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DRIVERS OF PLANT POPULATION DYNAMICS IN THREE ARID TO SUBHUMID
ECOSYSTEMS

by

Luke J. Zachmann

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

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2010

ABSTRACT

Drivers of Plant Population Dynamics in Three Arid to Subhumid Ecosystems

by

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Utah State University, 2010

Major Professor: Dr. Peter B. Adler
Department: Wildland Resources

Understanding the relative importance of density-dependent and density-independent factors in driving population dynamics is one of the oldest challenges in ecology, and may play a critical role in predicting the effects of climate change on populations. We used long-term observational data to describe patterns in plant population regulation for 57 forb and grass species from three different ecosystems (arid desert grassland, semiarid sagebrush steppe, and subhumid mixed-grass prairie). Using a hierarchical partitioning approach, we (i) quantified the relative influence of conspecific density, heterospecific composition, and climate on temporal variation in population growth rates, and (ii) asked how the relative importance of these drivers depends on site aridity, species growth form and life expectancy, and abundance and spatial patterns. The data from one of the sites in this analysis are presented in one of the chapters of this thesis.

We found that density-dependence had the strongest effect on species. Climate often had a significant effect, but its strength depended on growth form. Community

composition rarely explained significant variation in growth rates. The relative importance of density, composition, and climate did not vary among sites, but was related to species' life histories: compared to forbs, grasses were more sensitive to climate drivers. Abundance and spatial clustering were negatively correlated with the importance of density dependence, suggesting that local rarity is a consequence of self-limitation. Our results show that interspecific interactions play a weaker role than intraspecific interactions and climate variability in regulating plant populations. Forecasting the impacts of climate change on populations may require understanding how changes in climate variables will affect the strength of density-dependence, especially for rare species.

(78 pages)

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Luke J. Zachmann

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CHAPTER 1

INTRODUCTION

Disagreements about the importance of density-dependent vs. density-independent drivers of population dynamics dominated ecology in the middle of the 20th century (Hixon *et al.* 2002). Some investigators emphasized the apparent constancy of population sizes, while others emphasized the fluctuations. Those who emphasized constancy argued that we need to look for stabilizing forces within populations to explain why they do not increase without bounds or decline to extinction (e.g., Nicholson 1954). Those who emphasized the fluctuations looked to external factors, like weather, to explain the changes in population sizes (e.g., Andrewartha & Birch 1954). Andrewartha and Birch (1954) believed that the most important factor limiting the numbers of organisms in natural populations was the limited time in which the rate of increase in the population was positive. In other words, populations pass through a repeated sequence of setbacks and recovery.

In retrospect, it is clear that the first camp was preoccupied with density-dependent and the second with density-independent processes (Begon *et al.* 1996). Most ecologists today recognize that both processes play a role in determining species' population dynamics (Sibly & Hone 2002). Density-dependent processes (i.e., competition, predation, or disease) are the only mechanisms that can formally regulate populations. However, density-independent environmental conditions (e.g., temperature and precipitation) may have strong impacts on populations within the bounds set by carrying capacity and density-dependent regulation (Strong 1986).

Understanding the relative influence of density-dependent and independent factors

on populations (e.g., Coulson *et al.* 2001; Nowicki *et al.* 2009) will be crucial for predicting how species respond to climate change. Populations can respond directly to climate changes. But they can also respond indirectly to climate changes if shifts in climate alter community composition and species interactions (e.g., Tylianakis *et al.* 2008). In some cases, the indirect effects mediated by species interactions may influence population dynamics more than the direct effects of climate change (Dormann *et al.* 2004; Suttle *et al.* 2007).

Despite conceptual progress in teasing apart density-dependent and independent determinants of population growth and the direct and indirect effects of climate change, we still lack an empirical basis for generalizing across species and environmental gradients, especially for plant species (e.g., Adler & HilleRisLambers 2008). Most studies have focused on single species, or sets of closely-related species (e.g., Putman *et al.* 1996). As a result, we have not identified the species traits or environmental correlates that might predict the relative importance of density-dependent and independent drivers. This synthetic understanding could help us anticipate which sites or species are most vulnerable to climate change, even when few data are available.

This thesis consists of an analysis and a data chapter (see Chapters 2 and 3, respectively). In the analysis chapter, we used long-term datasets and hierarchical partitioning (Chevan & Sutherland 1991) to quantify the temporal variation in population growth rates explained by temporal variation in population density, community composition, and climate. Our primary objective was to quantify the relative importance of these three drivers of population growth for species of different growth forms (forbs and grasses) and from different ecosystems (arid desert grassland, semiarid sagebrush

steppe, and subhumid mixed-grass prairie). Our second objective was descriptive. We asked how the relative importance of population density, community composition, and climate depends on 1) aridity, 2) species growth form and life expectancy, and 3) abundance and spatial patterns. These are three factors we expected might explain general patterns in the relative importance of drivers of plant population dynamics.

In the data chapter we present one of the long-term datasets used in our analysis. The enormous ecological value, as well as the size and complexity of this data, justify its inclusion as a separate chapter in the thesis. Historically, observational and theoretical research in ecology has been limited by the availability of suitable long-term data (Fegraus *et al.* 2005). Collecting data for research on population dynamics, for example, is very time- and resource-intensive. Such “costs” have led to research focused on collection and analysis of individual datasets, which makes it difficult to formulate general theory and to investigate patterns across species, scales, and environmental gradients. Efforts to collect and share ecological data, such as time-series population data (see the Global Population Dynamics Database; Inchausti & Halley 2001), facilitate the discovery of general patterns and principles, advance the understanding of large-scale spatial and temporal patterns, and enable researchers to acquire a large number of datasets without undertaking repetitive, expensive, and time-consuming collection efforts.

The development of a database framework (Jones *et al.* 2001), as well as methods and software to create, manage, and share ecological data (Fegraus *et al.* 2005), has led to the creation of invaluable new resources, such as the Knowledge Network for Biocomplexity (KNB), a national network intended to facilitate research on biocomplexity. The journal *Ecology* also allows the publication of datasets. It hopes to

incentivize data collection and sharing by providing a high-profile outlet for data compilations and recognition to the ecologists who create them. Some of the data used in our analysis is already available online (Adler *et al.* 2007). The Idaho data presented in Chapter 3 will be made publicly available early 2010 with its publication in *Ecology* as a data paper and its release on the KNB. Our hope is that these data will enable users to test theory and describe patterns across species, ecosystems, and environmental gradients.

REFERENCES

- Adler, P. & HilleRisLambers, J. (2008). The influence of climate and species composition on the population dynamics of ten prairie forbs. *Ecology*, 89, 3049-3060.
- Adler, P.B., Tyburczy, W.R. & Lauenroth, W.K. (2007). Long-term mapped quadrats from Kansas prairie: demographic information for herbaceous plants. *Ecology*, 88, 2673-2673.
- Andrewartha, H. & Birch, L. (1954). *Distribution and abundance of animals*. University of Chicago Press, Chicago.
- Begon, M., Mortimer, M. & Thompson, D.J. (1996). *Population ecology: a unified study of animals and plants*. Wiley-Blackwell, Oxford.
- Chevan, A. & Sutherland, M. (1991). Hierarchical partitioning. *Am. Stat.*, 45, 90-96.
- Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock, T.H. *et al.* (2001). Age, sex, density, winter weather, and population crashes in Soay sheep. *Science*, 292, 1528-1531.
- Dormann, C.F., Wal, R.V.D. & Woodin, S.J. (2004). Neighbour identity modifies effects of elevated temperature on plant performance in the High Arctic. *Glob. Chang.*

Biol., 10, 1587-1598.

- Fegraus, E.H., Andelman, S., Jones, M.B. & Schildhauer, M. (2005). Maximizing the value of ecological data with structured metadata: an introduction to ecological metadata language (EML) and principles for metadata creation. *Bull. Ecol. Soc. Am.*, 86, 158-168.
- Hixon, M.A., Pacala, S.W. & Sandin, S.A. (2002). Population regulation: historical context and contemporary challenges of open vs. closed systems. *Ecology*, 83, 1490-1508.
- Inchausti, P. & Halley, J. (2001). Investigating long-term ecological variability using the global population dynamics database. *Science*, 293, 655-657.
- Jones, M.B., Berkley, C., Bojilova, J. & Schildhauer, M. (2001). Managing scientific metadata. *IEEE Internet Comput.*, 5, 59-68.
- Nicholson, A. (1954). An outline of the dynamics of animal populations. *Aust. J. Zool.*, 2, 9-65.
- Nowicki, P., Bonelli, S., Barbero, F. & Balletto, E. (2009). Relative importance of density-dependent regulation and environmental stochasticity for butterfly population dynamics. *Oecologia*, 161, 227-239.
- Putman, R., Langbein, J., Hewison, A.M. & Sharma, S. (1996). Relative roles of density-dependent and density-independent factors in population dynamics of British deer. *Mammal Rev.*, 26, 81-101.
- Sibly, R.M. & Hone, J. (2002). Population growth rate and its determinants: an overview. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.*, 357, 1153-1170.
- Strong, D.R. (1986). Density-vague population change. *Trends in Ecology & Evolution*,

1, 39-42.

Suttle, K.B., Thomsen, M.A. & Power, M.E. (2007). Species interactions reverse grassland responses to changing climate. *Science*, 315, 640-642.

Tylianakis, J., Didham, R., Bascompte, J. & Wardle, D. (2008). Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.*, 11, 1351-1363.

CHAPTER 2

DENSITY-DEPENDENCE AND CLIMATE, MORE THAN COMMUNITY
COMPOSITION, DRIVE PLANT POPULATION DYNAMICS¹**Abstract**

Understanding the relative importance of density-dependent and density-independent factors in driving population dynamics is one of the oldest challenges in ecology, and may play a critical role in predicting the effects of climate change on populations. We used long-term observational data to describe patterns in plant population regulation for 57 forb and grass species from three different ecosystems (arid desert grassland, semiarid sagebrush steppe, and subhumid mixed-grass prairie). Using a hierarchical partitioning approach, we (*i*) quantified the relative influence of conspecific density, heterospecific composition, and climate on temporal variation in population growth rates, and (*ii*) asked how the relative importance of these drivers depends on aridity, species growth form and life expectancy, and abundance and spatial patterns. We found that density-dependence had the strongest effect on species. Climate often had a significant effect, but its strength depended on growth form. Community composition rarely explained significant variation in growth rates. The relative importance of density, composition, and climate did not vary among sites, but was related to species' life histories: compared to forbs, grasses were more sensitive to climate drivers. Abundance and spatial clustering were negatively correlated with the importance of density dependence, suggesting that local rarity is a consequence of self-limitation. Our results show that interspecific interactions play a weaker role than intraspecific interactions and

¹ Coauthored by Luke Zachmann, Aldo Compagnoni, Mevin Hooten, Debra Peters, and Peter Adler.

climate variability in regulating plant populations. Forecasting the impacts of climate change on populations may require understanding how changes in climate variables will affect the strength of density-dependence, especially for rare species.

INTRODUCTION

Disagreements about the importance of density-dependent vs. density-independent drivers of population dynamics dominated ecology in the middle of the 20th century (Hixon *et al.* 2002). The most intense debate pitted Nicholson (1954), who claimed that interactions between individuals within populations regulate population growth, against Andrewartha and Birch (1954), who argued that external factors like weather determine growth. In hindsight, we recognize that the protagonists took extreme positions (Begon *et al.* 1996) and that both processes operate simultaneously (Sibly & Hone 2002).

The focus of contemporary research on the determinants of population growth is on disentangling the relative importance of density-dependent and independent determinants of population growth (e.g., Coulson *et al.* 2001; Nowicki *et al.* 2009). This information is essential to forecasts of future population trends, especially the response of plant and animal populations to climate change. Most efforts to forecast climate change impacts are based on the direct responses of individual species to climate (Walther *et al.* 2002). But species are also influenced by interactions with other species, and climate change can alter these interactions (Tylianakis *et al.* 2008). In some cases, the indirect effects mediated by species interactions can influence population dynamics more than the direct effects of climate change (Dormann *et al.* 2004; Suttle *et al.* 2007).

Despite conceptual progress in teasing apart density-dependent and independent

determinants of population growth and the direct and indirect effects of climate change, we still lack an empirical basis for generalizing across species and environmental gradients, especially for plant species (e.g., Adler & HilleRisLambers 2008). Most studies have focused on single species, or sets of closely-related species (e.g., Putman *et al.* 1996). As a result, we have not identified the species traits or environmental correlates that might predict the relative importance of density-dependent and independent drivers. This synthetic understanding could help us anticipate which sites or species are most vulnerable to climate change, even when few data are available.

At least three factors might explain general patterns in the relative importance of drivers of plant population dynamics. The first candidate factor is resource availability. Climatic controls on plant population growth may be relatively strong for species at arid sites where low and variable soil moisture constrains growth (Noy-Meir 1973; Huxman *et al.* 2004). At wetter sites, where resources are more abundant and reliable, density-dependent population regulation and species interactions may exert stronger control over plant growth and population growth rates (Grime 1979; Keddy 1989). On the other hand, species interactions might be important along the entire gradient of resource availability (Newman 1973; Tilman 1988, 1990).

The second factor potentially influencing the relative importance of density-dependent and independent processes on population dynamics is life history. For example, the strong morphological, life history, and ecophysiological differences between forbs and grasses in semiarid plant communities (Martin *et al.* 1991; Turner & Knapp 1996) could influence the relative importance of density-dependent and independent drivers. We might expect shorter-lived species to be more sensitive to climatic variability

than longer-lived species, which are buffered against such changes (Morris *et al.* 2008).

Finally, a species' abundance may influence whether density-dependent or independent processes are more important in regulating that species' population. Density dependence may be a stronger, more detectable force in more abundant species (Wills *et al.* 1997), perhaps because these species have reached carrying capacity. Since most species are rare, density-dependent population regulation may have little impact on most species most of the time (Grubb 1986). This hypothesis views differences in density-dependence as a consequence of differences in abundance. The alternative is that density-dependence could be the cause of differences in abundance: species may become abundant only if they are not strongly self-limiting. When testing these hypotheses, it may be important to consider the spatial scale at which abundance is estimated. Spatially averaged abundance may poorly characterize plant populations if the fate of individuals is determined by their local neighborhood and the spatial distribution of plants is non-random (Harper 1977). In fact, plants are often distributed non-randomly and spatial structure can have large impacts on plant population dynamics (Czaran & Bartha 1992). Growing interest in the link between plant spatial patterns and ecological processes (McIntire & Fajardo 2009), as well as methods to quantify spatial patterns (e.g., Wiegand & Moloney 2004), has enabled us to ask how the strength of density-dependence is related to spatial clustering.

We used long-term datasets and hierarchical partitioning (Chevan & Sutherland 1991) to quantify the temporal variation in population growth rates explained by temporal variation in population density, community composition, and climate. Our primary objective was to quantify the relative importance of these three drivers of population

growth for species of different growth forms (forbs and grasses) and from different ecosystems (arid desert grassland, semiarid sagebrush steppe, and subhumid mixed-grass prairie). Our second objective was descriptive. We asked how the relative importance of population density, community composition, and climate depends on 1) aridity, 2) species growth form and life expectancy, and 3) abundance and spatial patterns.

METHODS

Study site and dataset description

The data used in our analysis come from chart quadrats, which are permanent 1-m² quadrats in which all individual plants are identified and mapped each year using a pantograph (Hill 1920). Under Clements' (1907) influence, many range experiment stations across the western U.S. began mapping quadrats between the 1910s and the 1930s and continued annual censuses for decades. We used three chart quadrat datasets that represent widespread plant communities in the Western U.S.: sagebrush steppe at the USDA-ARS Sheep Station in Dubois, Idaho; mixed-grass prairie near Hays, Kansas; and Chihuahuan desert grassland at the Jornada Experimental Range in New Mexico. These sites differ in temperature and the timing and amount of precipitation, ranging from arid (New Mexico) to semiarid (Idaho) to subhumid (Kansas). Table 1 provides details about the climate and sampling coverage at each site. The original maps from each of the sites have been digitized. The data from KS and ID are available online in both spatial and tabular formats along with monthly precipitation and temperature data (Adler *et al.* 2007; Zachmann, Moffet, & Adler unpublished work).

We analyzed the population growth rates of 57 species across the three sites that

were common enough to provide a sufficient sample size for model fitting. The number of species included in the analysis varied by site. In Idaho, Kansas, and New Mexico, the number of forbs was 10, 17, and 8, respectively; the number of grasses was 7, 8, and 7, respectively.

Calculating population growth rates

For each species, population growth rate was calculated as

$$r_{jt} = \log \left(\frac{N_{jt}}{N_{jt-1}} \right) \quad (1)$$

where N_{jt} is the abundance of individuals in quadrat j at time t . For the forb species in our analysis, N represents the total density of the focal species per quadrat, while for grasses N represents the basal cover of the focal species per quadrat.

We analyzed the relative importance of population density, community composition, and climate in driving changes in population size, excluding colonization and extinction. Like many ecological datasets, ours contain many zero observations. This is a problem because $\log(0)$ is undefined and population growth rates calculated from zero observations result in undefined growth rates. Standard methods for handling zero observations, such as adding a constant to the whole series, can seriously distort data patterns by ignoring the natural scale of variation in the data (Steen & Haydon 2000, Turchin 2003) and more sophisticated statistical methods (Martin *et al.* 2005) would be difficult to implement for the number of species and models we wished to analyze. Therefore, we discarded zero observations in our samples before calculating r_{jt} and we restrict our inference to variation in species population growth rates calculated from consecutive presences.

Quantifying the relative importance of population density, community composition, and climate

We used hierarchical partitioning (HP) (Chevan & Sutherland 1991; Mac Nally 1996) to quantify the “independent” correlation of each species' population growth rate with conspecific population density, the composition of dominant heterospecifics, and climate. Our approach differs slightly from the way in which HP is generally used. Instead of looking at the effect of single predictor variables on some response variable, we look at the effect of *sets* of predictor variables that correspond to different endogenous and exogenous influences on population growth rate. We used the coefficient of determination (R^2) as our measure of fit.

Our approach was to fit the chart quadrat data with discrete-time models of the form

$$r = f(\textit{group}, \textit{lagged density}, \textit{community composition}, \textit{climate}, \varepsilon) \quad (2)$$

where the variable *lagged density* represents an endogenous feedback, while the other three variables represent known exogenous influences: *group* is a categorical variable for a spatial location effect, *community composition* is a site-specific set of predictors that describe the density and cover of heterospecifics in the quadrat, and *climate* is a set of parameters that represent climatic influences (i.e., growing- and dormant-season precipitation and temperature, and total annual precipitation in the previous year). Growing and dormant season differ by site (Table 2.1). ε represents the effects of stochastic factors and unknown exogenous influences (herbivory, disturbance, disease, etc.).

We fit the data to linear regression equations in a regression hierarchy derived

from eqn 1. With three sets of predictor variables, there are $2^3 = 8$ possible models. The first level of the hierarchy includes: a “density” model,

$$r_{ikt} = \beta_0 + \beta_G G_k + \beta_D N_{ikt-1} + \varepsilon_{ikt} \quad (3)$$

where β_0 is the intercept, G_k is the vector of dummy-coded group covariates from $k = 1, \dots, g$ groups, β_G is the vector of coefficients, and N_{ikt-1} is lagged density for observations $i = 1, \dots, n$ in group k at time $t-1$ for each species; a “composition” model,

$$r_{ikt} = \beta_0 + \beta_G G_k + \beta_H H_{ikt} + \varepsilon_{ikt} \quad (4)$$

where H_{ikt} is the vector of community composition covariates (generally forb density, grass cover, and shrub cover at time t , see Table 2.1) for observation i , in group k , at time t , and β_H is the vector of coefficients; and a “climate” model,

$$r_{ikt} = \beta_0 + \beta_G G_k + \beta_C C + \varepsilon_{ikt} \quad (5)$$

where C is the vector of climate covariates (growing- and dormant-season precipitation and temperature at time t , as well as total annual precipitation at time $t-1$ for observation i) and β_C is the vector of coefficients. Models in higher levels of the regression hierarchy were combinations of these three basic sets of predictors.

HP partitions variances so that the total independent influence (I) of a predictor variable, or set of predictor variables, on the response can be estimated. I -scores for density, composition, and climate are estimated for every species in the analysis. For example, to get the I -score for density, we would compare the following R^2 values: $R^2(\text{density})$ vs. $R^2(\text{intercept only})$, $R^2(\text{density, composition})$ vs. $R^2(\text{composition})$, $R^2(\text{density, climate})$ vs. $R^2(\text{climate})$, $R^2(\text{density, composition, climate})$ vs. $R^2(\text{composition, climate})$. The differences in R^2 values are averaged within each hierarchical level and then averaged across levels, providing a measure of the

independent effect of density on population growth rate (Christensen 1992).

We were interested in assessing the relative importance of density, community composition, and climate across sites and species, therefore we fit the same set of models for each species at each site. This approach carries the risk of poorly-specified models for species' population growth rates. A bias in our results toward one or another of the three factors could conceivably be created by a systematic mis-specification in one of our model sets (the density, composition, or climate models). However, because the exact form of the relationship between the density, composition, and climate and population growth rate varies from one species to the next in unpredictable ways, we have no reason to suspect such a bias. Instead, our results should be viewed as “conservative” because there is a penalty (in terms of R^2) for poorly fitted models (Korn & Simon 1991). All calculations were made using the hier.part package (Mac Nally & Walsh 2004) in the statistical software R, version 2.9.1.

Hierarchical partitioning and statistical significance

The coefficient of determination, R^2 , in linear models is the proportion of variability in a data set that is accounted for by the model. However, even models fit to random data have non-zero R^2 values. In fact, given random data, the percent of variation in some response variable explained by some predictor variable increases as sample size decreases, especially as the number of predictors included in the model increases. Our results are affected by this statistical artifact for three reasons. First, the sample sizes for species in this analysis were variable. Second, the number of predictors in the models for species differed (because the number of groups in our group covariate changed from one

species to the next). Finally, the number of predictor variables in the density, composition, and climate covariate sets differed – 1, 3, and 5 variables, respectively. To remove the effect of this statistical artifact, we constructed a null model.

We randomized the data matrix for each species 1000 times (Manly 1997), computing the “null” *I-scores* for each set of predictor variables at each run. The result was a distribution of null *I-scores* (I_{null}) for each species. We subtracted the mean of these null *I-scores* from the uncorrected, observed *I-scores* (I_{obs}) from the original HP run

$$\text{Corrected } I \text{ score} = I_{obs} - \bar{I}_{null} \quad (6)$$

to obtain the corrected *I-scores*. These *I-scores* represent variation explained by density, composition, and climate above and beyond any variation explained by chance.

The drivers (density, community composition, or climate) that independently explained a larger proportion of variance than would be expected by chance were identified by comparing uncorrected, observed *I-scores* to the population of null “*I*” values generated by the randomization procedure described above. Significance was accepted at the upper 95% confidence level ($Z\text{-score} \geq 1.65$; Mac Nally 2002).

Cross-species patterns in population drivers

To address our second objective, concerning factors that might explain general patterns in the relative importance of drivers of plant population dynamics, we assembled additional data on site aridity, species' life history traits, and abundance and spatial patterns. Precipitation records from each site characterize aridity (Table 2.1), and species' growth form data were obtained from the United States Department of Agriculture PLANTS Database (<http://plants.usda.gov/>). To estimate species' life expectancies and

abundance and spatial patterns, we used the chart quadrat data.

We estimated species life expectancies at one year of age using computer programs developed by Lauenroth and Adler (2008). The programs track the identity of individual genets based on their spatial locations in the permanent quadrats. They distinguish between new recruits and surviving individuals, and calculate the ages and life spans of the survivors.

Species' average population densities were calculated as the mean of the number of individuals per quadrat, per year in our sample, excluding years and quadrats in which a species was absent. Recognizing that spatial structure can have large impacts on plant population dynamics (Czaran & Bartha 1992), we extended the analysis by calculating a measure of the clustering of individuals within populations for each species.

We quantified population-level clustering as a point process for the forb species in our analysis using the O-ring statistic (Wiegand & Moloney 2004). We excluded grasses from this part of the analysis to avoid the complexities associated with the quantification of spatial patterns for features represented as polygons. The O-ring statistic averages the number of points counted within a ring of width w and radius r centered on each point found in a plot. Since each species occurred in several quadrats and years in our sample, we pooled the O-ring values from the plots in which species occurred and calculated a weighted average for each species (Diggle 2003). The O-ring depends on intensity, which is defined as number of points per unit area. The higher the intensity, the higher the O-ring statistic. Because every species had a different average intensity over the plots in which it occurred, we divided species' average O-ring statistic by its average intensity. This enabled us to compare our measure of clustering across species. To quantify point

patterns over several spatial scales, we carried out calculations holding w constant at 10 cm, but varying r from 5 to 30 cm in increments of 5 cm. This quantified spatial patterns over 6 spatial scales, or “bins.”

To evaluate the influence of site and species' growth form on the relative importance of density, composition, and climate, we regressed the corrected I -score for each driver on species' life expectancies and abundance and spatial patterns, aggregating species by site and growth form.

RESULTS

For the 57 species we analyzed, the sum of the uncorrected I -scores (observed variation explained) for density, community composition, and climate ranged from only 0.028 for *Phlox longifolia* to 0.600 for *Allionia incarnata*. The corrected I -scores (observed minus chance variation explained) ranged from 0 to 0.351 (Fig. 2.1). Variation explained by statistical artifact (chance alone) accounted for an average of 40.9% of uncorrected I -scores. Hereafter, we present only the corrected I -scores.

Mean density I -scores (0.115) were higher across species than mean I -scores for either climate (0.043) or composition (0.010). The relative influence of density, community composition, and climate depended on both site and growth form (Fig. 2.2). The density I -scores were higher for forbs than grasses at all sites, ranging from 0.129 for ID forbs to 0.187 for forbs in KS, and from 0.041 for NM grasses to 0.055 for grasses in KS. Density-dependence explained significant variance for 44 of the 57 species in the analysis (77%), but the percent of species showing significant density I -scores depended both on site and growth form (Fig. 2.2).

Climate had a stronger influence on grasses than on forbs, although the strength of this effect varied by site. The climate *I-scores* were higher for grasses than forbs at all sites, ranging from 0.037 for KS grasses to 0.083 for NM grasses, and from 0.031 for NM and ID forbs to 0.033 for forbs in KS. Climate explained a significant portion of variance for 26 of the 57 species in the analysis (46%). The percentage of species showing significant climate *I-scores* depended both on site and growth form, ranging from 12.5% in NM to 35.3% in KS for the forbs, and from 62.5% to 100% of the grasses in KS and ID, respectively (Fig. 2.2).

Community composition was the least influential of the three factors. Composition exhibited a significant independent contribution to variance for only 9 (16%) of the 57 species in the analysis. Composition *I-scores* ranged from 0.005 to 0.020 for the grasses and from 0.004 to 0.010 for the forbs. The percent of species showing significant composition *I-scores* ranged from 0% for ID and NM forbs to 11.8% for KS forbs, and from 4.3% to 42.9% of the grasses in NM and ID, respectively (Fig. 2.2).

We found a highly significant ($P < 0.001$) negative correlation between species' density *I-scores* and their life expectancies (Fig. 2.3), and the relationship remained significant ($P < 0.05$) after controlling for growth form (forb vs. grass). There was no significant correlation between species' composition or climate *I-scores* and their life expectancies. A significant ($P < 0.01$) correlation between the sum of the *I-scores* and species' life expectancies disappeared after controlling for growth form.

Forb species' density *I-scores* were negatively correlated with their average density in the quadrats ($P < 0.01$) (Fig. 2.4a). No such trend was found for the grasses. There was also a significant ($P < 0.05$) negative relationship across sites between forb

species' density *I-scores* and their spatial aggregation. Species that exhibit stronger clustering (larger clustering index scores) were relatively less sensitive to density-dependence than less clustered species. The results at $r = 10$ are presented in Fig. 2.4b, but this pattern existed for clustering measured at spatial scales from $r = 5$ to 30 cm.

DISCUSSION

The relative importance of conspecific density, heterospecific composition, and climate

Our primary objective was to determine the relative influence of intraspecific density-dependence, interspecific community composition, and climate on plant population growth rates. The high number (77%) of significant negative correlations between density and population growth rate and their strength (mean *I-score* = 0.115) suggest a strong role for density dependence in plant population dynamics, especially for forbs. This result is consistent with a recent study by Brook and Bradshaw (2006) that analyzed 30 plant species and concluded that density-dependence is a pervasive feature of population dynamics.

For most species, the effect of climate on growth rates was not as significant (46% of all species) nor as strong (mean *I-score* = 0.043) as the effect of density-dependence. However, the strength and importance of climate depended strongly on growth form. For forb species, climate was clearly less influential than density-dependence, while for grasses, climate had a stronger effect than density-dependence. We were surprised that climate was not more important across all species given previous evidence for its importance (Meyer *et al.* 2006; Adler & HilleRisLambers 2008; Lucas *et al.* 2008). One explanation is that forb species may respond to complex environmental cues involving

interactions among climate variables (Adler & Levine 2007; Levine *et al.* 2008), rather than to the general precipitation and temperature covariates we used.

Community composition was unambiguously the least important of the three drivers. It was the weakest (mean *I-score* = 0.010) and the least significant of all the drivers (only 9 of the 57, or 16% of species had significant composition *I-scores*). There are at least two potential explanations for this. First, the low importance of community composition may reflect a basic principle in classical coexistence theory: to promote coexistence, intraspecific interactions must be more limiting than interspecific interactions (Chesson 2000). Second, our community composition covariates reflect the combined effects of variation in the density and cover of the entire network of species in our quadrats, potentially masking the effects of certain strong individual competitor- or facilitator-species. However, the fact that the net effect of individual interactions is weak indicates that they may balance each other over the spatial and temporal scales of our data. While there is no question that plant species interact (Connell 1983; Schoener 1983; Goldberg & Barton 1992), the impact of such interactions on population dynamics is rarely quantified (Brooker & Kikvidze 2008). Our results suggest that interspecific interactions play a weaker role than intraspecific interactions and climate in driving plant population dynamics.

Differences between species in the relative influence of density, composition, and climate

Our second question concerned the potential for aridity, life history, and abundance to explain general patterns in the effects of density, composition, and climate on plant population dynamics. We found that the effects of population density,

community composition, and climate were remarkably consistent across sites. There are three potential explanations for this result. First, our models take into account changes in mean dormant- and growing-season precipitation as well as lagged annual precipitation, not the size and timing of precipitation events. The weak effect of site aridity may reflect the importance of patterns in the size and timing of precipitation events, which can exert a strong influence on plants (Knapp *et al.* 2002). Second, if resource availability is determined by plant uptake and not abiotic factors, we would expect species interactions to have similar effects on species across our aridity gradient (Goldberg & Novoplansky 1997). Finally, our three sites, which are all water-limited ecosystems, may not span a wide enough range of water availability to reveal an effect of aridity on the relative importance of population drivers.

The effect of plant growth form on the relative importance of density, composition, and climate appears to be strong. Density-dependence was overwhelmingly the most important driver of population growth for forbs, but the result was different for grasses. While the effects of density were significant for grasses, they were not as pervasive or as influential as the effects of climate, with the exception of the KS grasses. Differences in the magnitude and significance of density *I-scores* between forbs and grasses in this analysis could result from differences in sampling. We estimated population growth rates for forbs based on density, while growth rates for grasses were based on cover. Measures of cover may be more prone to observation error than density. On the other hand, there may be real differences between the growth forms. For example, Briggs and Knapp (1995) found that forb productivity may be more limited by biotic than abiotic factors in comparison to grass productivity in tallgrass prairie.

Species' life expectancies were negatively correlated with the importance of density-dependence: shorter-lived species were more limited by density than were longer-lived species. We speculate that this relationship may reflect differences in species' resistance to pathogens: annuals and biennials tend to accumulate more negative plant-soil feedbacks than perennials (Kulmatiski *et al.* 2008). These negative plant-soil feedbacks would be a potent form of density-dependence. Another potential explanation for this result is that the importance of unmeasured factors (e.g., herbivory, disturbance, or disease) is higher for longer-lived species.

Finally, the effect of density-dependence on forb species decreased at higher average densities and with more clustering. This finding may be the signature of intraspecific competition on the local distribution of populations (Kenkel 1988). Perhaps species become locally abundant and/or highly clustered only when they are not strongly self-limiting. In other words, density-dependence may be the cause, rather than the consequence, of patterns in abundance and aggregation.

In contrast with our results, previous studies have suggested that density dependence is more pervasive in more abundant species (Wills *et al.* 1997), presumably because they have reached their carrying capacity. However, this finding may be the result of a statistical artifact, since low sample sizes limit the detection of density-dependence for rare species. Our analysis controlled for the effect of sample size by using a null model. More clearly determining whether density-dependence is a cause or consequence of abundance may require an experimental approach.

Conclusion

Understanding the relative influence of density, composition, and climate on population growth may help prioritize management of high-risk populations. Species with strong direct responses to climate, like the grasses in our analysis, may be particularly sensitive to climate change. Species only loosely regulated by density-dependent processes may also be at greater risk of chance extinction (Ginzburg *et al.* 1990; Saita *et al.* 1991). The importance of intraspecific density-dependence in our data highlights the need to understand how changes in climate variables might affect self-limitation, especially for rare species. On the other hand, our results suggest that for many plant species it may be reasonable to ignore interactions with other plant species in bioclimate envelope models. Finally, the high proportion of variation in growth rates unexplained by our density, composition and climate covariates emphasizes the potential importance of other drivers of population dynamics, such as herbivory, disturbance, and disease.

REFERENCES

- Adler, P. & HilleRisLambers, J. (2008). The influence of climate and species composition on the population dynamics of ten prairie forbs. *Ecology*, 89, 3049-3060.
- Adler, P.B. & Levine, J.M. (2007). Contrasting relationships between precipitation and species richness in space and time. *Oikos*, 116, 221-232.
- Andrewartha, H. & Birch, L. (1954). *Distribution and Abundance of Animals*. University of Chicago Press, Chicago.
- Begon, M., Mortimer, M. & Thompson, D.J. (1996). *Population Ecology: A Unified*

Study of Animals and Plants. Wiley-Blackwell, Oxford.

- Briggs, J.M. & Knapp, A.K. (1995). Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. *Am. J. Bot.*, 82, 1024-1030.
- Brook, B.W. & Bradshaw, C.J.A. (2006). Strength of evidence for density dependence in abundance time series of 1198 species. *Ecology*, 87, 1445-1451.
- Brooker, R.W. & Kikvidze, Z. (2008). Importance: an overlooked concept in plant interaction research. *J. Ecol.*, 96, 703-708.
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*, 31, 343-366.
- Chevan, A. & Sutherland, M. (1991). Hierarchical partitioning. *Am. Stat.*, 45, 90-96.
- Christensen, R. (1992). Comment on Chevan and Sutherland. *Am. Stat.*, 46, 74.
- Clements, F.E. (1907). *Plant Physiology and Ecology*. H. Holt and Company, New York.
- Connell, J. (1983). On the prevalence and relative importance of interspecific competition - evidence from field experiments. *Am. Nat.*, 122, 661-696.
- Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock, T.H. *et al.* (2001). Age, sex, density, winter weather, and population crashes in Soay sheep. *Science*, 292, 1528-1531.
- Czaran, T. & Bartha, S. (1992). Spatiotemporal dynamic-models of plant-populations and communities. *Trends Ecol. Evol.*, 7, 38-42.
- Diggle, P.J. (2003). *Statistical Analysis of Spatial Point Patterns*. Arnold, London.
- Dormann, C.F., Wal, R.V.D. & Woodin, S.J. (2004). Neighbour identity modifies effects of elevated temperature on plant performance in the High Arctic. *Glob. Chang.*

Biol., 10, 1587-1598.

- Ginzburg, L.R., Ferson, S. & Akcakaya, H.R. (1990). Reconstructibility of density dependence and the conservative assessment of extinction risks. *Conserv. Biol.*, 4, 63-70.
- Goldberg, D. & Barton, A. (1992). Patterns and consequences of interspecific competition in natural communities - a review of field experiments with plants. *Am. Nat.*, 139, 771-801.
- Goldberg, D. & Novoplansky, A. (1997). On the relative importance of competition in unproductive environments. *J. Ecol.*, 85, 409-418.
- Grime, J.P. (1979). *Plant Strategies and Vegetation Processes*. John Wiley & Sons Ltd, Chichester.
- Grubb, P.J. (1986). Problems posed by sparse and patchily distributed species in species-rich plant communities. In: *Community Ecology* (eds Diamond, J. & Case, T.J.). Harper and Row, New York, pp. 207-228.
- Harper, J.L. (1977). *Population Biology of Plants*. Academic Press, London.
- Hill, R.R. (1920). Charting quadrats with a pantograph. *Ecology*, 1, 270-273.
- Hixon, M.A., Pacala, S.W. & Sandin, S.A. (2002). Population regulation: historical context and contemporary challenges of open vs. closed systems. *Ecology*, 83, 1490-1508.
- Huxman, T.E., Snyder, K.A., Tissue, D., Leffler, A.J., Ogle, K., Pockman, W.T. *et al.* (2004). Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia*, 141, 254-268.
- Keddy, P. (1989). *Competition*. Springer, New York.

- Kenkel, N.C. (1988). Pattern of self-thinning in jack pine: testing the random mortality hypothesis. *Ecology*, 69, 1017-1024.
- Knapp, A.K., Fay, P.A., Blair, J.M., Collins, S.L., Smith, M.D., Carlisle, J.D. *et al.* (2002). Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science*, 298, 2202-2205.
- Korn, E.L. & Simon, R. (1991). Explained residual variation, explained risk, and goodness of fit. *Am. Stat.*, 45, 201-206.
- Kulmatiski, A., Beard, K.H., Stevens, J.R. & Cobbold, S.M. (2008). Plant-soil feedbacks: a meta-analytical review. *Ecol. Lett.*, 11, 980-992.
- Lauenroth, W.K. & Adler, P.B. (2008). Demography of perennial grassland plants: survival, life expectancy and life span. *J. Ecol.*, 96, 1023-1032.
- Levine, J.M., McEachern, A.K. & Cowan, C. (2008). Rainfall effects on rare annual plants. *J. Ecol.*, 96, 795-806.
- Lucas, R.W., Forseth, I.N. & Casper, B.B. (2008). Using rainout shelters to evaluate climate change effects on the demography of *Cryptantha flava*. *Journal of Ecology*, 96, 514-522.
- Mac Nally, R. (1996). Hierarchical partitioning as an interpretative tool in multivariate inference. *Austral Ecol.*, 21, 224-228.
- Mac Nally, R. (2002). Multiple regression and inference in ecology and conservation biology: further comments on identifying important predictor variables. *Biodivers. Conserv.*, 11, 1397-1401.
- Mac Nally, R. & Walsh, C. (2004). Hierarchical partitioning public-domain software. *Biodivers. Conserv.*, 13, 659-660.

- Manly, B.F. (1997). *Randomization, Bootstrap and Monte Carlo Methods in Biology*. Chapman & Hall, London.
- Martin, C., Harris, F. & Norman, F. (1991). Ecophysiological responses of C3 forbs and C4 grasses to drought and rain on a tallgrass prairie in northeastern Kansas. *Bot. Gaz.*, 152, 257-262.
- Martin, T.G., Wintle, B.A., Rhodes, J.R., Kuhnert, P.M., Field, S.A., Low-Choy, S.J. *et al.* (2005). Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. *Ecol. Lett.*, 8, 1235-1246.
- McIntire, E.J.B. & Fajardo, A. (2009). Beyond description: the active and effective way to infer processes from spatial patterns. *Ecology*, 90, 46-56.
- Meyer, S.E., Quinney, D. & Weaver, J. (2006). A stochastic population model for *Lepidium papilliferum* (Brassicaceae), a rare desert ephemeral with a persistent seed bank. *Am. J. Bot.*, 93, 891-902.
- Morris, W.F., Pfister, C.A., Tuljapurkar, S., Haridas, C.V., Boggs, C.L., Boyce, M.S. *et al.* (2008). Longevity can buffer plant and animal populations against changing climatic variability. *Ecology*, 89, 19-25.
- Newman, E.I. (1973). Competition and diversity in herbaceous vegetation. *Nature*, 244, 310.
- Nicholson, A. (1954). An outline of the dynamics of animal populations. *Aust. J. Zool.*, 2, 9-65.
- Nowicki, P., Bonelli, S., Barbero, F. & Balletto, E. (2009). Relative importance of density-dependent regulation and environmental stochasticity for butterfly population dynamics. *Oecologia*, 161, 227-239.

- Noy-Meir, I. (1973). Desert ecosystems: environment and producers. *Annu. Rev. Ecol. Syst.*, 4, 25-51.
- Putman, R., Langbein, J., Hewison, A.M. & Sharma, S. (1996). Relative roles of density-dependent and density-independent factors in population dynamics of British deer. *Mammal Rev.*, 26, 81-101.
- Saila, S., Martin, B., Ferson, S., Ginzburg, L. & Millstein, J. (1991). *Demographic Modeling of Selected Fish Species with RAMAS*. EPRI-EN-7178, Electric Power Research Inst., Palo Alto, CA; Applied Biomathematics, Inc., Setauket, NY.
- Schoener, T. (1983). Field experiments on interspecific competition. *Am. Nat.*, 122, 240-285.
- Sibly, R.M. & Hone, J. (2002). Population growth rate and its determinants: an overview. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.*, 357, 1153-1170.
- Steen, H. & Haydon, D. (2000). Can population growth rates vary with the spatial scale at which they are measured? *J. Anim. Ecol.*, 69, 659-671.
- Suttle, K.B., Thomsen, M.A. & Power, M.E. (2007). Species interactions reverse grassland responses to changing climate. *Science*, 315, 640-642.
- Tilman, D. (1990). Constraints and tradeoffs: toward a predictive theory of competition and succession. *Oikos*, 58, 3-15.
- Tilman, D. (1988). *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton.
- Turchin, P. (2003). *Complex Population Dynamics: A Theoretical/Empirical Synthesis (MPB-35)*. Princeton University Press, Princeton.
- Turner, C.L. & Knapp, A.K. (1996). Responses of a C4 Grass and Three C3 Forbs to

Variation in Nitrogen and Light in Tallgrass Prairie. *Ecology*, 77, 1738.

Tylianakis, J., Didham, R., Bascompte, J. & Wardle, D. (2008). Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.*, 11, 1351-1363.

Walther, G., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C. *et al.* (2002). Ecological responses to recent climate change. *Nature*, 416, 389-395.

Wiegand, T. & Moloney, K.A. (2004). Rings, circles, and null-models for point pattern analysis in ecology. *Oikos*, 104, 209-229.

Wills, C., Condit, R., Foster, R. & Hubbell, S. (1997). Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. *Proc. Natl. Acad. Sci. U.S.A.*, 94, 1252-1257.

Table 2.1 Information about the three chart quadrat datasets used in this study

Site	Location	Vegetation	Mean annual temperature	Mean annual precipitation	Growing season	Composition covariates	Number of quadrats	Sampling period
Jornada, NM	32.6° N, 106.7° W	Desert grassland	14°C	246 mm (summer-fall rain)	July – October	forb density, grass cover, shrub cover	69	1915-1950
Dubois, ID	44.2° N, 112.2° W	Sagebrush steppe	6°C	325 mm (winter-spring snow and rain)	April – July	forb density, grass cover, shrub cover	26	1926-1957
Hays, KS	38.8° N, 99.3° W	Mixed-grass prairie	12°C	580 mm (spring-summer rain)	April – September	forb density, shortgrass cover, midgrass cover	47	1937-1972

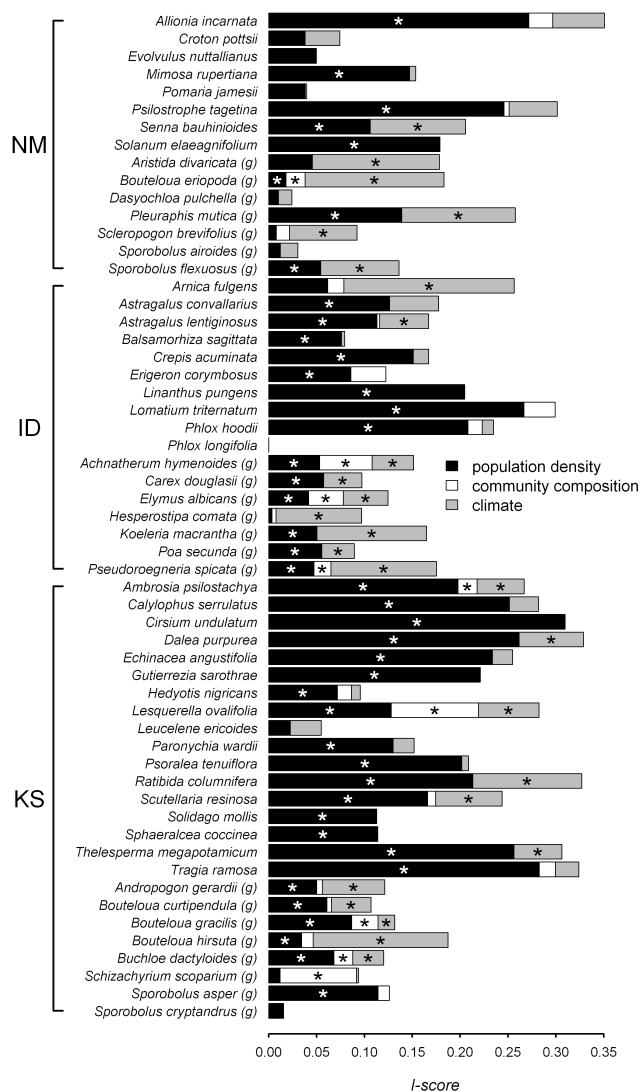


Figure 2.1 Proportion of variation in population growth rate explained by variations in population density (black bars), community composition (white bars), and climate (gray bars) for species ordered by site and growth form. Shown are corrected *I-scores*, the proportion of variability in growth rates explained above and beyond chance alone. Sites are New Mexico (NM), Idaho (ID), and Kansas (KS). A “(g)” next to species name denotes grasses. Asterisks in bars denote significant Z-scores ($P < 0.05$) from randomizations for each factor.

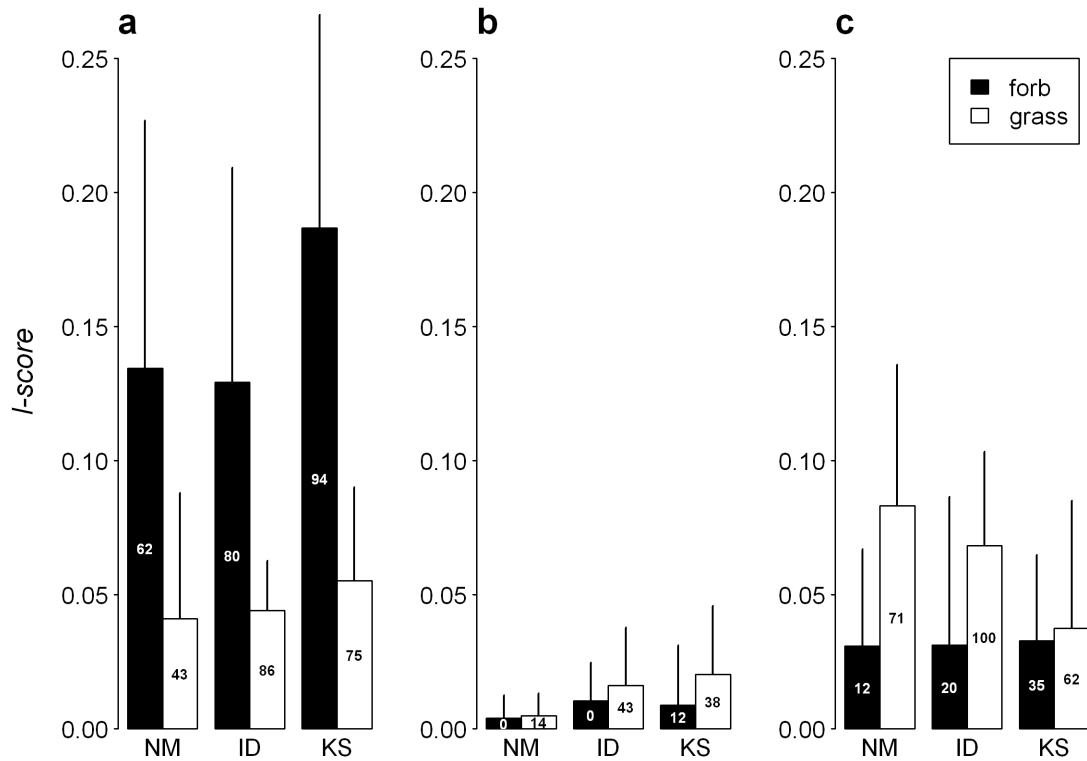


Figure 2.2 Corrected *I*-scores (mean + SE) averaged over species by growth form and site for: a) population density, b) community composition, and c) climate. Numbers in bars denote percent of species, by site and growth form, with significant Z-scores ($P < 0.05$) from randomizations for each factor.

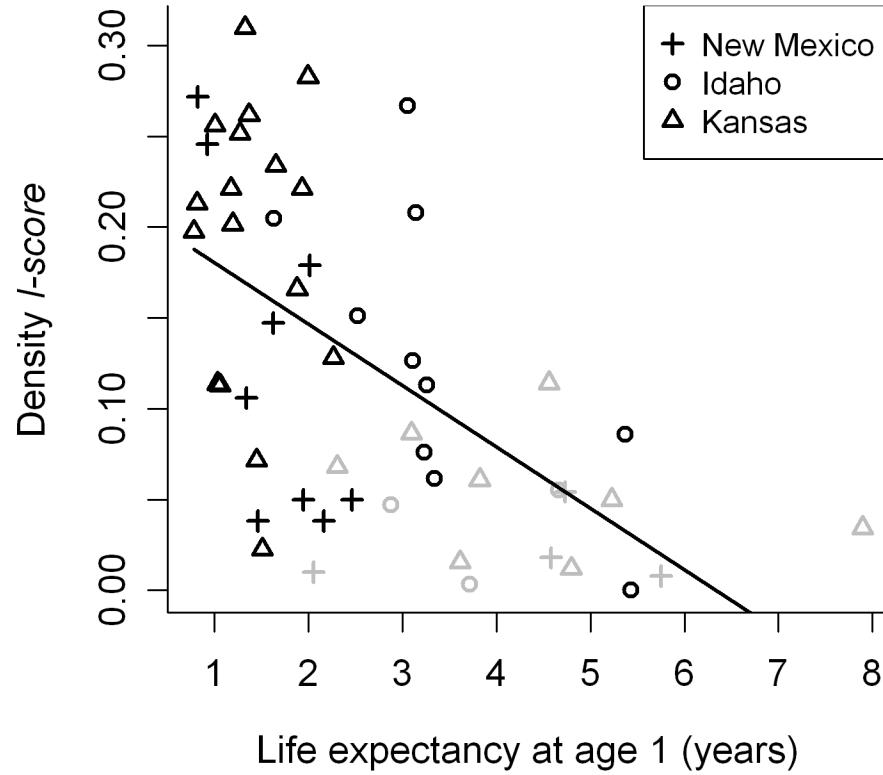


Figure 2.3 Linear regression ($P < 0.01$) between species' life expectancies at age 1 and corrected density *I-scores*. Forbs and grasses are represented by black and gray symbols, respectively.

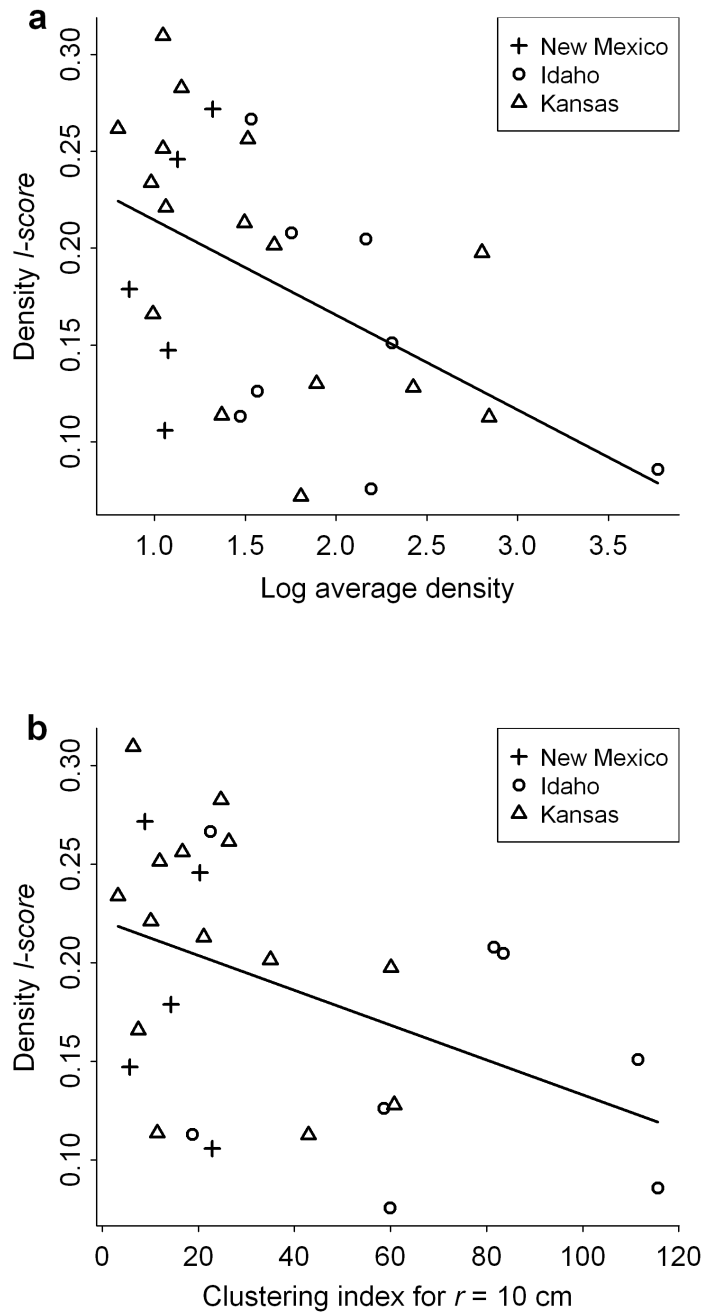


Figure 2.4 Linear regression of: a) logged average density ($P < 0.01$), and b) clustering ($P < 0.05$ at $r = 10$) on corrected density *I*-scores for all forb species with significant density *I*-scores. Larger clustering index scores indicate more clustering.

CHAPTER 3

MAPPED PLANT COMMUNITY TIME SERIES, DUBOIS, ID, 1923-1973¹**INTRODUCTION**

Chart quadrats are permanent 1-m² quadrats in which all individual plants are identified and mapped using a pantograph (Hill 1920). Under Clements' (1907) influence, many range experiment stations across the western U.S. began mapping quadrats between the 1910's and the 1930's and continued annual censuses for decades. We previously published a chart quadrat dataset from southern mixed-prairie in western Kansas (Adler et al. 2007). The dataset described here, from sagebrush steppe in eastern Idaho, is the second in the series, with Chihuahuan desert (Wright and Van Dyne 1976), Sonoran desert (Canfield 1957), and northern mixed-prairie datasets (Olson et al. 1985) in preparation. Taken together, these datasets represent some of the most widespread plant communities in the Western U.S. Combining chart quadrat data from multiple sites may enable users to test ecological theory and describe patterns across species and ecosystems or environmental gradients.

Chart quadrat data are unique in several ways. First, the fine spatial resolution of the maps makes it possible to track the fates of individual plants, providing detailed demographic information that is rare for herbaceous plants (Lauenroth and Adler 2008). Such demographic information is often essential for understanding community and ecosystem patterns and will be important for predicting how plant populations and communities respond to climate change. Second, the maps enable analysis of spatial

¹ Coauthored by Luke Zachmann, Corey Moffet, and Peter Adler.

patterns and interactions among plants in local neighborhoods (e.g., Purves and Law 2002). Third, the long-term nature of the data can reveal temporal variability in demographic performance and spatial interactions. And finally, these data are available for all species in the community.

Chart quadrat data have a rich history in ecological research. The Idaho dataset, for example, has been used to evaluate the effect of climate and grazing on range vegetation (Pechanec et al. 1937, Craddock and Forsling 1938, Blaisdell 1958). A second focus of chart quadrat analyses has been the survival of perennial plants (Canfield 1957, Wright and Van Dyne 1976, West et al. 1979). These survival analyses and subsequent re-analyses (Sarukhán and Harper 1973, Fair et al. 1999) contributed much to our current knowledge about the demography of herbaceous perennial plants (White 1985).

Contemporary chart quadrat analyses take advantage of Geographic Information Systems and modern statistical techniques. For example, we have automated analyses of the survival, life expectancies, and life spans of perennial grassland plants (Lauenroth and Adler 2008). Such demographic data can then be used to address additional research questions: Can life history traits predict the vulnerability of forb populations to increased climate variability (Dalglish et al. *unpublished manuscript*)? Does climate variability affect coexistence (Adler et al. 2006, Adler et al. *unpublished manuscript*)? What is the relative influence of biotic and abiotic drivers of population dynamics (Adler and HilleRisLambers 2008, Zachmann et al. *unpublished manuscript*)? Do patterns of species diversity differ in space and time (Adler and Lauenroth 2003, Adler 2004, Adler and Levine 2007)?

This dataset contains the following data and data formats: 1) image files (*.tif) of

the original, scanned maps; 2) the digitized maps in shapefile format; 3) a tabular version of the entire dataset (a table with no spatial information except an x,y coordinate for each individual plant record); 4) a species list, containing information on plant growth forms and shapefile geometry type; 5) quadrat information, such as grazing information and original quadrat names (the names as they appear in the original, scanned maps); 6) an inventory of the years each quadrat was sampled; 7) monthly precipitation, temperature, and snowfall records; and 8) counts of annuals in the quadrats.

METADATA

CLASS I. DATA SET DESCRIPTORS

A. Data set identity: Mapped plant community time series, Dubois, ID, 1923-1973

B. Data set identification code: Not applicable (N/A)

C. Data set description

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2. Abstract: This historical dataset consists of a series of permanent 1-m² quadrats located on the sagebrush steppe in eastern Idaho, USA. The key

aspect of the data is that during each growing season, all individual plants in each quadrat were identified and mapped. The combination of a long time-series with full spatial resolution allows analyses of demographic processes and intra- and interspecific interactions among individual plants. This dataset contains the following data and data formats: 1) the digitized maps in shapefile format; 2) a tabular version of the entire dataset (a table with no spatial information except an x,y coordinate for each individual plant record); 3) a species list, containing information on plant growth forms and shapefile geometry type; 4) quadrat information, such as grazing information; 5) an inventory of the years each quadrat was sampled; 6) monthly precipitation, temperature, and snowfall records; and 7) counts of annuals in the quadrats.

D. Key words: *sagebrush steppe; plant community; demography; species interactions; climate; Geographic Information Systems (GIS); Idaho*

CLASS II. RESEARCH ORIGIN DESCRIPTORS

A. Overall project description: We digitized the Idaho dataset as part of a National Science Foundation project to digitize, distribute, and analyze four historical chart quadrat datasets.

B. Specific subproject description

1. Site description: The U.S. Sheep Experiment Station is located on the upper Snake River plain at the foothills of the Centennial Mountains, approximately 6 miles north of Dubois, ID. The station headquarters sit on 27,930 acres of ARS land at elevations ranging from 5,500 to 6,000 feet.

Permanent quadrats were established on station land in 1923.

a. Site type: N/A

b. Geography: The study site is located approximately 6 miles north of Dubois, ID (44.2° N, 112.2° W)

c. Habitat: Blaisdell (1958), Craddock and Forsling (1938), and Pechanec et al. (1937) describe the vegetation at the site. The vegetation type is sagebrush steppe, though the cover of vegetation is discontinuous with numerous patches of bare ground and exposed rock. The most conspicuous components of the vegetation where the quadrats are located are the shrubs, including threetip sagebrush (*Artemisia tripartita*), spineless horsebrush (*Tetradymia canescens*), antelope bitterbrush (*Purshia tridentata*), and yellow rabbitbrush (*Chrysothamnus viscidiflorus*). Beneath and between these shrubs are grasses, such as bluebunch wheatgrass (*Pseudoroegneria spicata*), needle and thread (*Hesperostipa comata*), Indian ricegrass (*Achnatherum hymenoides*), Sandberg bluegrass (*Poa secunda*), and other wheatgrass species (*Elymus spp.*), as well as forbs, such as arrowleaf balsamroot (*Balsamorhiza sagittata*), tapertip hawksbeard (*Crepis acuminata*), tailcup lupine (*Lupinus caudatus*), and mountain dandelion (*Agoseris taraxacifolia*). The forbs are more diverse than the grasses, but their distribution on the landscape is much less uniform.

d. Geology: In relatively recent geologic time (during Pliocene and Pleistocene epochs), a lava flow covered the station range and surrounding territory, creating a flat to gently rolling surface (Craddock and Forsling

1938, Blaisdell 1958). The soil is a fine basaltic, sandy loam a few inches to several feet in depth with frequent exposed reefs of basalt (Pechanec et al. 1937, Craddock and Forsling 1938). These soils are relatively low in nitrogen and organic matter, but have undergone little leaching as a result of the low precipitation (Blaisdell 1958).

e. Watersheds/hydrology: There is an absence of surface water except where an intermittent stream crosses the northwest corner of the sheep station (Craddock and Forsling 1938).

f. Site history: Most of the quadrats (18 of 26 total) are located in small fenced areas in which grazing was excluded. The other quadrats (the remaining 8) are located in two 80-acre “paddocks.” The paddocks are located within a short distance of the station headquarters and are fairly similar with respect to plant cover, topography, and soil. Historically, a different system of grazing was applied to each paddock.

g. Climate: Mean annual precipitation is 325 mm and mean annual temperature is 6°C. Craddock and Forsling (1938), as well as Blaisdell (1958), provide an excellent review of the climate at the site. Temperatures are generally favorable for plant growth from early April until late October. Somewhat less than half the precipitation falls as snow during the late fall and winter; rains are most common in spring and summer. During late spring, and especially through the summer months, rainless periods are common, during which the soil becomes thoroughly dried for weeks at a time.

2. Experimental or sampling design

a. Design characteristics: 26 permanent quadrats were located in both grazed and ungrazed units. The two grazed paddocks contain 4 quadrats each. The four ungrazed units contain a total of 18 quadrats (anywhere from 4 to 6 quadrats per enclosure).

b. Permanent plots: See quadrat information data file in IV.

c. Data collection: Quadrats were mapped annually from 1923 to 1957 and once again in 1973, with some exceptions (see the quadrat sampling schedule data file in IV). Quadrats were mapped late in the growing season each summer (generally between late May and early July, depending on the year).

3. Research Methods

a. Field / laboratory: The data were collected in the field using pantographs (Hill 1920), a mechanical device used to make scale drawings. The original paper maps were first scanned and then stored as TIFF image files. These images were then converted into shapefiles by heads-up digitization in ArcGIS. For a complete digitization protocol, contact Peter Adler. Monthly climate data was obtained from the National Climatic Data Center (<http://www.ncdc.noaa.gov/oa/ncdc.html>).

b. Instrumentation: Pantographs, scanners, and computers running ArcGIS, Python, and R.

c. Taxonomy and systematics: Originally assigned plant names were corrected for synonyms based on the USDA Plants Database

(<http://plants.usda.gov/>).

d. Permit history: N/A

e. Legal / organizational requirements: None.

CLASS III. DATA SET STATUS AND ACCESSIBILITY

A. Status

1. Latest Update: 11 November 2009.

2. Latest Archive date: 11 November 2009.

3. Metadata status: The metadata are complete and up to date.

4. Data verification: After the initial digitizing phase, all maps were checked for completeness and accuracy. In addition, time series of species abundances were generated to identify outlier maps. Luke Zachmann made the following changes to the original (digitized) GIS dataset (stored shapefiles) between 2007 and 2008:

- 1) Shapefiles were rotated to have a consistent North-South vertical orientation;
- 2) Species names for large unlabeled or obviously mislabeled polygons were assigned based on species names assigned to the same features in previous or later years;
- 3) Shapefiles were processed using R and Python scripts to cut polygons and point features at the map borders and remove any small polygon “slivers” generated accidentally while digitizing;
- 4) Other miscellaneous corrections based on visual inspection of the

shapefiles;

5) All species were then classified as either density- or cover-type features. All forbs, with the exception of two species, show up as point features. All grasses as polygon features. All shrubs show up as both point and polygon features. Small, young shrubs without significant canopy cover were mapped in the field as point features, so they remain point-features in the shapefiles. The canopies of larger shrubs were mapped in the field, so these show up as polygon features in the shapefiles. Many of these larger shrubs have stems that are mapped as points features, but linked to the canopy using a common identifier in the shapefile attribute table;

6) Plant names were corrected for synonyms based on the USDA PLANTS Database (<http://plants.usda.gov/>). Some questionable, infrequent taxa lumped into "spp." categories; and

7) x,y coordinates of each polygon centroid were added to shapefile attribute tables.

B. Accessibility

1. Storage location and medium: The data are available from the Ecological Society of America's data archives. Duplicate copies of the data are being stored at Utah State University and on the Knowledge Network for Biocomplexity (KNB).

2. Contact person: Peter Adler, Department of Wildland Resources and the Ecology Center, Utah State University, Logan, UT, 84322 USA,

peter.adler@usu.edu.

3. Copyright restrictions: None.

4. Proprietary restrictions: None, although we would like to hear how the data are being used (e.g., for what research questions or teaching exercises).

5. Costs: None.

CLASS IV. DATA STRUCTURAL DESCRIPTORS

SPATIAL DATA

A. Data Set File

1. Identity: shapefiles.zip

2. Size: 51,097,147 bytes.

3. Format and storage mode: Shapefiles compressed and submitted together in a zipped directory.

4. Header information: The fields within the attribute tables for each shapefile are described in the tabular data, see "Records of all individual plants mapped as points" and "Records of all individual plants mapped as polygons" for the density and cover shapefiles, respectively.

B. Variable information: This is a zipped directory, containing a series of subdirectories, each corresponding to one quadrat. Within the subdirectories are individual shapefiles for each year that the quadrat was mapped. File names reflect the quadrat (Q#), year (YY), and geometry (C or D) of each shapefile. C refers to "cover" while D refers to "density." Features in cover files (generally grasses and shrubs) are mapped as polygons, while features in density files (generally forbs and small shrubs, mapped shrub stems, and shrub

seedlings) are mapped as points. Each feature in these shapefiles has attributes that describe the individual, such as species name and location within the quadrat. The size of this zip file is 48.7 Mb.

RECORDS OF ALL INDIVIDUAL PLANTS MAPPED AS POINTS

A. Data Set File

- 1. Identity:** allrecords_density.csv
- 2. Size:** 40,837 records, 3,161,211 bytes.
- 3. Format and storage mode:** ASCII text, comma separated. No compression scheme was used.
- 4. Header information:** The first row of the file contains the variable names below.

B. Variable information: See Table 3.1.

RECORDS OF ALL INDIVIDUAL PLANTS MAPPED AS POLYGONS

A. Data Set File

- 1. Identity:** allrecords_cover.csv
- 2. Size:** 80,233 records, 7,425,597 bytes.
- 3. Format and storage mode:** ASCII text, comma separated. No compression scheme was used.
- 4. Header information:** The first row of the file contains the variable names below.

B. Variable information: See Table 3.2.

QUADRAT INFORMATION

A. Data Set File

1. **Identity:** quad_info.csv
2. **Size:** 26 records, 593 bytes.
3. **Format and storage mode:** ASCII text, comma separated. No compression scheme was used.
4. **Header information:** The first row of the file contains the variable names below.

B. Variable information: See Table 3.3.

QUADRAT SAMPLING SCHEDULE

A. Data Set File

1. **Identity:** quad_inventory.csv
2. **Size:** 29 records, 2957 bytes.
3. **Format and storage mode:** ASCII text, comma separated. No compression scheme was used.
4. **Header information:** The first row of the file contains the variable names below.

B. Variable information: See Table 3.4.

SPECIES LIST

A. Data Set File

1. **Identity:** species_list.csv
2. **Size:** 97 records, 3,686 bytes.
3. **Format and storage mode:** ASCII text, comma separated. No compression scheme was used.

4. Header information: The first row of the file contains the variable names below.

B. Variable information: See Table 3.5.

MONTHLY TEMPERATURES

A. Data Set File

1. Identity: monthly_mean_temp.csv

2. Size: 83 records, 5,800 bytes.

3. Format and storage mode: ASCII text, comma separated. No compression scheme was used.

4. Header information: The first row of the file contains the variable names below.

B. Variable information: See Table 3.6.

MONTHLY PRECIPITATION

A. Data Set File

1. Identity: total_monthly_ppt.csv

2. Size: 83 records, 5,410 bytes.

3. Format and storage mode: ASCII text, comma separated. No compression scheme was used.

4. Header information: The first row of the file contains the variable names below.

B. Variable information: See Table 3.7.

MONTHLY SNOWFALL

A. Data Set File

1. Identity: total_monthly_sno.csv

2. Size: 84 records, 4,199 bytes.

3. Format and storage mode: ASCII text, comma separated. No compression scheme was used.

4. Header information: The first row of the file contains the variable names below.

B. Variable information: See Table 3.8.

COUNTS OF ANNUALS

A. Data Set File

1. Identity: annuals_counts_v3.csv

2. Size: 1361 records, 48,259 bytes.

3. Format and storage mode: ASCII text, comma separated. No compression scheme was used.

4. Header information: The first row of the file contains the variable names below.

B. Variable information: See Table 3.9.

CLASS V. SUPPLEMENTAL DESCRIPTORS

A. Data acquisition

1. Data forms: N/A

2. Location of completed data forms: The original chart quadrat data sheets are archived at the U.S. Sheep Experiment Station.

3. Data entry verification procedures: See II.3.

B. Quality assurance/quality control procedures: The procedures described above (II.3) ensured accurate transfer of information from the original to the digital maps and correction of some errors introduced at the original mapping stage. Nevertheless, future

users must become familiar enough with the raw data provided here to determine whether or not it is appropriate for their particular research question.

C. Related materials: Zip files containing the scanned images of the original maps (TIFF format, *.tif) may be found at the Knowledge Network for Biocomplexity: <http://knb.ecoinformatics.org/index.jsp/>.

D. Computer programs and data processing algorithms: N/A

E. Archiving

1. Archival Procedures: Data files and associated metadata have been archived on the Knowledge Network for Biocomplexity (KNB). The current link for the metadata is (<http://knb.ecoinformatics.org/knb/metacat?action=read&qformat=knb&sessionid=8BF741E0A743813407453AF34173CA30&docid=lzachmann.6.36>). Data files may also be retrieved from this site.

2. Redundant Archival Sites: Data on the KNB is automatically replicated onto the Long-Term Ecological Research Network site (<http://metacat.lternet.edu/knb/index.jsp>).

F. Publications and results: subset the literature cited

G. History of data set usage

1. Data request history: N/A

2. Data set update history: N/A

3. Review history: N/A

4. Questions and comments from secondary users: N/A

LITERATURE CITED

- Adler, P., and J. HilleRisLambers. 2008. The influence of climate and species composition on the population dynamics of ten prairie forbs. *Ecology* 89:3049-3060.
- Adler, P. B. 2004. Neutral models fail to reproduce observed species-area and species-time relationships in Kansas grasslands. *Ecology* 85:1265-1272.
- Adler, P. B., J. HilleRisLambers, P. C. Kyriakidis, Q. Guan, and J. M. Levine. 2006. Climate variability has a stabilizing effect on the coexistence of prairie grasses. *Proceedings of the National Academy of Sciences of the United States of America* 103:12793-12798.
- Adler, P. B., and W. K. Lauenroth. 2003. The power of time: spatiotemporal scaling of species diversity. *Ecology Letters* 6:749-756.
- Adler, P. B., and J. M. Levine. 2007. Contrasting relationships between precipitation and species richness in space and time. *Oikos* 116:221-232.
- Adler, P. B., W. R. Tyburczy, and W. K. Lauenroth. 2007. Long-term mapped quadrats from Kansas prairie: demographic information for herbaceous plants. *Ecology* 88:2673-2673.
- Blaisdell, J. P. 1958. Seasonal development and yield of native plants on the Upper Snake River Plains and their relation to certain climatic factors. *USDA Technical Bulletin* 1190:1-68.
- Canfield, R. H. 1957. Reproduction and life span of some perennial grasses of southern Arizona. *Journal of Range Management* 10:199-203.

- Clements, F. E. 1907. Plant physiology and ecology. H. Holt and Company, New York, New York, USA.
- Craddock, G. W., and C. L. Forsling. 1938. The influence of climate and grazing on spring-fall sheep range in southern Idaho. USDA Technical Bulletin 600:1-42.
- Fair, J., W. Lauenroth, and D. Coffin. 1999. Demography of *Bouteloua gracilis* in a mixed prairie: analysis of genets and individuals. *Journal of Ecology* 87:233-243.
- Hill, R. R. 1920. Charting quadrats with a pantograph. *Ecology* 1:270-273.
- Lauenroth, W. K., and P. B. Adler. 2008. Demography of perennial grassland plants: survival, life expectancy and life span. *Journal of Ecology* 96:1023-1032.
- Olson, K. C., R. S. White, and B. W. Sindelar. 1985. Response of vegetation of the Northern Great Plains to precipitation amount and grazing intensity. *Journal of Range Management* 38:357-361.
- Pechanec, J. F., G. D. Pickford, and G. Stewart. 1937. Effects of the 1934 drought on native vegetation of the Upper Snake River Plains, Idaho. *Ecology* 18:490-505.
- Purves, D. W., and R. Law. 2002. Fine-scale spatial structure in a grassland community: quantifying the plant's-eye view. *Journal of Ecology* 90:121-129.
- Sarukhán, J., and J. L. Harper. 1973. Studies on plant demography: *Ranunculus repens* L., *R. bulbosus* L. and *R. acris* L.: I. Population flux and survivorship. *Journal of Ecology* 61:675-716.
- West, N. E., K. H. Rea, and R. O. Harniss. 1979. Plant demographic studies in sagebrush-grass communities of southeastern Idaho. *Ecology* 60:376-388.
- White, J. 1985. The census of plants in vegetation. Pages 33–88 in J. White, editor. The population structure of vegetation. Dr. W. Junk Publishers, Dordrecht, The

Netherlands.

Wright, R. G., and G. M. Van Dyne. 1976. Environmental factors influencing semidesert grassland perennial grass demography. *The Southwestern Naturalist* 21:259-273.

TABLE 3.1. Records of all individual plants mapped as points

Variable name	Variable definition	Unit/Format	Storage type	Precision	Variable codes and definitions
quad	Name of the quadrat	N/A	Character	N/A	N/A
year	The year of the observation (just the last 2 digits). All observations are from the 1900's.	YY	Integer	1	N/A
OBJECTID	Identification of each record (an individual point in a shapefile) within a given quadrat in a given year. If the value in the "stem" column of the table is "Y", the point is a stem for a shrub in the cover shapefile for the same quadrat and year, and the OBJECTID for that record relates to the "stemID" in cover shapefiles and records. Most investigators will want to remove any records with "stem" = "Y" from the dataset before analysis.	N/A	Integer	N/A	N/A
species	Latin name of the plant species (<i>genus, species</i>) or other label ("unknown", for example).	N/A	Character	N/A	N/A
seedling	Indicates whether an individual was mapped as a seedling by the original surveyors.	N/A	Character	N/A	N – Age/stage of the individual is unknown Y – The individual is a seedling
stem	Indicates whether the individual is the stem of a shrub in the cover shapefiles.	N/A	Character	N/A	N – The individual is not a stem for a shrub in the cover shapefile Y – The individual is a stem for a shrub in the cover shapefile
x	Location of the record in the East-West direction within the quadrat.	m	Fixed Point	1.00E-015	N/A
y	Location of the record within the plot in the North-South direction.	m	Fixed Point	1.00E-015	N/A

TABLE 3.2. Records of all individual plants mapped as polygons

Variable name	Variable definition	Unit/Format	Storage type	Precision	Variable codes and definitions
quad	Name of the quadrat	N/A	Character	N/A	N/A
year	The year of the observation (just the last 2 digits). All observations are from the 1900's.	YY	Integer	1	N/A
SP_ID	Identification of each record (an individual polygon in a shapefile) within a given quadrat in a given year.	N/A	Integer	N/A	N/A
species	Latin name of the plant species (<i>genus, species</i>) or other label ("unknown", for example).	N/A	Character	N/A	N/A
area	Area of individual polygons	m ²	Fixed Point	1.00E-015	N/A
stemID	A non-null stemID indicates that a polygon (shrub) feature has a mapped stem in the density shapefile layer (D.shp) for the same quad and same year. The number in this field relates to the number in the "OBJECTID" field of the density shapefile for the same quadrat and year.	N/A	Character	N/A	null – the polygon has no mapped stem non-null integer – see Variable definition
x	Location of the polygon centroid in the East-West direction within the quadrat	m	Fixed Point	1.00E-015	N/A
y	Location of the polygon centroid within the plot in the North-South direction	m	Fixed Point	1.00E-015	N/A

TABLE 3.3. Quadrat information

Variable name	Variable definition	Unit/Format	Storage type	Precision	Variable codes and definitions
quadrat	Quadrat name	N/A	Character	N/A	N/A
shapefiles	Quadrat name for shapefiles: shapefiles have naming restrictions which required abbreviated versions of the original quadrat names	N/A	Character	N/A	N/A
grazing	Presence or absence of sheep grazing	N/A	Character	N/A	No – No grazing (quadrat is located inside livestock enclosure) Yes – Grazing (quadrat is located outside livestock enclosure)

TABLE 3.4. Quadrat sampling schedule

Variable name(s)	Variable definition	Unit/ Format	Storage type	Precision	Variable codes and definitions
year	The year of the observation (just the last 2 digits). All observations are from the 1900's.	YY	Integer	1	N/A
[quadrat name] (Q1, Q2, Q3, etc. See Quadrat Information data file for complete list)	Year values (YY) indicate that the named quadrat was sampled that year. NAs indicate the year specified by the "year" column was not sampled for the named quadrat.	YY	Integer	1	See Variable definition

TABLE 3.5. Species list

Variable name	Variable definition	Unit/Format	Storage type	Precision	Variable codes and definitions
species	Latin name of a plant species (<i>genus, species</i>), and miscellaneous "unknown" labels	N/A	Character	N/A	N/A
density	The total number of individuals of each species in the dataset (all quadrats and all years) mapped as points. These individuals can be found in shapefiles with file names ending "D.shp." An "NA" entry in "density" for a species indicates that it shows up only as cover-type features in cover shapefiles, which have file names ending "C.shp." Some shrub species are represented in both density and cover shapefiles.	N/A	Integer	1	See Variable definition
cover	The total number of individuals of each species in the dataset (all quadrats and all years) mapped as polygons. These individuals can be found in shapefiles with file names ending "C.shp." An "NA" entry in "cover" for a species indicates that it shows up only as density in density-type features shapefiles, which have file names ending "D.shp."	N/A	Integer	1	See Variable definition
growthForm	Classification of species by growth form. Information about species growth form was taken from the USDA PLANTS Database (http://plants.usda.gov/).	N/A	Character	N/A	forb – Perennial forbs (non-graminoid herbaceous plants) grass – Perennial graminoid shrub – Woody perennial plants unknown – unknown growth form lichen – lichen moss – moss

TABLE 3.6. Monthly temperatures

Variable name(s)	Variable definition	Unit/ Format	Storage type	Precision	Variable codes and definitions
YEAR	Calendar year in which the temperatures were recorded	YYYY	Integer	N/A	N/A
JAN, FEB, MAR, APR, MAY, JUN, JUL, AUG, SEP, OCT, NOV, DEC	Mean monthly temperature for that month, respectively	Fahrenheit	Floating Point	0.01	N/A

TABLE 3.7. Monthly precipitation

Variable name(s)	Variable definition	Unit/ Format	Storage type	Precision	Variable codes and definitions
YEAR	Calendar year in which the precipitation measurements were recorded	YYYY	Integer	N/A	N/A
JAN, FEB, MAR, APR, MAY, JUN, JUL, AUG, SEP, OCT, NOV, DEC	Total precipitation for that month, respectively	inch	Floating Point	0.01	N/A

TABLE 3.8. Monthly snowfall

Variable name(s)	Variable definition	Unit/ Format	Storage type	Precision	Variable codes and definitions
YEAR	Calendar year in which the snowfall measurements were recorded	YYYY	Integer	N/A	N/A
JAN, FEB, MAR, APR, MAY, JUN, JUL, AUG, SEP, OCT, NOV, DEC	Total precipitation for that month, respectively	inch	Floating Point	0.1	N/A

TABLE 3.9. Counts of annuals

Variable name	Variable definitions	Unit/ Format	Storage type	Precision	Variable codes and definitions
quad	Name of the quadrat	N/A	Character	N/A	N/A
year	The year of the observation (just the last 2 digits)	YY	Integer	1	N/A
species	Latin name of the plant species (genus, species) or other label ("unknown", for example)	N/A	Character	N/A	N/A
count	Number of individuals of each species in a given quadrat and year	individuals per m2	Integer	1	N/A
notes	Notes made by map surveyors in map margins	N/A	Character	N/A	2 X 50% cruise – Number of individuals of a species estimated by surveying only half of the quadrat 5 X 20% cruise – Number of individuals of a species estimated by surveying only one-fifth of the quadrat

CHAPTER 4

CONCLUSIONS

Ecology, as a discipline, is moving away from small-scale empirical observations and experiments to interdisciplinary and collaborative research at broad temporal and spatial scales (Thompson *et al.* 2001; Palmer *et al.* 2005). Making this transition successfully is going to require increased data sharing and mechanisms to enable long-term community access to data (Olson & McCord 2000; Andelman *et al.* 2004). Increased data sharing and access can improve our ability to reliably forecast ecosystem change, which in turn improves planning and decision-making (Clark *et al.* 2001).

Recognizing the importance of both sharing data and creating adequate metadata to describe its content, organization, and structure (Michener *et al.* 1997), we presented a chart quadrat dataset from Idaho in Chapter 3 of this thesis. Pulling this data together was the product of two years of effort in the lab and three decades of work in the field. The ecological value of the Idaho dataset lies in its long temporal extent, its fine spatial resolution, and in the existence of other chart quadrat datasets, one of which is already available to the public (Adler *et al.* 2007). These attributes of the data make it possible to model the influence of historical climate variability and on many co-occurring plant species (Adler *et al.* 2006; Adler & HilleRisLambers 2008), and to ask questions about ecological patterns and processes across sites and environmental gradients.

In Chapter 2 of this thesis, we used the chart quadrat data to ask a question about the relative importance of density-dependent and density-independent factors in driving population dynamics. Understanding this feature of population dynamics is one of the

oldest challenges in ecology, and may play a critical role in predicting the effects of climate change on populations. We used chart quadrat data to describe patterns in plant population regulation for 57 forb and grass species from three different ecosystems (arid desert grassland, semiarid sagebrush steppe, and subhumid mixed-grass prairie). Using a hierarchical partitioning approach, we (i) quantified the relative influence of conspecific density, heterospecific composition, and climate on temporal variation in population growth rates, and (ii) asked how the relative importance of these drivers depends on aridity, species growth form and life expectancy, and abundance and spatial patterns.

We found that density-dependence had the strongest effect on species. Climate often had a significant effect, but its strength depended on growth form. Community composition rarely explained significant variation in growth rates. The relative importance of density, composition, and climate did not vary among sites, but was related to species' life histories: compared to forbs, grasses were more sensitive to climate drivers. Abundance and spatial clustering were negatively correlated with the importance of density dependence, suggesting that local rarity is a consequence of self-limitation. Our results show that interspecific interactions play a weaker role than intraspecific interactions and climate variability in regulating plant populations.

Understanding the relative influence of density, composition, and climate on population growth may help prioritize management of high-risk populations. Species with strong direct responses to climate, like the grasses in our analysis, may be particularly sensitive to climate change. Species only loosely regulated by density-dependent processes may also be at greater risk of chance extinction (Ginzburg *et al.* 1990; Saila *et al.* 1991). The importance of intraspecific density-dependence in our data

highlights the need to understand how changes in climate variables might affect self-limitation, especially for rare species. On the other hand, our results suggest that for many plant species it may be reasonable to ignore interactions with other plant species in bioclimate envelope models. Finally, the high proportion of variation in growth rates unexplained by our density, composition and climate covariates emphasizes the potential importance of other drivers of population dynamics, such as herbivory, disturbance, and disease.

REFERENCES

- Adler, P. & HilleRisLambers, J. (2008). The influence of climate and species composition on the population dynamics of ten prairie forbs. *Ecology*, 89, 3049-3060.
- Adler, P.B., HilleRisLambers, J., Kyriakidis, P.C., Guan, Q. & Levine, J.M. (2006). Climate variability has a stabilizing effect on the coexistence of prairie grasses. *Proc. Natl. Acad. Sci. U.S.A.*, 103, 12793-12798.
- Adler, P.B., Tyburczy, W.R. & Lauenroth, W.K. (2007). Long-term mapped quadrats from Kansas prairie: demographic information for herbaceous plants. *Ecology*, 88, 2673-2673.
- Andelman, S.J., Bowles, C.M., Willig, M.R. & Waide, R.B. (2004). Understanding environmental complexity through a distributed knowledge network. *BioScience*, 54, 240-246.
- Clark, J.S., Carpenter, S.R., Barber, M., Collins, S., Dobson, A., Foley, J.A. *et al.* (2001). Ecological Forecasts: An Emerging Imperative. *Science*, 293, 657-660.
- Ginzburg, L.R., Ferson, S. & Akcakaya, H.R. (1990). Reconstructibility of density

dependence and the conservative assessment of extinction risks. *Conserv. Biol.*, 4, 63-70.

Michener, W.K., Brunt, J.W., Helly, J.J., Kirchner, T.B. & Stafford, S.G. (1997).

Nongeospatial Metadata for the Ecological Sciences. *Ecol. Appl.*, 7, 330-342.

Olson, R.J. & McCord, R.A. (2000). Archiving ecological data and information. In:

Ecological Data: Design, Management and Processing (eds Michener, W. & Brunt, J.). Blackwell Science, Malden, Massachusetts, pp. 117-141.

Palmer, M.A., Bernhardt, E.S., Chornesky, E.A., Collins, S.L., Dobson, A.P., Duke, C.S.

et al. (2005). Ecological science and sustainability for the 21st century. *Front. Ecol. Environ.*, 3, 4-11.

Saila, S., Martin, B., Ferson, S., Ginzburg, L. & Millstein, J. (1991). *Demographic*

Modeling of Selected Fish Species with RAMAS. EPRI-EN-7178, Electric Power Research Inst., Palo Alto, CA; Applied Biomathematics, Inc., Setauket, NY.

Thompson, J.N., Reichman, O.J., Morin, P.J., Polis, G.A., Power, M.E., Sterner, R.W. *et*

al. (2001). Frontiers of Ecology. *BioScience*, 51, 15-24.

APPENDIX

16 November 2009

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Dear Aldo Compagnoni,

I am in the process of preparing my thesis in the Department of Wildland Resources at Utah State University. I defend on Wednesday, December 9, 2009. I hope to graduate in the spring of 2010.

I am requesting your permission to include the attached material as shown. I will include acknowledgments to your work as shown. You will be cited as a co-author on the title page of each chapter of which you are a co-author. Please advise me of any changes you require.

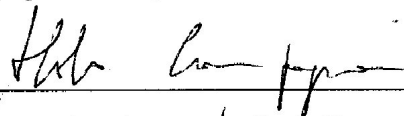
Please indicate your approval of this request by signing in the space provided, attaching any other form or instruction necessary to confirm permission. If you have any questions, please call me at the number above.

Thank you for your cooperation,
Luke Zachmann

I, Aldo Compagnoni, hereby give permission to Luke Zachmann to reprint the following material in his thesis,

Zachmann, L., A. Compagnoni, M. Hooten, D. Peters, P. Adler. 2010. Chapter 2: Density-dependence and climate, more than community composition, drive plant population dynamics. Master's Thesis. Utah State University, Logan, UT.

Signed



Date

11/16/2009

16 November 2009

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Dear Mevin Hooten,

I am in the process of preparing my thesis in the Department of Wildland Resources at Utah State University. I defend on Wednesday, December 9, 2009. I hope to graduate in the spring of 2010.

I am requesting your permission to include the attached material as shown. I will include acknowledgments to your work as shown. You will be cited as a co-author on the title page of each chapter of which you are a co-author. Please advise me of any changes you require.

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Zachmann, L., A. Compagnoni, M. Hooten, D. Peters, P. Adler. 2010. Chapter 2: Density-dependence and climate, more than community composition, drive plant population dynamics. Master's Thesis. Utah State University, Logan, UT.

Signed 

Date 11/17/09

16 November 2009

Luke Zachmann Utah State University College of Natural Resources 5230 Old Main Hill
Logan, UT 84322-5230 612.859.4983

Dear Debra Peters,

I am in the process of preparing my thesis in the Department of Wildland Resources at Utah State University. I defend on Wednesday, December 9, 2009. I hope to graduate in the spring of 2010.

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Signed



Date November 19, 2009

17 November 2009

Luke Zachmann
 Utah State University
 College of Natural Resources
 5230 Old Main Hill
 Logan, UT 84322-5230
 612.859.4983

Dear Dr. Gregory Lewis,

I am in the process of preparing my thesis in the Department of Wildland Resources at Utah State University. I defend on Wednesday, December 9, 2009. I hope to graduate in the spring of 2010.

I am requesting your permission, as the research leader of the U.S. Sheep Experiment Station, to include the attached material as shown. I will include acknowledgments to Dr. Corey Moffet's work as shown. He will be cited as a co-author on the title page of each chapter of which he is a co-author. Please advise me of any changes you require.

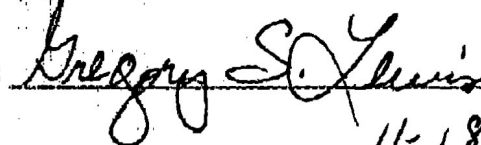
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Date

11-18-09