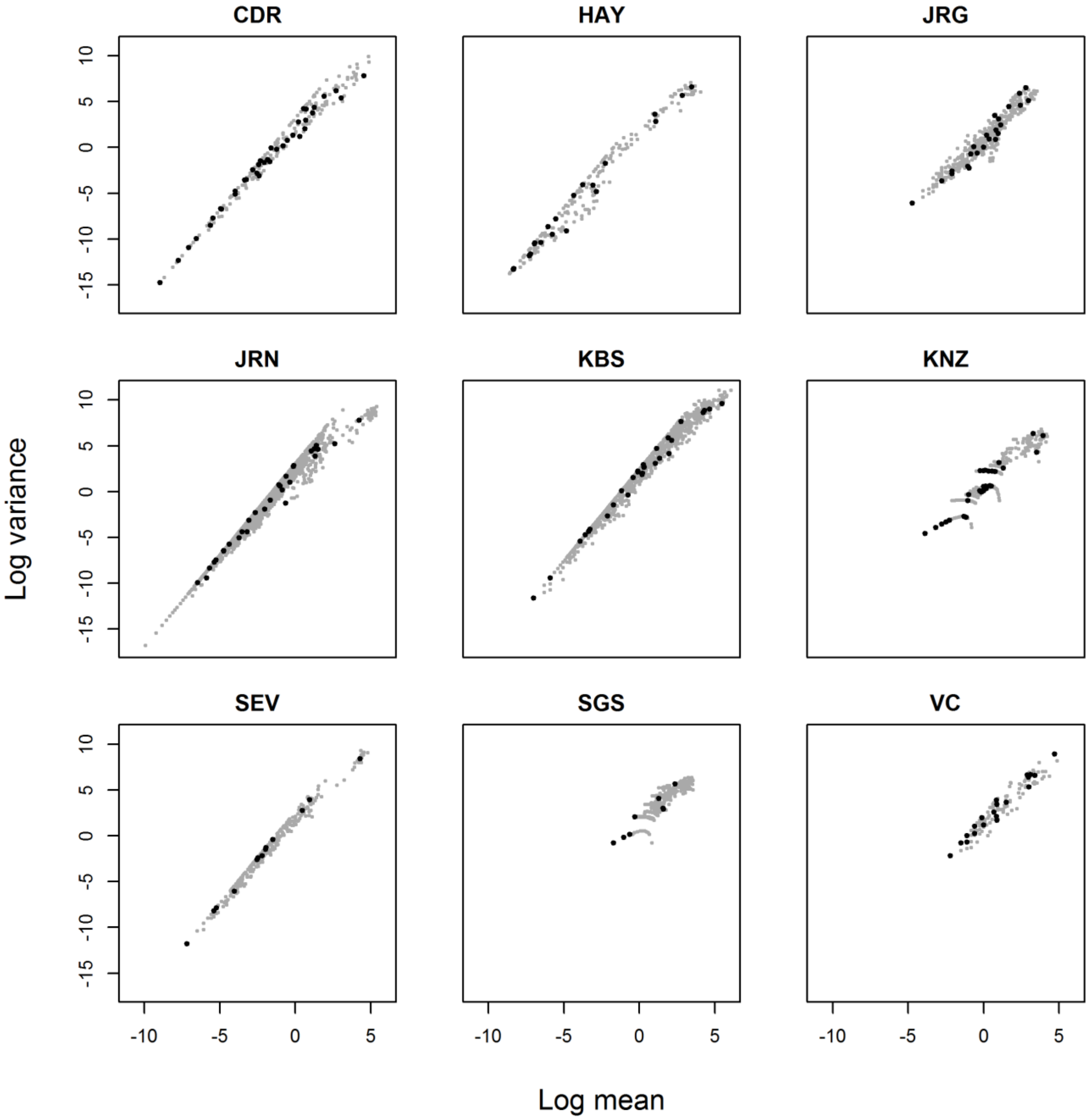
Appendix 2. Time-series of plant species abundances over time from a representative replicate within each of nine grassland sites analyzed in Chapter 1 (and described in Appendix 1). Different colors represent different species within each site; colors are not consistent across sites.



Appendix 3. Mean-variance scaling relationships of plant species at each of nine grassland sites analyzed in Chapter 1 (and described in Appendix 1). Data from all plots within a site are in gray, species within a representative plot are highlighted in black.



Appendix 4. Population size in relation to the number of years since gopher disturbance for six annual serpentine species described in Chapter 4. Lines represent a logistic growth curve fit to each species.