DRIVERS OF PLANT POPULATION DYNAMICS IN THREE ARID TO SUBHUMID ECOSYSTEMS

by

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ABSTRACT

Drivers of Plant Population Dynamics in Three Arid to Subhumid Ecosystems

by

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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.
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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.

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CHAPTER 2

DENSITY-DEPENDENCE AND CLIMATE, MORE THAN COMMUNITY COMPOSITION, DRIVE PLANT POPULATION DYNAMICS

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

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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

\[
 r_{jt} = \log \left( \frac{N_{jt}}{N_{jt-1}} \right) \tag{1}
\]

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

$$r = f\left\{\text{group, lagged density, community composition, climate, } \varepsilon\right\}$$  \hspace{1cm} (2)

where the variable $\text{lagged density}$ represents an endogenous feedback, while the other three variables represent known exogenous influences: $\text{group}$ is a categorical variable for a spatial location effect, $\text{community composition}$ is a site-specific set of predictors that describe the density and cover of heterospecifics in the quadrat, and $\text{climate}$ 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). $\varepsilon$ 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,

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

where $\beta_0$ is the intercept, $G_k$ is the vector of dummy-coded group covariates from $k = 1, \ldots, g$ groups, $\beta_G$ is the vector of coefficients, and $N_{ikt-1}$ is lagged density for observations $i = 1, \ldots, n$ in group $k$ at time $t-1$ for each species; a “composition” model,

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

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 $\beta_H$ is the vector of coefficients; and a “climate” model,

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

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 $\beta_C$ 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:

$R^2$(density) vs. $R^2$(intercept only), $R^2$(density, composition) vs. $R^2$(composition), $R^2$(density, climate) vs. $R^2$(climate), $R^2$(density, composition, climate) vs. $R^2$(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*<sub>null</sub>) for each species. We subtracted the mean of these null *I*-scores from the uncorrected, observed *I*-scores (*I*<sub>obs</sub>) from the original HP run

\[
\text{Corrected } I \text{ score} = I_{\text{obs}} - \overline{I}_{\text{null}} \quad (6)
\]

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-score ≥ 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; 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


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1490-1508.


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

<table>
<thead>
<tr>
<th>Site</th>
<th>Location</th>
<th>Vegetation</th>
<th>Mean annual temperature</th>
<th>Mean annual precipitation</th>
<th>Growing season</th>
<th>Composition covariates</th>
<th>Number of quadrats</th>
<th>Sampling period</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jornada, NM</td>
<td>32.6° N, 106.7° W</td>
<td>Desert grassland</td>
<td>14°C</td>
<td>240 mm (summer-fall rain)</td>
<td>July – October</td>
<td>forb density, grass cover, shrub cover</td>
<td>69</td>
<td>1915-1950</td>
</tr>
<tr>
<td>Dubois, ID</td>
<td>44.2° N, 112.2° W</td>
<td>Sagebrush steppe</td>
<td>8°C</td>
<td>325 mm (winter-spring snow and rain)</td>
<td>April – July</td>
<td>forb density, grass cover, shrub cover</td>
<td>26</td>
<td>1926-1957</td>
</tr>
<tr>
<td>Hays, KS</td>
<td>38.8° N, 99.3° W</td>
<td>Mixed-grass prairie</td>
<td>12°C</td>
<td>580 mm (spring-summer rain)</td>
<td>April – September</td>
<td>forb density, shortgrass cover, midgrass cover</td>
<td>47</td>
<td>1937-1972</td>
</tr>
</tbody>
</table>
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.
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

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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 (Dalgleish 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**

1. **Principal Investigators**:

Luke Zachmann, Department of Wildland Resources and the Ecology Center, Utah State University, Logan, UT 84322, USA

Corey Moffet, Research Rangeland Scientist, US Department of Agriculture–Agricultural Research Service, US Sheep Experiment Station, Dubois, ID 83423, USA

Peter Adler, Department of Wildland Resources and the Ecology Center, Utah State University, Logan, UT 84322, USA

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 6ºC. 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 exclosure).

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


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
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,
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


Netherlands.

TABLE 3.1. Records of all individual plants mapped as points

<table>
<thead>
<tr>
<th>Variable name</th>
<th>Variable definition</th>
<th>Unit/Format</th>
<th>Storage type</th>
<th>Precision</th>
<th>Variable codes and definitions</th>
</tr>
</thead>
<tbody>
<tr>
<td>quad</td>
<td>Name of the quadrat</td>
<td>N/A</td>
<td>Character</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>year</td>
<td>The year of the observation (just the last 2 digits). All observations are from the 1900's.</td>
<td>YY</td>
<td>Integer</td>
<td>1</td>
<td>N/A</td>
</tr>
<tr>
<td>OBJECTID</td>
<td>Identification of each record (an individual point in a shapefile) within a given quadrat in a given year. If the value in the &quot;stem&quot; column of the table is &quot;Y&quot;, 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 &quot;stemID&quot; in cover shapefiles and records. Most investigators will want to remove any records with &quot;stem&quot; = &quot;Y&quot; from the dataset before analysis.</td>
<td>N/A</td>
<td>Integer</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>species</td>
<td>Latin name of the plant species (genus, species) or other label (&quot;unknown&quot;, for example).</td>
<td>N/A</td>
<td>Character</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>seedling</td>
<td>Indicates whether an individual was mapped as a seedling by the original surveyors.</td>
<td>N/A</td>
<td>Character</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>stem</td>
<td>Indicates whether the individual is the stem of a shrub in the cover shapefiles.</td>
<td>N/A</td>
<td>Character</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>x</td>
<td>Location of the record in the East-West direction within the quadrat.</td>
<td>m</td>
<td>Fixed Point</td>
<td>1.00E-015</td>
<td>N/A</td>
</tr>
<tr>
<td>y</td>
<td>Location of the record within the plot in the North-South direction.</td>
<td>m</td>
<td>Fixed Point</td>
<td>1.00E-015</td>
<td>N/A</td>
</tr>
</tbody>
</table>
### TABLE 3.2. Records of all individual plants mapped as polygons

<table>
<thead>
<tr>
<th>Variable name</th>
<th>Variable definition</th>
<th>Unit/Format</th>
<th>Storage type</th>
<th>Precision</th>
<th>Variable codes and definitions</th>
</tr>
</thead>
<tbody>
<tr>
<td>quad</td>
<td>Name of the quadrat</td>
<td>N/A</td>
<td>Character</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>year</td>
<td>The year of the observation (just the last 2 digits). All observations are from the 1900's.</td>
<td>YY</td>
<td>Integer</td>
<td>1</td>
<td>N/A</td>
</tr>
<tr>
<td>SP_ID</td>
<td>Identification of each record (an individual polygon in a shapefile) within a given quadrat in a given year.</td>
<td>N/A</td>
<td>Integer</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>species</td>
<td>Latin name of the plant species (<em>genus, species</em>) or other label (&quot;unknown&quot;, for example).</td>
<td>N/A</td>
<td>Character</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>area</td>
<td>Area of individual polygons</td>
<td>m²</td>
<td>Fixed Point</td>
<td>1.00E-015</td>
<td>N/A</td>
</tr>
<tr>
<td>stemID</td>
<td>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 &quot;OBJECTID&quot; field of the density shapefile for the same quadrat and year.</td>
<td>N/A</td>
<td>Character</td>
<td>N/A</td>
<td>null – the polygon has no mapped stem, non-null integer – see Variable definition</td>
</tr>
<tr>
<td>x</td>
<td>Location of the polygon centroid in the East-West direction within the quadrat</td>
<td>m</td>
<td>Fixed Point</td>
<td>1.00E-015</td>
<td>N/A</td>
</tr>
<tr>
<td>y</td>
<td>Location of the polygon centroid within the plot in the North-South direction</td>
<td>m</td>
<td>Fixed Point</td>
<td>1.00E-015</td>
<td>N/A</td>
</tr>
<tr>
<td>Variable name</td>
<td>Variable definition</td>
<td>Unit/Format</td>
<td>Storage type</td>
<td>Precision</td>
<td>Variable codes and definitions</td>
</tr>
<tr>
<td>---------------</td>
<td>---------------------</td>
<td>-------------</td>
<td>--------------</td>
<td>-----------</td>
<td>-------------------------------</td>
</tr>
<tr>
<td>quadrat</td>
<td>Quadrat name</td>
<td>N/A</td>
<td>Character</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>shapefiles</td>
<td>Quadrat name for shapefiles: shapefiles have naming restrictions which required abbreviated versions of the original quadrant names</td>
<td>N/A</td>
<td>Character</td>
<td>N/A</td>
<td>N/A</td>
</tr>
</tbody>
</table>
| grazing       | Presence or absence of sheep grazing | N/A | Character | N/A | **No** – No grazing (quadrat is located inside livestock exclosure)  
**Yes** – Grazing (quadrat is located outside livestock exclosure) |
TABLE 3.4. Quadrat sampling schedule

<table>
<thead>
<tr>
<th>Variable name(s)</th>
<th>Variable definition</th>
<th>Unit/Format</th>
<th>Storage type</th>
<th>Precision</th>
<th>Variable codes and definitions</th>
</tr>
</thead>
<tbody>
<tr>
<td>year</td>
<td>The year of the observation (just the last 2 digits). All observations are from the 1900's.</td>
<td>YY</td>
<td>Integer</td>
<td>1</td>
<td>N/A</td>
</tr>
<tr>
<td>[quadrat name]</td>
<td>Year values (YY) indicate that the named quadrat was sampled that year. NAs indicate the year specified by the &quot;year&quot; column was not sampled for the named quadrat.</td>
<td>YY</td>
<td>Integer</td>
<td>1</td>
<td>See Variable definition</td>
</tr>
<tr>
<td>Variable name</td>
<td>Variable definition</td>
<td>Unit/Format</td>
<td>Storage type</td>
<td>Precision</td>
<td>Variable codes and definitions</td>
</tr>
<tr>
<td>---------------</td>
<td>---------------------</td>
<td>-------------</td>
<td>--------------</td>
<td>-----------</td>
<td>------------------------------</td>
</tr>
<tr>
<td>species</td>
<td>Latin name of a plant species (<em>genus</em>, <em>species</em>), and miscellaneous &quot;unknown&quot; labels</td>
<td>N/A</td>
<td>Character</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>density</td>
<td>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 &quot;D.shp.&quot; An &quot;NA&quot; entry in &quot;density&quot; for a species indicates that it shows up only as cover-type features in cover shapefiles, which have file names ending &quot;C.shp.&quot; Some shrub species are represented in both density and cover shapefiles.</td>
<td>N/A</td>
<td>Integer</td>
<td>1</td>
<td>See Variable definition</td>
</tr>
<tr>
<td>cover</td>
<td>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 &quot;C.shp.&quot; An &quot;NA&quot; entry in &quot;cover&quot; for a species indicates that it shows up only as density in density-type features shapefiles, which have file names ending &quot;D.shp.&quot;</td>
<td>N/A</td>
<td>Integer</td>
<td>1</td>
<td>See Variable definition</td>
</tr>
</tbody>
</table>
| 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>
<thead>
<tr>
<th>Variable name(s)</th>
<th>Variable definition</th>
<th>Unit/Format</th>
<th>Storage type</th>
<th>Precision</th>
<th>Variable codes and definitions</th>
</tr>
</thead>
<tbody>
<tr>
<td>YEAR</td>
<td>Calendar year in which the temperatures were recorded</td>
<td>YYYY</td>
<td>Integer</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>JAN, FEB, MAR, APR, MAY, JUN, JUL, AUG, SEP, OCT, NOV, DEC</td>
<td>Mean monthly temperature for that month, respectively</td>
<td>Fahrenheit</td>
<td>Floating Point</td>
<td>0.01</td>
<td>N/A</td>
</tr>
</tbody>
</table>
TABLE 3.7. Monthly precipitation

<table>
<thead>
<tr>
<th>Variable name(s)</th>
<th>Variable definition</th>
<th>Unit/Format</th>
<th>Storage type</th>
<th>Precision</th>
<th>Variable codes and definitions</th>
</tr>
</thead>
<tbody>
<tr>
<td>YEAR</td>
<td>Calendar year in which the precipitation measurements were recorded</td>
<td>YYYY</td>
<td>Integer</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>JAN, FEB, MAR, APR, MAY, JUN, JUL, AUG, SEP, OCT, NOV, DEC</td>
<td>Total precipitation for that month, respectively</td>
<td>inch</td>
<td>Floating Point</td>
<td>0.01</td>
<td>N/A</td>
</tr>
</tbody>
</table>
TABLE 3.8. Monthly snowfall

<table>
<thead>
<tr>
<th>Variable name(s)</th>
<th>Variable definition</th>
<th>Unit/Format</th>
<th>Storage type</th>
<th>Precision</th>
<th>Variable codes and definitions</th>
</tr>
</thead>
<tbody>
<tr>
<td>YEAR</td>
<td>Calendar year in which the snowfall measurements were recorded</td>
<td>YYYY</td>
<td>Integer</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>JAN, FEB, MAR, APR, MAY, JUN, JUL, AUG, SEP, OCT, NOV, DEC</td>
<td>Total precipitation for that month, respectively</td>
<td>inch</td>
<td>Floating Point</td>
<td>0.1</td>
<td>N/A</td>
</tr>
<tr>
<td>Variable name</td>
<td>Variable definitions</td>
<td>Unit/ Format</td>
<td>Storage type</td>
<td>Precision</td>
<td>Variable codes and definitions</td>
</tr>
<tr>
<td>---------------</td>
<td>---------------------------------------------------------------------------------------</td>
<td>--------------</td>
<td>--------------</td>
<td>-----------</td>
<td>------------------------------</td>
</tr>
<tr>
<td>quad</td>
<td>Name of the quadrat</td>
<td>N/A</td>
<td>Character</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>year</td>
<td>The year of the observation (just the last 2 digits)</td>
<td>YY</td>
<td>Integer</td>
<td>1</td>
<td>N/A</td>
</tr>
<tr>
<td>species</td>
<td>Latin name of the plant species (genus, species) or other label (&quot;unknown&quot;, for example)</td>
<td>N/A</td>
<td>Character</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>count</td>
<td>Number of individuals of each species in a given quadrat and year</td>
<td>individuals per m2</td>
<td>Integer</td>
<td>1</td>
<td>N/A</td>
</tr>
</tbody>
</table>

Notes made by map surveyors in map margins

**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
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-limitedness. 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


APPENDIX
16 November 2009

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

Dear Aldo Compagnoni,

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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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Luke Zachmann

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Date 11-18-09