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Direct and Indirect Effects of Climate Change on Plant Populations and Communities in Sagebrush Steppe

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DIRECT AND INDIRECT EFFECTS OF CLIMATE CHANGE ON PLANT

POPULATIONS AND COMMUNITIES IN SAGEBRUSH STEPPE

by

Andrew R. Kleinhesselink

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

of

DOCTOR OF PHILOSOPHY

in

Ecology

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UTAH STATE UNIVERSITY
Logan, Utah

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ABSTRACT

Direct and Indirect Effects of Climate Change on Plant Communities

by

Andrew R. Kleinhesselink, PhD Ecology

Utah State University, 2017

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

Forecasting the effects of climate change on plant and animal populations is a high priority in ecology. We studied the effects of climate on plant populations through the use of observational and experimental data, as well as analytical models. Our research questions were: (1) Do the effects of interannual climate variation on the population growth rates of widespread species show a coherent pattern across gradients of mean annual climate? (2) How well can population models fit to observational data predict the response of populations to field experiments that manipulate climate? And (3) does niche overlap between competitors predict the magnitude of competition-mediated indirect effects in mechanistic resource competition models? To test the first question, we assessed how interannual variation in climate affected the abundance of big sagebrush (*Artemisia tridentata*) at 131 monitoring sites across its range. We found that years of above average temperature increased sagebrush abundance at cold sites, but decreased sagebrush abundance at hot sites. This pattern indicates that sagebrush distribution may be limited by hot and cold temperatures at the extremes of its distribution. We addressed

our second research question by fitting statistical models to over 25 years of observational data on the performance of four dominant plant species in a sagebrush steppe community. We then experimentally manipulated soil moisture in this community and tested how well the statistical models fit to observational data could predict species' responses to the experimental treatments. In two out of four species, we found that including climate effects in our models helped us predict the population-level responses to the experiment. Moreover, effects of historical soil moisture variation on vital rates were generally consistent with the effects of drought and irrigation treatments. Our results provide some evidence that observational data can be used to predict species' responses to climate change in the future. We addressed our third question by simulating environmental change in analytical models of resource competition and quantifying the size of direct and competition-mediated indirect effects that resulted. We showed that the magnitude of indirect effects increased as the niche overlap between competitors increased.

(194 pages)

PUBLIC ABSTRACT

Direct and Indirect Effects of Climate Change on Plant Communities

Andrew R. Kleinhesselink

Rapid climate change presents humanity with a number of big problems. Foremost among these is the sad fact that the climate we will pass on to our children will likely be nothing like the climate that we inherited from our parents. Ecologists have collected solid evidence that climate change has already begun to affect the living things around us and the ecosystems humans depend on. Unfortunately, predicting the future effects of climate change on life on earth is not easy. We focused on three research goals as part of an effort to improve our ability to predict how plants and animals will be affected by climate change.

First, we studied the effects of yearly variation in temperature on an important shrub from the western US: sagebrush. We found that sagebrush abundance increased in cold places after relatively hot years, but decreased in warm places after hot years. In contrast, we did not see the same pattern for precipitation—sagebrush actually decreased in dry places in response to wet years and increased in wet places in response to wet years. This pattern hints that sagebrush is limited more by temperature at the edges of its range than by precipitation.

Second, we studied how the growth and survival of thousands of individual grasses and shrubs varied from year to year at field site in eastern Idaho. Using this information, we developed a model that related plant growth and survival in each year to the amount of rain and snow that year. Next we set up an experiment to directly control

the amount of water available to plants. We ran the experiment for five years and then we used the plant growth and survival model we built from the observational data to predict how each species would respond in the experiment. We found that we could predict two out of the four species responses to the experiment. Overall we found that the direction that species responded to the experimental treatments was generally the same as how they responded to natural precipitation.

Third, we used mathematical models to examine the indirect effects of climate change on competing plants. Climate change can affect a species directly by decreasing or increasing its population growth rate. But climate change can also affect its competitors. If competition is strong then it is possible that an environmental change with positive direct effects on the first species, but that also causes positive direct effects on its competitor, can actually be a net negative for the first species. This complicated back and forth among competitors can make predicting the effects of climate change difficult. Fortunately, we show that some mathematical properties of species competition can help predict when indirect effects are large. One benefit of this work will be helping researchers figure out when the response of species to climate change can be safely predicted from single species population models rather than complicated multi-species models.

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Andrew Kleinhesselink

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CHAPTER 1

INTRODUCTION

Global climate change has already had large effects on populations and distributions of species across the globe (Parmesan and Yohe 2003, Chen et al. 2011) and the shifting distributions and abundances of species will have important consequences for the future of biodiversity (Pachauri et al. 2015). To anticipate the effects of climate change, we need detailed species-specific models that quantify how climate affects populations, and enough confidence in these models to use them to predict the future (Ehrlén and Morris 2016). But achieving this goal is an immense challenge.

The problem of estimating climate change impacts on populations can be tackled with species distribution models, observational data on the temporal dynamics of populations and controlled climate change experiments. Each approach has its own limitations—distribution models lack population dynamics and usually cannot predict changes in population abundance (Ehrlén and Morris 2015). Population models fit to temporal data require long time series to detect the effects of climate (Teller et al. 2016), and such data are usually only available for a limited set of research sites and species. Moreover, both species distribution models and population models usually rely on observational data to infer the effects of climate on populations. However, any inference based on correlations and observations alone is susceptible to spurious relationships between climate and species distribution and performance (Dormann 2007, Hilborn 2016). Climate change experiments solve some of these problems but come with their own issues: climate change experiments are expensive, are sometimes impossible to

conduct at large enough scales, and are not always good analogues for the effects of

natural climate change (Wolkovich et al. 2012).

Another challenge confronting any would-be predictor of the effects of climate

change is the complexity of each species' interactions with other organisms including

predators, pathogens and competitors (Tylianakis et al. 2008, Adler et al. 2012).

Biotically-mediated indirect effects may alter population responses to environmental

change (Jiang and Morin 2004, Adler et al. 2009), sometimes even reversing the direct

effects of environmental change on a given species (Suttle et al. 2007).

The need for better predictions of the effects of climate change is especially great

for the dominant plants of sagebrush steppe in western North America. Sagebrush

dominated habitats are among the most widely distributed in North America (Kuchler

1970) and the growth of sagebrush (*Artemisia spp.*) appears to be sensitive to climate

(Perfors et al. 2003, Dalgleish et al. 2010, Apodaca 2013)**.** Moreover, sagebrush steppe

provides critical habitat for many endemic species, including some threatened and iconic

species such as the greater sage-grouse (*Centrocercus urophasianus*; Coates et al. 2016).

Species distribution models for sagebrush indicate that the area these ecosystems span

may be greatly diminished due to climate change in the future (Neilson et al. 2005,

Bradley 2010, Schlaepfer et al. 2012, Still and Richardson 2015). Climate change in this

region will lead to warmer temperatures, less snow cover, increased evaporation and

changes in precipitation (Garfin et al. 2014). Throughout most of this region this will

likely lead to a decrease in soil moisture during the growing season which could reduce

the growth of sagebrush and other plants (Schlaepfer et al. 2012). Unfortunately, many

of the limitations inherent in using species distribution models, long-term observational

data and experimental approaches to predict the effects of climate change on populations

apply to the sagebrush steppe as well. Moreover, the potential for indirect effects

between the closely competing plant species in sagebrush steppe are also great. Thus we

are left with a high degree of uncertainty about the ultimate effects of climate change.

We believe that predicting the effects of climate change on sagebrush steppe

communities will benefit from considering data from multiple spatial scales and through

the use of long term observational data, experiments and theory. Moreover, before we

have confidence in any regional predictions of the effects of climate change we should

also evaluate whether we can predict the population responses of the plant species that

inhabit the sagebrush steppe at much smaller scales. Finally, getting a better theoretical

grasp on the potential for indirect effects to modify the direct effects of climate change on

plant communities will be critical to increasing our confidence in predictions for this and

all other communities.

Towards the goal of improving our understanding of climate effects on plant

populations in sagebrush steppe, we have three main research goals: first we hope to

demonstrate how repeat measurements of species abundance over time across a species

range can be used to predict that species' sensitivity to the long-term impacts of climate

change. We applied this approach to thousands of observations of big sagebrush

(*Artemisia tridentata*) cover from over one hundred monitoring sites in order to estimate

this species' sensitivity to annual climate variation in hot, cold, wet and dry parts of its

range. Our primary research question was whether the population response to annual

climate variation at each site would be consistent with the position of that site across

large-scale climate gradients. We hypothesize that populations at cold sites respond

positively to above average temperatures, while populations at warm sites respond negatively to the same. The answer to this question will be a valuable contribution to efforts aimed at forecasting the future abundance and distribution of this species.

Our second research goal was to go beyond simply predicting the effects of climate change on plant populations, but also to test quantitative predictions with an experiment. Our primary research question was whether detailed demographic models relating the growth, survival and recruitment of dominant plant species to annual variation in precipitation can be used to predict how species respond to experimental climate manipulations. We fit demographic models to observational data for four important plants of sagebrush steppe: three-tip sagebrush, (*Artemisa tripartita*), needle-and-thread, (*Hesperostipa comata*), Sandberg's bluegrass, (*Poa secunda*), and bluebunch wheatgrass, (*Pseudoroegneria spicata*). We then tested whether demographic models based on observational data could predict the response of each of these species to a five-year rain-out shelter and irrigation experiment.

Our third research objective was to use analytical models to investigate competition-mediated indirect effects of climate change. Our work builds on recent theoretical work showing that the mathematical properties that determine stable competitor coexistence in phenomenological competition models also determine the magnitude of indirect effects between species (Adler et al. 2012). However, these analyses were based on extremely abstract models. We brought this theoretical work one step closer to reality by examining indirect effects in mechanistic, rather than phenomenological, competition models. Our results will help reduce the uncertainty

associated with predicting the effects of climate change in sagebrush steppe and other plant communities.

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CHAPTER 2

SAGEBRUSH (*ARTEMISIA TRIDENTATA*) RESPONSE TO INTERANNUAL

CLIMATE VARIATION CHANGES ACROSS THE SPECIES RANGE[1]

Abstract

Understanding how annual climate variation affects population growth rates across a species' range may help us anticipate the effects of climate change on species. We predict that populations in warmer or wetter parts of a species' range should respond negatively to periods of above average temperature or precipitation, respectively, whereas populations in colder or drier areas should respond positively to periods of above average temperature or precipitation. To test this, we estimated the sensitivity of a common shrub species, big sagebrush (*Artemisia tridentata*), to annual climate variation across its range. Our analysis includes 7934 observations of year-to-year change in sagebrush cover or production from 131 monitoring sites in western North America. We coupled these observations with seasonal weather data for each site and analyzed the effects of spring through fall temperatures and fall through spring accumulated precipitation on annual changes in sagebrush abundance. Sensitivity to annual temperature variation supported our hypothesis: sagebrush responded negatively to warmer years in hotter locations but positively to warmer years in colder locations. In contrast, sensitivity to precipitation ran counter to our hypothesis: sagebrush responded negatively to above average precipitation in drier sites and positively in wetter sites. This pattern of responses suggests that patterns of regional abundance of this species may be more limited by temperature than

[1]Coauthored with Peter B. Adler.

precipitation. Our model predicts that a short-term temperature increase of 2°C would

increase sagebrush cover by a factor of 0.67 at the coldest sites and decrease cover by a

factor of 0.21 at the warmest sites. This prediction is qualitatively consistent with

predictions from species distribution models for sagebrush based on spatial occurrence

data, but it provides new mechanistic insight and produces estimates for how much and

how fast sagebrush cover may change within its range.

Introduction

Global climate change is causing species to go extinct in locations where they

once thrived and become common in areas where they never before occurred (Parmesan

and Yohe 2003, Chen et al. 2011). Changing species distributions and abundances will

have profound consequences for ecosystem functioning, the spread of diseases and the

future of biodiversity on earth (Pachauri et al. 2015). To anticipate the future effects of

climate change, we need detailed species-specific understanding of how climate

determines where species will be found in the future, but also how much and how fast

their abundances will change (Ehrlén and Morris 2015).

One approach for determining how species are affected by climate is to assume

that spatial patterns of occurrence are determined by climatic constraints. This is the

assumption underlying use of species distribution models (SDMs) to project climate

change impacts in biodiversity. But using SDMs to predict how any species will respond

to climate change may be problematic. Species distributions are shaped by non-climatic

factors such as dispersal barriers, physical variables such as soil type, and stochastic

population extinction. Moreover, species may occur in areas outside of their climate

niche due to immigration or because remnant populations do not immediately go extinct

after climate change (Guisan and Thuiller 2005, Holt and Keitt 2005). Even if species occurrence does coincide with the climate niche, using occurrence alone would still be problematic for predicting the ecological impacts of climate change. Species distribution models are likely to identify as important variables which have no direct connection to individual performance or population growth rates. When projected into the future, these spurious correlations could lead to unreliable forecasts (Dormann 2007).

An alternative approach is to study changes in species abundance over time to infer how populations respond to short-term climate variation (Dalgleish et al. 2010, Chen et al. 2010, Munson et al. 2013, Lunn et al. 2016). In many ecosystems, differences in rainfall or temperature between two subsequent years may be as large as the difference in long-term average climate between two locations at opposite ends of a species range, or the difference between the climate of a site today and the projected climate of that site in the distant future (Mora et al. 2013). Studying the effects of short-term variation in climate may help us understand how long-term changes in average climate could affect populations at a local scale (Barber et al. 2000, McLaughlin et al. 2002, Maschinski et al. 2006, Bigler et al. 2007, Jenouvrier et al. 2009, Dalgleish et al. 2010, Pol et al. 2010, Chen et al. 2010, Lunn et al. 2016, Searcy and Shaffer 2016). Of course, such local-scale population studies rarely address the landscape to regional scales relevant to management.

Applying the temporal, population modeling approach at multiple locations across a species range could link it to the SDM approach and address the scaling challenge (Doak and Morris 2010, Ehrlén and Morris 2015). For example, Ettinger et al. (2011) showed that annual climate variation was more strongly correlated with growth at the

upper elevation range limit of several tree species than at their lower elevation range limit. The implication is that climate limits the growth and, by extension, the upper elevation range limit of these tree species, but that climate does not directly influence their lower elevation range limit. This mechanistic insight into the role of temperature and climate would be hidden in a purely spatial SDM approach. Similarly, temporal analyses can strengthen our confidence in the use of SDMs for prediction. For instance, Searcy and Shaffer (2016) analyzed time series of annual recruitment data from salamander populations and found that the same annual climate variables that were most influential for this local population-level process matched the long-term average climate variables identified by a SDM as being most important in controlling that species' geographic distribution.

We propose that the population response of a species to annual climate variation across its range can provide valuable insight about how that species' abundance and distribution will change in response to long-term climate change. For example, if a species is sensitive to temperature, we would expect that at the hottest parts of its range, populations will decrease after warmer than average years, whereas in colder parts of its range, populations will increase after warmer than average years (Fig. 2.1 upper plots). Such a pattern can be tested statistically by examining whether the short-term effect of a climate driver changes from positive to negative with increases in the average of that climate driver (Fig. 2.1 a middle plot). This pattern indicates a strong link between climate driver and the species' long-term abundance and distribution. On the other hand, if sensitivity to short-term climate variation is always positive or negative or is unrelated to average climate, we would conclude that while the climate variable may influence

local population dynamics, it may not play an important role in determining the species'

geographic distribution. Of course it would still be possible that long-term effects may

actually be different or even the reverse of short-term sensitivity (Suttle et al. 2007), but

we would argue that the simpler hypothesis that short-term sensitivity of species vital

rates, behavior, or population change, should be a good indicator of the direction of long-

term response (Ludwig et al. 2006).

Case study with Big Sagebrush (*Artemisia tridentata***)**

Big sagebrush is a dominant shrub found across much of western North America,

occurring from forest edges to prairies and from low elevation deserts to high elevation

mountains (Kuchler 1970). Sagebrush provides unique and critical habitat for many

endemic species of conservation concern such as the greater sage-grouse (*Centrocercus

urophasianus*) (Davies et al. 2011). Distribution models for sagebrush typically indicate

that climate change will cause large decreases in the total area suitable for sagebrush in

the future (Neilson et al. 2005, Bradley 2010, Schlaepfer et al. 2012a, Still and

Richardson 2015). Climate change could cause a decrease in snow cover and an increase

in evaporation, both of which would lead to decreased soil moisture during the growing

season and reduce sagebrush growth (Schlaepfer et al. 2012a, 2012b).

Direct evidence for the effects of short-term climate variation on sagebrush come

from a multi-year global warming experiment, analysis of sagebrush growth rings and

new remote sensing data. Harte et al. (2015) found that sagebrush cover increased

substantially in response to 20 years of artificial warming at high elevation in the

southern Rocky Mountains. This increase was linked to a longer snow-free growing

season at higher elevations with warming (Perfors et al. 2003). Likewise, Tredennick et

al. (2016) found a positive response of sagebrush cover to growing season temperature in a 30-year remote sensing dataset from southwestern Wyoming. In contrast, at lower elevation sites that are warmer and drier, sagebrush growth appears to decrease in response to warmer than average years (Poore et al. 2009, Apodaca 2013).

Complicating detection of relationships between climate and sagebrush performance is the fact that sagebrush comprises many different ecologically distinct subspecies or varieties. The three most common subspecies, mountain big sagebrush (*A. t. var. vaseyana*), basin big sagebrush (*A. t. var. tridentata*), and Wyoming big sagebrush (*A. t. var. wyomingensis*), have more or less distinct climate niches (Bonham et al. 1991, Rosentreter 2001). Mountain sagebrush is dominant where snowfall is high, basin big sagebrush is found in warmer areas with moderate amounts of rainfall, and Wyoming big sagebrush dominates the most arid regions (Rosentreter 2001). These subspecies also appear to have physiological differences related to drought adaptation (Kolb and Sperry 1999) and may have differences in phenology and temperature response as well (Hansen et al. 2008). Given these differences, subspecies may respond differently to the effects of annual climate variation.

Based on our conceptual model (Fig. 2.1), we predicted that sagebrush abundance will decrease after warmer than average years in the hottest parts of its range, whereas populations will increase after warmer than average years in the coldest sites. Similarly, if sagebrush distribution is limited by precipitation, we expected sagebrush abundance would increase after wetter than average years in the drier areas but decrease after wetter than average years in wetter areas. We also expected that sagebrush subspecies might show distinct patterns of response to annual climate variation, with Wyoming big

sagebrush showing a strong response to annual variation in water availability, whereas

mountain sagebrush, found on the cooler, wetter end of the regional climate gradient,

would show a stronger response to annual variation in temperature. Finding these patterns

would support a link between local population dynamics and the climate niche of

sagebrush and suggest that the future distribution and abundance of sagebrush will be

sensitive to climate change.

Materials and Methods

Multi-year sagebrush cover datasets

We assembled multi-year data on sagebrush cover or sagebrush production

through literature searches and by contacting rangeland and natural resource managers at

federal and state land management agencies. Only datasets that directly measured big

sagebrush (*Artemisia tridentata*) cover or production in permanent monitoring plots for at

least two consecutive years were included in the analysis. From each study, we extracted

information on the exact plot location (latitude and longitude), the year of data collection,

the plot size, the subspecies of sagebrush in the plot, the measurement type (% cover or

g/m^2 production), the measurement method (e.g. line-intercept, point intercept, visual

estimate), and any experimental treatments that affected the plots. For studies that

reported multiple plots from multiple locations we preserved plot groupings or location

identifiers as reported by the original study authors.

The complete database of sagebrush cover and production estimates included

7934 observations of annual changes in sagebrush cover from 1083 plots, in 131

locations across the western United States (Fig. 2.2; Table 2.1). The data adequately

capture the full range of climates occupied by sagebrush from cold mountains to arid

shrublands (Fig. A1) and range from sites with mean annual temperatures of 1ºC to 15ºC

and mean annual precipitation from 180 mm to 883 mm (Fig. A2). Wyoming big

sagebrush was the most common subspecies in the data (N = 2989), sagebrush that was

not identified to subspecies was the next most common (N =3824), mountain sagebrush

was the third most common (N = 871) and basin big sagebrush was the least common (N

= 250).

A complete list of the data sources and references describing methods for each

dataset are included in the supplementary information (Appendix B).

Auto-regressive model for sagebrush cover

We used a discrete time Gompertz population model to analyze the cover and

production time-series and draw inference about the effects of interannual climate

variation on sagebrush abundance (Ives et al. 2003). In this model, cover or production at

the plot or transect level in year t is dependent on cover or production in the previous

year t − 1 via the following relationship,

$$n_t = n_{t-1} exp[\quad a + (b - 1) \ ] \log n_{t-1} \tag{1}$$

where n_t is the abundance (e.g. percent cover or density) in year t, a is the

intrinsic rate of increase and b is the dependence on previous year's population

abundance. Log transforming the abundance values results in a simple linear model,

$$y_t = a + b y_{t-1} \tag{2}$$

where $y_t = \log n_t$. Importantly this model predicts a stable long-term equilibrium

abundance $\hat{y}$ for the population at

$$\hat{y} = a/(1-b). \tag{3}$$

Annual climate covariates can be incorporated in this model as simple additive effects on the log-transformed cover, y_t, during the transition from year $t-1$ to year t.

$$y_t = a + by_{t-1} + x'_{t-1} * \theta \tag{4}$$

where x_{t-1} is a vector of annual weather variables in year t and θ is a vector of coefficients describing the effects of each variable on the population growth rate.

Climate covariates

We modeled inter-annual changes in cover as a function of annual climate. For each study site, we extracted monthly historical weather data from the NASA Daymet data set (http://daymet.ornl.gov/). For data prior to 1980 we used monthly historic weather data from the monthly PRISM dataset (http://www.prism.oregonstate.edu/). For each site, we adjusted the pre-1980 PRISM data to better match the Daymet data by regressing the available Daymet data (1980-2014) against the equivalent PRISM data and then using the slope and intercept from these site specific regressions to adjust the pre-1980 PRISM values.

For each year and site with sagebrush cover data we calculated annual climate variables from the Daymet or from the adjusted PRISM datasets. We focused on growing season temperature at two different time windows: average daily maximum temperature of the spring of year t (*tmax*), and average daily maximum temperature for the spring through fall season for years -1 to -3 (*tmax_{lag}*), where *t* is the year of the current observation of sagebrush cover. Likewise, we considered seasonal water availability at two different time windows: winter and spring (Nov. to May) in year (*ppt*), and for all

months of years -1 through -3 (*ppt_{lag}*).

We evaluated three different measures of seasonal water availability: cumulative seasonal precipitation, net water balance, and standardized precipitation evapotranspiration index (SPEI). Cumulative seasonal precipitation is simply the total of monthly total precipitation (in cm) for each month during the seasonal window. Net water balance is calculated as total precipitation minus total potential evapotranspiration (in cm). We estimated potential evapotranspiration using the Hargreaves formula which takes into account monthly minimum and maximum temperatures, monthly precipitation and site latitude (Hargreaves and Samani 1985). SPEI takes a time series of net water balance values and standardizes them using the log-logistic distribution. We calculated potential evapotranspiration and SPEI in the SPEI package in R (Beguería and Vicente-Serrano 2013).

Cumulative precipitation, net water balance, spring temperature and growing season temperatures were centered by subtracting the site-specific average for the period (1984 to 2014). We also calculated the mean spring through fall monthly maximum temperature (*tmax_{avg}*) and average winter through spring precipitation (*ppt_{avg}*) for each site for the period 1984 to 2014.

We included the interaction of the two precipitation variables with long-term average precipitation (*ppt:ppt_{avg}*, *ppt_{lag}:ppt_{avg}*) and the interaction of the two temperature variables with long-term average temperature at each site (*tmax:tmax_{avg}*, *tmaxlag:tmax_{avg}*). These interaction effects are key to testing our hypothesis that annual climate effects should change systematically across gradients in average climate (Fig. 2.1). If sagebrush distribution is limited by temperature or precipitation, then we expect

to find negative interaction effects.

Statistical model

      To fit the autoregressive population model, we used a general linear mixed effects model (GLMM) implemented with the lme4 package in R (Bates et al. 2015, R Core Team 2015). Our model included random effects to reflect spatial and temporal grouping factors in the data: each unique plot or transect, location of plots, and year. Locations were designated in the original studies, but generally group plots at the scale of around 1-5 km. Year effects were unique to each location so that only plots near one another and exposed to similar conditions experienced the same year effects. We allowed the intercept of the Gompertz model to vary with each of these grouping factors. Likewise, we allowed the relationship between the previous year's abundance (y_{t-1}) and the current year's abundance (y_t) to vary with the random effect for plot, reflecting variation between plots in the strength of density dependence.

      We also allowed the intercept and slope of the Gompertz model to vary with the sagebrush subspecies type in each plot, reflecting differences in the average abundance and growth rates of each subspecies. The dataset is mainly comprised of absolute percent cover estimates (N = 7735), but there were also some datasets that reported annual production estimates for sagebrush in g per m^2 (N = 199). We fit a separate intercept and slope for each of these data types indicated by the variable *dtype*.

      Finally, we added the four annual weather variables (*ppt_lag, ppt, tmax, tmaxlag*) and their interaction with long-term average climate variables (*ppt_avg, tmax_avg*) to model the effects of climate. The full model written in **lmer** notation was,

$$y_t \sim (y_{t-1}|plot) + (1|loc) + (1|loc/year) + y_{t-1} + spp$$

$$+dtype + y_{t-1}:spp + y_{t-1}:dtype$$

$$+ppt + ppt_{lag} + \text{tmax} + \text{tmax}_{lag} + ppt:ppt_{avg}$$

$$+ppt_{lag}:ppt_{avg} + \text{tmax}:\text{tmax}_{avg} + \text{tmax}_{log}:\text{tmax}_{avg}$$

We fit separate models with each of the three seasonal water availability measures (total precipitation, net water balance or SPEI) and with untransformed and log-transformed average climate variables (*tmaxavg* and *pptavg*) resulting in six possible models. After fitting each of these models separately we compared models using Aikake Information Criteria (AIC) and chose one model with which to test our hypotheses. We judged an interaction effect between average climate and annual deviation in climate as significant with likelihood ratio tests ($P(\chi 2) < 0.05$) comparing the models with and without the interaction effect.

After fitting models to the full data set, we explored whether sagebrush subspecies responded differently to annual variation in climate by fitting separate models to data for each subspecies.

Climate change sensitivity

We used the fitted model to predict how perturbations in temperature or precipitation would affect sagebrush abundance across the sites observed in the dataset. For each site we predicted the effect of either temperatures 2ºC above average, or precipitation ten percent above average. These perturbations change the values of *tmax, tmaxlag, ppt* and *pptlag* but do not affect the values of *tmaxavg* and *pptavg*.

We generated predictions for each location without incorporating the plot,

location and year-specific random effects in the model. Predictions and bootstrapped

prediction intervals were plotted against the site mean annual temperature and mean

annual precipitation to show the direction of sagebrush climate sensitivity across its

range. We show prediction as proportional change in sagebrush abundance from baseline

abundance. Baseline abundance at each location was set as the equilibrium abundance

predicted by equation (3). We generated predictions and bootstrapped 95% confidence

intervals around predictions using the bootMer function in lme4 (Bates et al. 2015).

Results

   The best fitting model in terms of AIC included total net water balance for the

water availability measure while the worst fitting model used the standardized

evapotranspiration index (SPEI). However, all six models had AIC values within three of

the of best fitting model (five were within two), suggesting that all six models were

equivalent in terms of fit. For simplicity of interpretation, we chose to focus our analysis

on the model that used centered total precipitation in mm as a measure of annual water

availability (*ppt* and *ppt*$_{lag}$), centered average seasonal temperature in °C (*tmax* and

tmax$_{lag}$) as a measure of annual temperature, and average spring through fall maximum

temperature and average winter through spring total precipitation in m as the measures of

average local climate (*tmax*$_{avg}$ and *ppt*$_{avg}$ respectively).

   Fixed effects for measurement type (*dtype*), sagebrush subspecies (*ssp*) and their

interaction with last year's abundance were significant in affecting sagebrush cover

(Table 2.2). Using the fixed effects estimates of the model intercept (a) and the effect of

last year's abundance (b) allowed us to calculate an equilibrium abundance using

equation of 6.2%, 2.7%, 6.9%, 6.3% for cover of unidentified, basin, mountain and

Wyoming sagebrush subspecies. These equilibrium values appeared to slightly

underestimate the actual observed mean cover for each subspecies: 10.2%, 9.6%, 12.1%,

10.5% for cover of unidentified, basin, mountain and Wyoming sagebrush, respectively.

This underestimate in equilibrium cover may reflect a bias towards overestimating

density dependence in analyses of population time series (Freckleton et al. 2006).

Two of the four annual climate measures showed a significant interaction with

long-term average climate, average maximum growing season temperature in the three

years preceding sagebrush measurement (*tmax*$_{lag}$ x tmax$_{avg}$ interaction) and cumulative

annual precipitation during those years (*ppt*$_{lag}$ x *ppt*$_{avg}$ interaction; Table 2.2). The effect

of *ppt*$_{lag}$ was negative at drier sites and positive at wetter sites (Fig. 2.3c) --meaning

sagebrush cover increased after wet years in wet sites but decreased after wet years in dry

sites. The effect of *tmax*$_{lag}$ was negative at the hottest sites but positive at coldest sites--

sagebrush cover increased after warm years at cold sites, but decreased after warm years

at hot sites (Fig. 2.3d).

In contrast, the effects of spring average maximum temperature and total cool

season precipitation in the period immediately preceding sagebrush measurement (*tmax*

and *ppt*) did not interact significantly with average climate (Table 2.2; Fig. 2.3a, b).

Fitting a separate model to Wyoming big sagebrush showed a significant negative

interaction between *ppt* and *ppt*$_{avg}$, meaning the effect of *ppt* was positive at the drier sites

but negative at the wetter sites (Table A1; Fig. A3-a). The effect of *ppt*$_{lag}$ was the

opposite, negative in dry sites but neutral to positive in wetter sites (Table A1; Fig. A3-c).

A model fit just to mountain sagebrush showed a significant interaction between

tmax$_{lag}$ and tmax$_{avg}$ and a positive response to *ppt* at all sites (Table A2). Mountain

sagebrush responded positively to increased temperatures in the colder parts of its range but showed little to no response in the warmer parts of its range (Fig. A3d).

There were only observations of basin big sagebrush in the dataset, much less than the other subspecies, and none of the interaction effects were significant (Table A3; Fig. A4).

Using only the fixed effects from the model, we predicted that a 2ºC increase in spring and growing season temperature would increase sagebrush cover at the coldest sites and decrease cover at the hottest sites (Fig. 2.4). The predicted effect of a 10% increase in precipitation across all sites was an increase in sagebrush cover in the wetter sites and no change in the driest sites (Fig. 2.4). However, for both scenarios, bootstrapped 95% confidence intervals around predictions widely overlapped zero at nearly all locations across the gradient (Fig. 2.4).

Discussion

We found mixed support for our conceptual model that the response of sagebrush populations to annual climate would vary systematically across its geographic range. Sagebrush response to temperatures matched our hypothesis well, but sagebrush response to precipitation ran counter to our expectation (Fig. 2.3). A significant negative interaction effect between average growing season temperature and annual temperature deviation (Table 2.2) shows that sagebrush cover decreased in response to warmer than average years in hot sites but increased in response to warmer than average years in cold sites. This supports the idea that average growing season temperatures may broadly control where sagebrush can grow. An implication is that growing season temperature may be a good variable for modeling the future of sagebrush distributions. The data

suggest that sagebrush has a growing season temperature threshold, or climate pivot point (Munson et al. 2013), of 20ºC (corresponding to about 8ºC mean annual temperature) above which sagebrush growth is becomes increasingly limited by temperatures (Figs. 2.3d & 2.4a).

Effects on soil moisture and plant water status (Kwon et al. 2008, Schlaepfer et al. 2012c) or more direct effects on the growth and respiration of sagebrush are both potential mechanisms for the observed effect of temperature (Hansen et al. 2008). Using a model of leaf respiration and anabolic growth, Hansen et al. (2008) found an optimum growth rate for sagebrush at around 20C: above this temperature growth rates declined. Apodaca (2013) and Poore et al. (2009) both found significant negative correlations between sagebrush growth ring width and spring through summer temperatures at sites in Nevada and Colorado respectively, indicating that warm temperatures, either directly or indirectly, appear to inhibit sagebrush growth.

In colder climates, however, both experimental evidence and some observational data show that warmer temperatures can enhance sagebrush growth (Perfors et al. 2003, Harte et al. 2015, Tredennick et al. 2016). In cold regions, cold temperatures may be especially detrimental for sagebrush if they lengthen the duration of snow-cover and shorten the growing season (Harte et al. 2015).

The effects of precipitation were inconsistent with our conceptual mode for sagebrush. The interaction effect between lag precipitation and average precipitation was significantly positive (Table 2.2). This means that periods of above average precipitation had a negative effect on sagebrush in drier sites, but a positive effect in wetter sites. If we accept this result, it would suggest that low annual precipitation is not a limiting factor

for sagebrush populations at the dry edge of its range. This result could help explain cases where precipitation shows up as a weak predictor in sagebrush species distribution models (Still and Richardson 2015). However, it contradicts some other models (Bradley 2010, Schlaepfer et al. 2012a).

In the wettest sites on the precipitation gradient, we found that sagebrush should benefit from years with above average precipitation (Fig. 2.3c). In fact, there is some support for this pattern in the literature: Poore et al. (2009) found that sagebrush growth ring width increased in years with greater winter precipitation at a high elevation site with relatively high precipitation (mean annual precipitation ≈ 500 mm). Similarly, at a high elevation site with 385 mm annual precipitation, experimental watering increased sagebrush stem water potential and net photosynthesis (Loik 2007, Reed and Loik 2016). That sagebrush benefits from more water even in the wettest sites suggest that extra precipitation may not be a direct factor in limiting sagebrush distribution. Over longer time periods however, precipitation may still play a role in limiting sagebrush if it promotes competition with other species such as trees (Leffler and Caldwell 2005).

On the other extreme of the precipitation gradient, our result that sagebrush is inhibited by wet years at dry sites seems unlikely. For instance, sagebrush growth rings at relatively dry sites (mean annual precipitation = 250 to 300 mm) in Nevada were greatest in years with above average precipitation (Apodaca 2013). Likewise, in an experimental study at a dry site in Idaho (mean annual precipitation 220 mm) sagebrush cover increased in response to winter irrigation (Germino and Reinhardt 2014). However, in shallow soils at this site, winter irrigation actually did have a negative effect on sagebrush cover. Reduced soil oxygen in wetter soils may be a mechanism for this effect. Sagebrush

root growth is very sensitive to low oxygen (Lunt et al. 1973) and sagebrush has been known to die off rapidly in response to flooding (Lunt et al. 1973, Ganskopp 1986).

We saw important differences in how sagebrush subspecies responded to annual temperature and precipitation across the climate gradient. We expected precipitation would have a stronger positive effect on Wyoming big sagebrush, which grows in drier climates, while temperature would have a stronger positive effect on mountain sagebrush, which grows in colder and wetter climates. While the effects of temperature were more or less in line with our expectations (Fig. A3d, Fig. A4d), the effects of precipitation were not (Fig. A3c, Fig. A4c). Both drought adaptation and response to temperature are known to vary with sagebrush ecotypes and subspecies (Kolb and Sperry 1999, Hansen et al. 2008). The positive response of mountain sagebrush to precipitation could reflect more vulnerability in this subspecies to drought stress than Wyoming sagebrush (Kolb and Sperry 1999). Conversely, factors which make Wyoming sagebrush more tolerant of drought could reduce its tolerance of soil saturation and low soil oxygen (Lunt et al. 1973, Ganskopp 1986) and possibly cause it to be inhibited by wetter conditions-- although this would not explain why it responded positively to precipitation in the wetter sites where it was found (Fig. 2.3c).

Implications for the future of sagebrush

Species distribution models for sagebrush predict that regional warming will result in large areas of current sagebrush habitat becoming warmer than areas currently occupied by sagebrush (Neilson et al. 2005, Bradley 2010, Schlaepfer et al. 2012a, Still and Richardson 2015). One interpretation of this prediction is that sagebrush populations in these areas will no longer fall within the species' climate niche and should decline.

Likewise, warming could bring cold regions currently without sagebrush within the climate niche of sagebrush. This could make these areas more suitable for sagebrush colonization and increases in abundance (Schlaepfer et al. 2012a). The results of our analysis broadly support this projected pattern--sagebrush cover is predicted to decrease slightly in the hottest sites and increase in the coldest sites.

While our model cannot predict population extinction or colonization it does at least suggest that population growth rates will change at the warm and cold edges of sagebrush distribution in ways that would promote extinction and colonization. Even without changes in the occurrence of sagebrush, changes in the abundance of sagebrush where it already exists could have real impacts on other species and ecosystem function. For instance, the threatened greater sage-grouse requires 10-30% cover of sagebrush for winter habitat (Connelly et al. 2000). Our model predicts that before large scale shifts in sagebrush distribution become apparent, several years of anomalously warm weather could lower sagebrush cover and decrease habitat quality for this species in warmer areas and increase habitat quality in colder areas (Fig.4).

Our model leaves out numerous factors that could influence the future of sagebrush. The most obvious omissions are the effects of climate on fire and the effects of climate on sagebrush germination and seedling survival. Fires usually result in mortality of adult plants and catastrophic loss of sagebrush cover at the landscape scale (Hosten and West 1994). The probability of fires in sagebrush ecosystems is closely tied to cheatgrass (*Bromus tectorum*) invasion, which may increase with climate change (Bradley 2009, Balch et al. 2013, Compagnoni and Adler 2014). Recovery of sagebrush populations following fire requires germination and seedling survival in burned areas,

demographic processes that are both influenced by annual climate (Maier et al. 2001).

Reduced seedling survival in warmer years in hot sites could exacerbate the population-

level effects of reduced sagebrush cover we predict for those sites (Schlaepfer et al.

2014); while in colder sites, increases in mountain sagebrush recruitment in warmer years

(Maier et al. 2001) may reinforce the increases in sagebrush abundance we predict for

colder sites (Fig. 2.4). Unfortunately, our data are likely to miss the effects of climate on

these processes because the growth and survival of tiny seedlings are unlikely to have

much influence on sagebrush cover at the scale of plots and transects. We also confined

our analysis to effects of temperature during the growing season, but winter temperatures

either directly, or through their effects on snow pack, could also have importance

consequences for sagebrush (Hanson et al. 1982, Loik and Redar 2003, Schlaepfer et al.

2012b). At longer time scales, changes in the distribution of sagebrush subspecies,

hybridization between subspecies and evolutionary adaptation within populations may

give sagebrush potential to adapt to warmer temperatures. Our results indicate different

sagebrush subspecies respond differently to the effects of annual climate variation

(Tables A2-A3) -- a finding which agrees with some physiological and demographic

differences between subspecies (Harniss and McDonough 1975, Wang et al. 1997, Maier

et al. 2001, Lambrecht et al. 2007). Mountain big sagebrush cover was most strongly

influenced by variation in temperature, while Wyoming big sagebrush showed a stronger

response to precipitation. Our results suggest that mountain sagebrush may decline in

response to warmer temperatures at lower elevations. This could create an opportunity for

lower elevation subspecies, such as Wyoming and basin big sagebrush to invade higher

elevation sites. Likewise, hybridization between subspecies could allow the flow of genes

conferring local adaptation between subspecies. In experiments in Utah, basin and

Mountain big sagebrush showed strong patterns of local adaptation whereas hybrids had

high fitness where the subspecies overlapped (Wang et al. 1997, Miglia et al. 2005).

Conclusion

The challenges of understanding the effects of climate change on local population

abundance and large scale spatial distributions should not be tackled separately.

Understanding the full ecological effects of climate change will require drawing

inference from multiple data sources that span a range of temporal and spatial scales.

Towards this goal, our work presents a new statistical framework that could be used for

many species to connect the short-term effects of annual climate variability with the long-

term impacts of climate change on species' abundances and distributions.

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Tables

TABLE 2.1. Summary of datasets used in the analysis

dataset	measure type	method	no. locations	no. plots	no. obs.
BCD	cover	point intercept	3	70	130
CAMPWILLIAMS	cover	point intercept	1	81	354
ARID_LANDS	cover	cover estimate	36	92	737
BLACK_THUNDER	production	production estimate	1	18	52
GRAZING_SYSTEMS	cover	cover estimate	3	77	174
GERMINO	cover	point intercept	1	3	30
GRCAMEVE	cover	cover estimate	2	11	22
MILLSUT	cover	point intercept	1	3	34
MTHOME	cover	line intercept	1	12	107
MUNSON	cover	cover estimate	4	9	72
OCTC	cover	point intercept	1	134	2185
PARKERMT	cover	line intercept	1	4	24
PASSEY	production	weight estimates	8	16	131
REYNOLDS	cover	point intercept	7	16	116
RMBL	production	point intercept	1	1	16
SAGEMAP	cover	point intercept	24	98	98
SAGESTEP	cover	point intercept	20	248	2766
SEOR	cover	line intercept	14	25	176
WYQB	cover	cover estimate	3	165	710
Total			132	1083	7934

TABLE 2.2. Coefficients from a linear mixed effects model fit to the annual sagebrush data (n = 7934). Production indicates the difference between data estimating sagebrush cover (%) and production (g per m^2). Estimates for *a* and *b* correspond to the variables in the Gompertz population model described in 1. LRT and P(χ^2) give the likelihood ratio and p-value of the likelihood ratio test on the climate interaction effects. Climate variables are defined in the main text.

	Estimate	Std. Error	t value	LRT	P(χ^2)	
a	0.88	0.09	10.07			
b	0.52	0.02	24.87			
production	1.33	0.29	4.62			
production:b	-0.34	0.08	-4.07			
basin	-0.37	0.25	-1.48			
mountain	0.81	0.18	4.53			
Wyoming	0.42	0.14	3.12			
basin:b	-0.03	0.08	-0.37			
mountain:b	-0.39	0.05	-7.59			
Wyoming:b	-0.23	0.04	-6.19			
ppt	0.00	0.01	0.59			
ppt_lag	-0.00	0.00	-1.79			
tmax	-0.15	0.09	-1.70			
tmax_lag	0.72	0.27	2.63			
ppt:ppt_avg	-0.00	0.01	-0.03	0	0.98	
ppt_lag:ppt_avg	0.02	0.01	2.00	4.04	0.04	*
tmax:tmax_avg	0.01	0.00	1.51	2.33	0.13	
tmax_lag:tmax_avg	-0.03	0.01	-2.47	6.07	0.01	*

Figures
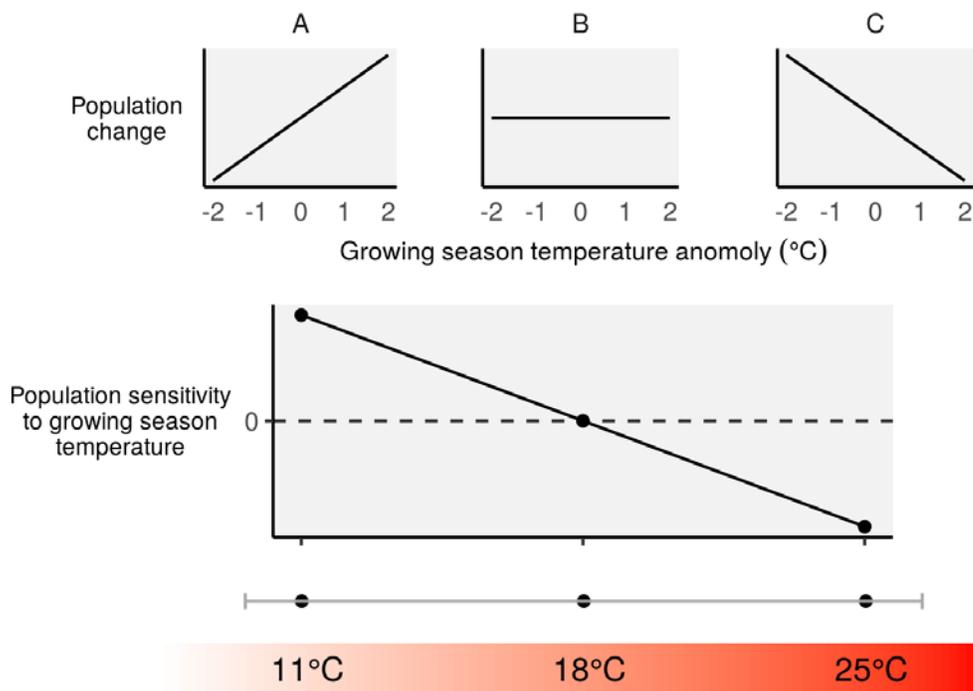
FIG. 2.1. Hypothetical effects of interannual climate variation on species' populations across its range. The bottom axis corresponds to average climate at each site. Figures in the top row show change in cover on the y-axis and annual temperature anomalies at each site on the x-axis. Years of above average temperatures are expected to increase population size at the coldest site (A), but decrease population size at the warmest site (C). The middle panel plots the sensitivities of each site against the average climate gradient. We interpret a negative slope between sensitivities to annual climate variation and average climate as support for the hypothesis that temperature controls the species' distribution. ⌈SEP⌉
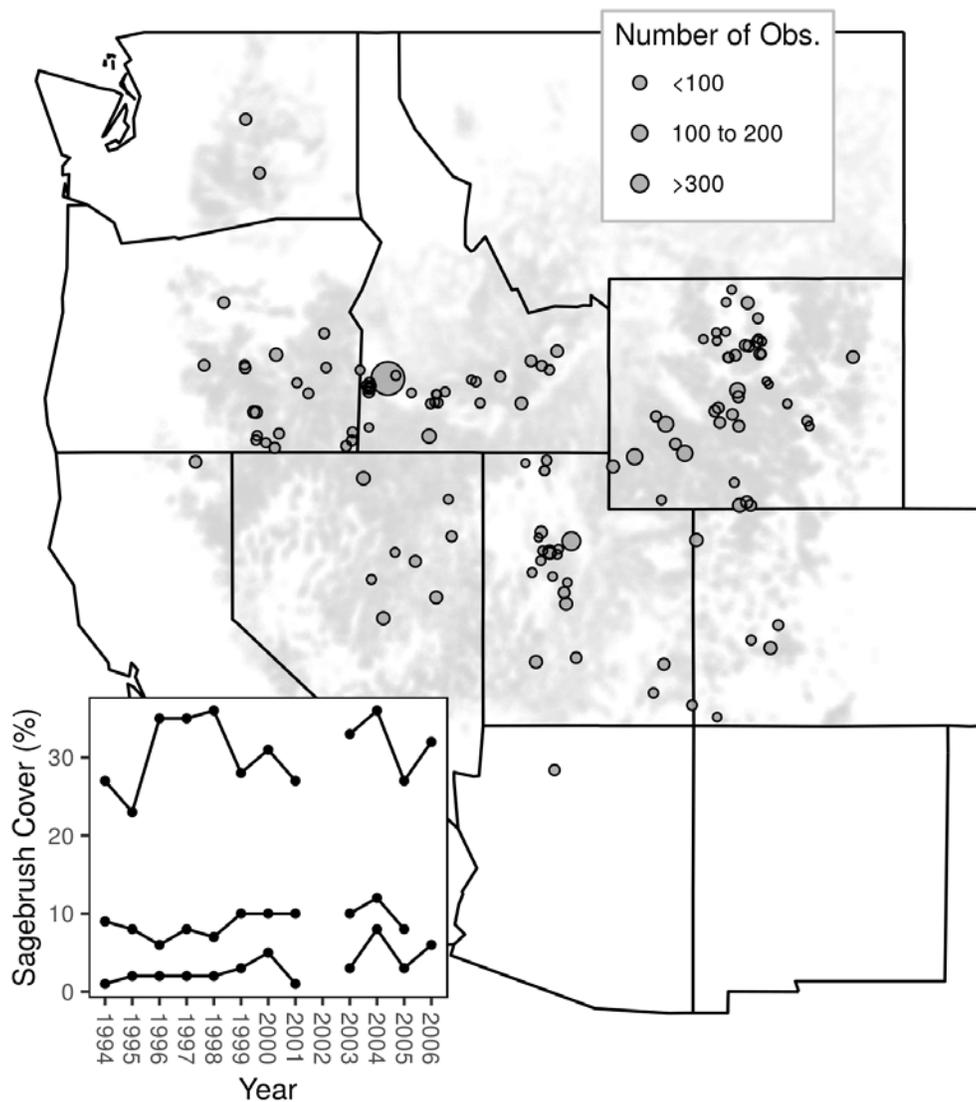
FIG. 2.2. Map of sites with multi-year sagebrush cover data in the western USA. Point size corresponds to number of observations at each site. Gray areas show the distribution of sagebrush based on the USGS SAGEMAP dataset (http://sagemap.wr.usgs.gov/). Inset shows an example of multi-year sagebrush cover data from three monitoring plots at Camp Williams, Utah. ⌞SEP⌟
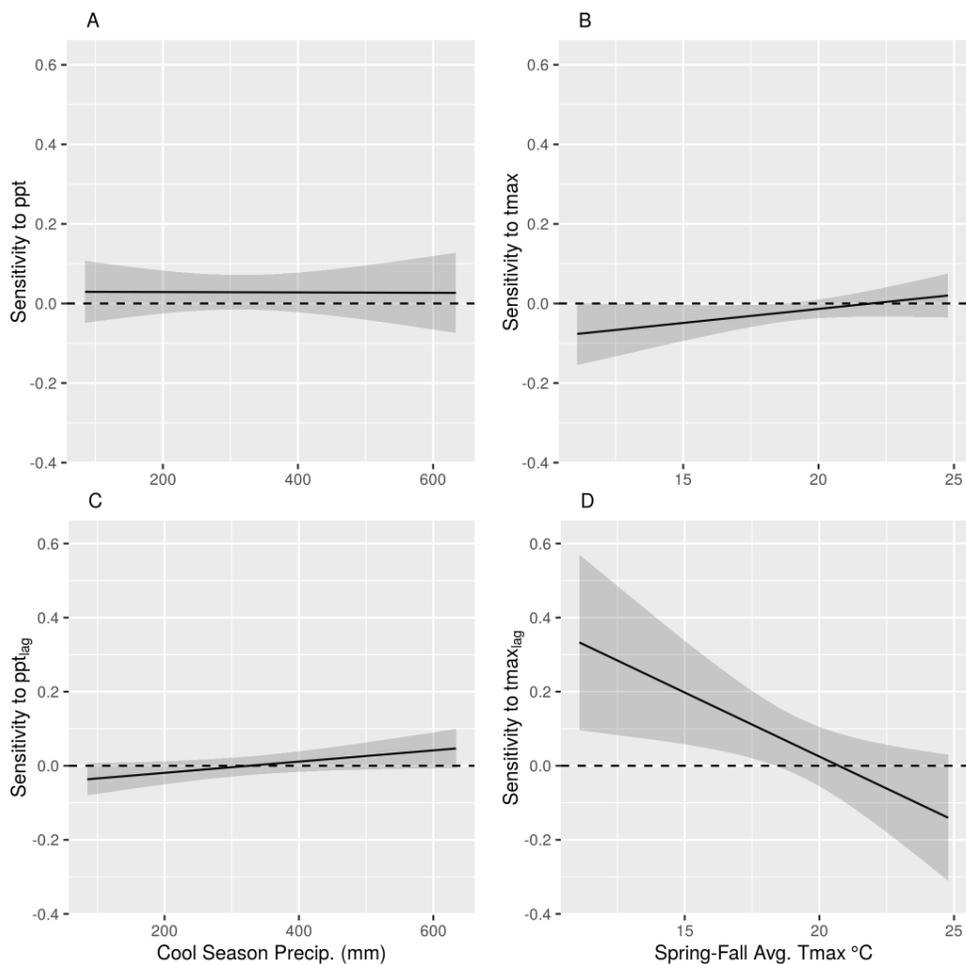
FIG. 2.3. Sensitivity of sagebrush abundance to annual climate covariates plotted against average site climate. Sensitivity is defined as the log change in sagebrush abundance produced by a 10 cm increase in precipitation (A, C) or a 1°C increase in temperature (B, D). Effects below zero indicate where above average temperatures or precipitation would decrease population size, while effects above zero indicate where above average annual temperature or precipitation would increase population size. Gray areas show 95% confidence intervals. SEP
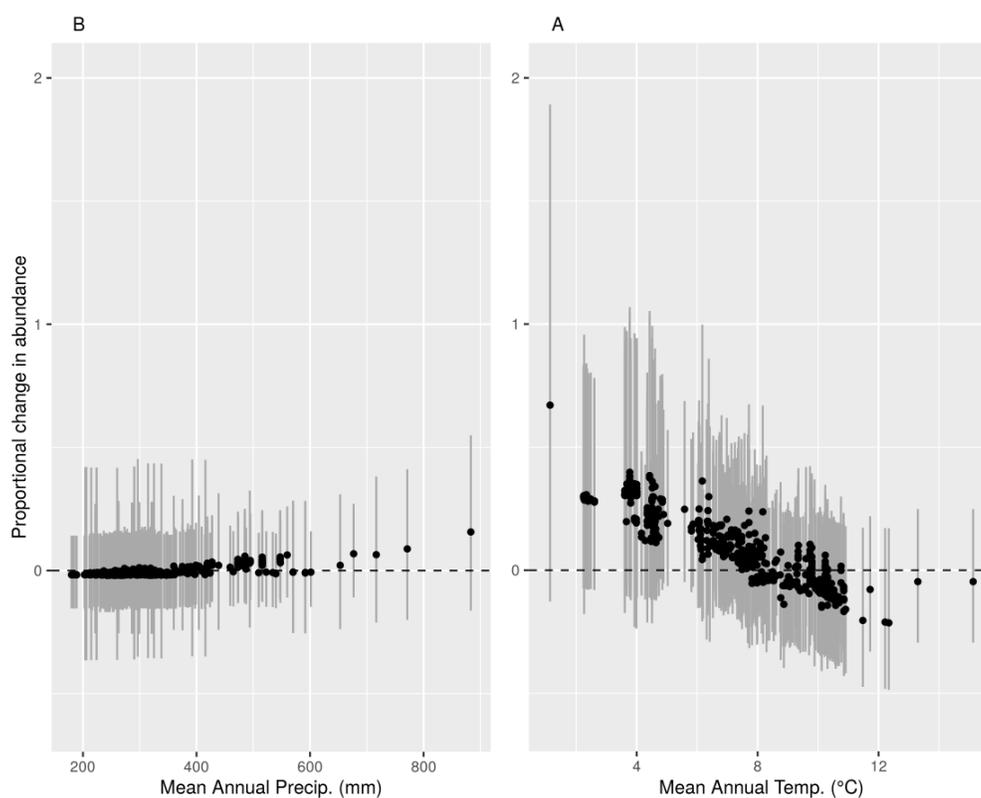
FIG. 2.4. Predicted effects of a short-term increase in precipitation (A) or temperature (B) on sagebrush abundance at each of the monitoring sites. Panel A shows the predicted proportional change after four years with 10% above average precipitation plotted against site mean annual precipitation. Panel B shows the predicted proportional change after four years of 2°C above average temperatures plotted against site mean annual temperature. Gray bars show bootstrapped 95% confidence intervals. Confidence intervals do not take into account uncertainty in random effects.

CHAPTER 3

CAN OBSERVATIONAL DATA PREDICT POPULATION RESPONSES TO

CLIMATE CHANGE EXPERIMENTS?[1]

Abstract

Climate is an important driver of population dynamics and annual variation in

demographic rates often correlate with variation in weather. However, the predictive

potential of such correlations is largely unknown. We used rainout shelters and automatic

sprinklers to manipulate the soil moisture in sixteen plots in a sagebrush steppe

community at the US Sheep Experiment Station in Dubois, ID. We report how the

growth, survival and recruitment of a dominant shrub (*Artemisia tripartita*) and three

dominant perennial grasses (*Hesperostipa comata*, *Poa secunda* and *Pseudoroegneria

spicata*) responded to the experimental drought and irrigation treatments after five years.

We then attempted to predict these treatment responses using two models fit to long-term

observational data collected at this site prior to the experiment: a baseline model that only

included the effects of plant size and local crowding on plant performance, and a climate

model that also included the effects of three seasonal soil moisture variables. We

compared predictions made by the baseline and climate models to the actual experimental

responses. We also used an individual-based population model to generate one-step-

ahead predictions of cover in each experimental plot for each year of the experiment and

compared these predictions to observed cover.

Over the course of the experiment, average cover of *H. comata* and *P. spicata*

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declined significantly in the drought treatment. At the level of individual vital rates, experimental drought reduced the survival of *H. comata* and *P. spicata* and the growth of *P. secunda*. In contrast, drought increased the growth of the shrub *A. tripartita*. The climate model made better predictions of the experimental responses than the baseline model in six out of twelve cases. Across all species and vital rates, there was a strong positive correlation between the observed responses to the treatments and the responses predicted by the climate model. At the population-level, the climate model predicted changes in species cover more accurately than the baseline model for *P. secunda* and *P. spicata*.

Observational climate data held valuable information for predicting species' responses to a climate change experiment in this ecosystem. Treatment responses often matched the direction of predicted responses even when the effects were not significant. We were better able to predict species' responses to the drought treatment than to the control and irrigation treatments, suggesting that soil moisture is an important factor for predicting the population dynamics of these species but only when water is truly limiting.

Introduction

Climate is one of the most powerful drivers of changes in species abundance across space and time (Davis and Shaw 2001, Post and Forchhammer 2002, Walther et al. 2002). The effects of climate on populations and ecosystems are most apparent at large scales: climate determines the distribution of ecosystems (Whittaker 1975), tree lines (Körner 2012) and the range limits of many species (Davis and Shaw 2001, Parmesan and Yohe 2003). Understanding and predicting the effects of climate on populations is an increasingly important goal if we are to anticipate the effects of climate change on earth's

ecosystems (Petchey et al. 2015, Ehrlén et al. 2016, Teller et al. 2016, Tredennick et al.

2016).

Ecologists often resort to one of two methods for predicting the effects of future

climate change on populations and communities: they may use experiments to manipulate

aspects of climate directly and observe the response of populations (Compagnoni and

Adler 2014, Elmendorf et al. 2015, Knapp et al. 2016) or they may use long term

observational data on species performance and abundance and relate this to ambient

annual variation in climate (Jenouvrier et al. 2009, Dalgleish et al. 2010, Koons et al.

2012, Lunn et al. 2016). The strength of the experimental approach is in the stronger

inference that comes from manipulating some aspects of climate while controlling for

other factors; for instance, knowing that loss of snow cover, and not changes in soil

temperature or moisture are factors causing species performance to change with warming

(Compagnoni and Adler 2014). It also allows for the creation of conditions that may be

more extreme than those observed historically (Knapp et al. 2016) but that are possible in

the future. However, it is often expensive to control climate at even the smallest scales,

and larger scale climate manipulation is often impossible. Moreover, experimental

manipulation can come with artifacts that may make them less than ideal models for

understanding and predicting the effects of future variation in climate (Wolkovich et al.

2012).

One important advantage of using observational data is cost: analyses of already

existing long-term ecological data and ever increasingly detailed climate data are cheaper

than experiments. Observational studies may also be the only way to study the effects of

climate on large and or migratory species, for which it would be difficult to manipulate

climate (Jenouvrier et al. 2009, Koons et al. 2012, Aubry et al. 2013). The principal disadvantage is the reliance on correlative relationships between species performance and climate to predict future species' responses. First, many years of data are needed to reliably detect climate effects, especially when annual variation in demographic rates is high (Gerber et al. 2015, Teller et al. 2016). Teller et al. (2016) estimate that even cutting edge statistical approaches for fitting relationships between climate and species performance require at least 20-25 years of independent climate observations before they perform well. Moreover, strong correlations between species performance and the climate covariates we choose to include in population models may not reflect direct causation, leading to failures when predicting future, out of sample data (Hilborn 2016).

The extrapolation of climate-demography correlations presents another potential problem. In many systems, future precipitation and temperature will fall outside the range of historical variation. If species performance responds non-linearly to these drivers, fitting linear models for species responses to climate may produce large errors when future conditions are outside the range of observed variation (Doak and Morris 2010). In addition, climate change will not only alter mean temperature and precipitation, but is also likely to increase the variance in precipitation and the frequency of extreme events, which will have their own consequences independent of changes in means (Jentsch et al. 2007, Gherardi and Sala 2015). Any models based on observations drawn from the historical range of variation will therefore be extrapolating beyond both the range of observed averages and variances when used to predict the future (Williams and Jackson 2007).

Here, we combine the strengths of experimental and observational approaches by

testing the ability of models fit to historical data to predict the effects of experimental

climate manipulations that generate extreme conditions. A demonstration that the

observational approach can skillfully predict experimental responses would provide

strong confirmation that observed climate-demography correlations are not spurious and

will hold in the future (Adler et al. 2013). Work with forbs in tallgrass prairie system,

Adler et al. (2013) showed that population models based on observed correlations

between plant population growth rates and precipitation did have some predictive power

in describing species response to a short-term climate manipulation. Three species

showed responses to experimentally imposed drought and irrigation that were well

predicted by population models fitted to historical observations. However, the responses

of another three species were not well predicted by historical observations.

Among plant populations, annual variation in precipitation and or soil moisture

often drive variation in net primary productivity (Knapp and Smith 2001, Hsu and Adler

2014), the annual growth rates of the woody tissue in trees and shrubs (Srur and Villalba

2009, Franklin 2013, Yang et al. 2014), and the germination and reproductive output of

annuals (Venable 2007). Despite clear signs that precipitation should be important for

plant populations, there have been relatively few studies that clearly link observed

variation in precipitation to species performance in population models (Ehrlén et al.

2016).

The sagebrush steppe plant community at the US Sheep Experiment Station near

Dubois, Idaho offers an ideal opportunity to test whether the climate effects derived from

observational data can also be used to predict species responses to controlled

precipitation experiments. The demography of three perennial bunchgrasses and a shrub

species at the USSES have been described in detail in six different studies since 2009,

several of which report significant effects of seasonal precipitation on the vital rates and

overall population growth rates of these species (Adler et al. 2009, Adler et al. 2010,

Adler et al. 2012, Dalgleish et al. 2010, Chu and Adler 2015, Chu et al. 2016).

In this study, we report how the four dominant plant species at the USSES

responded to a five-year drought and irrigation experiment and use the results to address

two research questions: (1) How much do the growth, recruitment and survival of our

target species differ between the precipitation manipulation treatments? Significant

experimental effects on species vital rates imply that future changes in precipitation will

impact populations. (2) Can we predict each species' response to the experimental

conditions based on how they respond to natural climate variation in the observational

data? If models based on observational data can predict the response of species to this

experiment, we will gain confidence in using long-term population monitoring data to

predict species responses to future climate change.

Methods

Study site and data set description

The U.S. Sheep Experiment Station (USSES) is located at Dubois, Idaho (44.2°N,

112.1°W), 1500 m above sea level. During the historical period of data collection, mean

annual precipitation was 270 mm and mean temperatures ranged from -8°C (January) to

21°C (July). The vegetation is dominated by a shrub, *Artemisia tripartita*, and three

perennial C3 grasses: *Pseudoroegneria spicata*, *Hesperostipa comata*, and *Poa secunda*.

These dominant species account for over 70% of basal cover and 60% of canopy cover at

this site.

Scientists at the USSES established 26 1-m^2 quadrats between 1926 and 1932. Eighteen quadrats were distributed among four ungrazed exclosures, and eight were distributed in two paddocks grazed at medium intensity spring through fall. All quadrats were located on similar topography and soils. In most years until 1957, all individual plants in each quadrat were mapped using a pantograph (Blaisdell 1958). The historical data set is public and available online (Zachmann et al. 2010). In 2007, we located 14 of the original quadrats, all of which are inside permanent livestock exclosures, and resumed annual mapped censusing using the traditional pantograph method. Daily temperature and precipitation has been monitored throughout this period at a climate station located at the USSES headquarters (station id: GHCND:USC00102707) located within 2 km of the research plots. We downloaded daily and monthly tmin, tmax, and precipitation data for this site from the National Climate Data Centers online database.

We extracted data on survival, growth, and recruitment from the mapped quadrats based on plants' spatial locations. Our approach tracks genets representing individual plants. For the shrub, each genet is associated with the basal position of a stem. For the bunchgrasses, each genet represents a spatially distinct polygon of basal cover in the mapped quadrat. These genets may fragment and/or coalesce over time. Each mapped polygon is classified as a surviving genet or a new recruit based on its spatial location relative to genets present in previous years (Lauenroth and Adler 2008).

Precipitation experiment

In spring 2011, we selected locations for an additional 16 quadrats for the

precipitation experiment. We located these in a large exclosure containing six of the historical permanent quadrats. We avoided plots falling on hill slopes, areas with greater than 20% bare rock, or with over 10% cover of the woody shrubs *Purshia tridentata* or *Amelanchier utahensis*. New plots were established in pairs, and one plot per pair was randomly assigned to either the precipitation reduction or the precipitation addition treatment. We mapped the quadrats in June, 2011 and then built the rainfall shelters and set-up the irrigation systems in the fall of 2011. We used a rain-out shelter and automatic irrigation design described in (Gherardi and Sala 2013). Each rain-out shelter covered an area of 2.5 by 2 m and consisted of transparent acrylic shingles held up 1.5 to 1 m over the plot to channel 50% of incoming rainfall off of the plot and into 75 L reservoirs. The collected water was pumped out of reservoirs and sprayed onto paired irrigation treatment plots. Pumping was initiated automatically with float switches that were triggered when water levels in the reservoirs were approximately 20 L, or equivalently irrigation was triggered once for every 6 mm of rainfall collected. We disconnected the irrigation pumps in late fall each year and re-connected them in April. The drought shelters remained in place throughout the year.

We monitored soil moisture and air temperature in four of the precipitation experiment plot pairs using Decagon Devices (Pulman Washington) 5TM and EC-5 soil moisture sensors and 5TE temperature sensors. We installed two soil moisture sensors in each monitored plot at 5 cm and two at 25 cm deep in the soil. Air temperature was measured underneath the roofing on the northern side of the shelter at 30 cm above ground. For each pair of manipulated plots, we also installed sensors in a nearby area to measure ambient rainfall and temperature. Data were logged automatically every four

hours. We augmented automatic monitoring of the climate in these plots with direct

measurements of soil moisture with a handheld EC-5 soil moisture sensor at six points

around all 16 plots on 6/6/2012, 4/29/2015, 5/7/2015, 6/9/2015 and 5/10/2016. We

analyzed these spot measurements for significant treatment effects on soil moisture using

a linear mixed effects model with the *lmer* package in *R*, with plot, plot group, and date

as random effects in the model (Bates et al. 2015).

To determine the net effect of the experimental treatments on cover in the

experiment we calculated the log change in cover for each of the four focal species in

each quadrat from the start of the experiment in spring prior to manipulation, to the last

year of the experiment. Log change in cover was defined as $log(\text{Cover}_{2016}/\text{Cover}_{2011})$

where Cover_{2016} is the cover of each species in 2016 and Cover_{2011} is cover in 2011. We

tested for the effect of precipitation treatment on this measure with a linear model in R (R

Core Team 2016).

Soil moisture modeling

We expected that our precipitation manipulation experiment would affect plants

by altering available soil moisture during the growing season. Because we do not have

direct soil moisture measures for the years of observed plant cover in the historical

record, we used the SOILWAT soil moisture model to estimate daily soil moisture at the

USSES from 1925 to the present (Sala et al. 1992). We used an enhanced version of

SOILWAT that has recently been developed for use in semi-arid shrubland ecosystems

(Bradford et al. 2014). SOILWAT uses daily weather data, ecosystem specific vegetation

properties and site specific soil properties to estimate water balance processes.

SOILWAT specifically estimates rainfall interception by vegetation, evaporation of intercepted water, snow melt and snow redistribution, infiltration into the soil, percolation through the soil, bare-soil evaporation, transpiration from each soil layer, and drainage. We parameterized SOILWAT with the generic sagebrush steppe vegetation parameters and site specific soil texture and bulk density data. We used daily weather data collected at the USSES from 1925 until the present as weather forcing data for the SOILWAT predictions.

We averaged daily soil moisture predictions from SOILWAT from the upper 40 cm of soil and then averaged these seasonally to serve as the covariates in the vital rate regressions for each species. Because we did not monitor soil moisture directly in all control, drought and irrigation plots, we used another model to describe the average treatment effects on soil moisture that we observed with the automatic data loggers during the course of the experiment. To do this we first averaged observed soil moisture by day and plot and then standardized these by the mean and standard deviation of the control soil moisture conditions observed within each plot group. We found the difference between soil moisture in the treated plots and the ambient conditions and then modeled these treatment effects as a function of season and whether a day was rainy or dry. We expected that our drought and irrigation treatments might be more effective during rainy weather than during dry weather. Rainy days were defined as any days when any precipitation was recorded and average temperature was above 3 degrees C. The day immediately following rainfall was also classified as rainy. We fit this model using the *lmer* package in *R* with random effects for plot group and date (Bates et al. 2015). Finally, we used this model to predict the treatment effects on soil moisture for each day

of the study period based on the ambient soil moisture values predicted from the

SOILWAT model. These adjusted soil moisture values reflected the average season and

rainfall dependent effects of the experimental treatments on soil moisture and could be

used as covariates for predicting the effects of our manipulation on each species

demographic rates.

Overview of the demographic analyses

Our analysis consists of two separate datasets and three different categories of

vital rate models. We refer to the first dataset as the observational data. It consists of all

the historical data collected from 1925 to 1957 as well as the contemporary data collected

from the same plots from 2007 to 2010. These data record the response of plants in each

plot to the ambient climate variation. We refer to the second dataset as the experimental

data. It consists of the data collected from 2011 to 2016 from the 16 new experimentally

manipulated plots, as well as from 14 of the original historical plots that were monitored

during the experiment to serve as ambient climate controls. Each data set comprises

hundreds to thousands of observations of individual genets of each species (Table 3.1).

To serve as a point of comparison for our predictions, we fit "treatment" models

to the all of the observational and experimental data together. The treatment models

included parameters representing the effects of the drought and irrigation treatments on

each vital rate. We fit these models using all experimental and all observational data

combined. We combined the datasets because we wanted to focus our predictions on the

effects of the experimental treatments on the vital rates, rather than any differences

between the historical and contemporary periods in effects of crowding and plant size on

the vital rates.

Next, in order to test how well we could predict the responses in the experimental plots, we fit two classes of models to the observational dataset only. The "baseline" models include parameters for the effects of competition on each vital rate and the size dependence of survival and growth but they do not include climate or treatment effects. The "climate" models are the same but also model the effects of annual variation in soil moisture on each vital rate. The baseline models give us a point of comparison by which to measure the accuracy of predictions from the climate model. Because much of the variation in growth, survival and recruitment in this system can be explained by plant size and competition, we expect that these two models will make similar predictions for individual plant performance in the experiment. However, if the climate model makes more accurate predictions than the baseline model, this indicates that the soil moisture effects that it estimates contain useful information for prediction. Note that because these models are fit using only the observation dataset, when we use these models to predict experimental responses we are generating true out-of-sample predictions.

Statistical models of vital rates

All three categories of models described above follow the same basic structure and differ only in how they treat climate and treatment effects (Adler et al. 2010, Chu and Adler 2015). We model the survival probability of an individual genet as a function of genet size, the neighborhood-scale crowding experienced by the genet from both conspecific and heterospecific genets, temporal variation among years, and permanent spatial variation among groups of quadrats ('group' here means a set of nearby quadrats located within one pasture or grazing exclosure). In this analysis, we only include crowding from the four main focal species.

Formally, we modeled the survival probability, S, of genet i in species j, group g, and from time t to $t + 1$ as

$$\text{Logit}(S_{ijg,t}) = \varphi_{jg}^{S} + \gamma_{j,t}^{S} + \beta_{j,t}^{S} u_{ij,t} + \langle \boldsymbol{\omega}_{j,t}^{S}, \boldsymbol{W}_{ij,t} \rangle, \qquad (1)$$

where φ is the spatial group dependent intercept, γ is a year-effect, β is a year-dependent coefficient that represents the effect of log genet size, u, on survival in year t. $\boldsymbol{\omega}$ is a vector of interaction coefficients which determine the impact of crowding, $\boldsymbol{W}$, by each species on the focal species. In this model, γ and β where modeled as hierarchical random year effects drawn from random normal distributions. The vector $\boldsymbol{W}$ includes crowding from the four dominant species, *A. tripartita*, *P. spicata*, *H. comata*, and *Poa secunda*. $\langle \boldsymbol{x}, \boldsymbol{y} \rangle$ denotes the inner product of vectors $\boldsymbol{x}$ and $\boldsymbol{y}$, calculated as sum(x*y) in R. This model is the baseline model for survival.

In the treatment model, a new term is added to the above model, $\boldsymbol{T}\boldsymbol{\chi}_{j}^{S}$ where $\boldsymbol{\chi}$ is a vector of treatment effect coefficients for each experimental treatment level on the survival rate, and $\boldsymbol{T}$ is a design matrix indicating the treatment level of each observation in the data. The design matrix also includes terms for the interaction between plant size u and the treatment effects which allow the effect of each treatment to vary with plant size.

In the climate model, the treatment term is replaced with $\boldsymbol{M}_{t}\boldsymbol{\xi}_{j}^{S}$, where $\boldsymbol{\xi}$ is a vector of coefficients describing the effects of a set of soil moisture covariates $\boldsymbol{M}$ in each year t on the survival rate of species j. $\boldsymbol{M}$ can include interaction effects between plant size, u, and the soil moisture covariates allowing the effects of soil moisture to vary with plant size.

Our growth model has a similar structure. The genet size u in year $t + 1$, conditional on survival, is given by:

$$u_{ijg,t+1} = \varphi_{jg}^{G} + \gamma_{j,t}^{G} + \beta_{j,t}^{G}u_{ij,t} + \langle \omega_{j,t}^{G}, W_{ij,t} \rangle. \tag{2}$$

As in the survival regression above, parameters describing the treatment effects on growth are added in the treatment model, $T\chi_{j}^{G}$, where χ is a treatment effect describing the effect of each experimental treatment on growth, including treatment by size interactions. Similarly, in the climate model, the above term is replaced with $M\xi_{j}^{G}$, where ξ is a vector of coefficients describing the effects of soil moisture covariates in the matrix M for treatment h and year t on growth of species j. Again this can include interactions between soil moisture and plant size u.

The main focus of the current analysis is the effects of soil moisture, however, we also modeled the effects of inter- and intra-specific competition in our vital rate models. We model the crowding experienced by a focal genet as a function of the distance to and size of neighbor genets. This approach is well described in previous work (Teller et al. 2016, Adler et al. in prep.). Briefly, we model the crowding experienced by genet i of species j from neighbors of species m as the sum of neighbor areas across a set of concentric annuli, k, centered at the plant,

$$w_{ijm,k} = F_{jm}(d_k)A_{i,k}, \tag{3}$$

where F_{jm} is the competition kernel (described below) for effects of species m on species j, d_k is the average of the inner and outer radii of annulus k, and $A_{im,k}$ is the total area of genets of species m in annulus k around genet i. The total crowding on genet i exerted by species m is

$$W_{ijm} = \sum_{k} w_{ijm,k}. \tag{4}$$

Note that W_{ijj} gives intraspecific crowding. The W's are then the components of the W

vectors introduced as covariates in the survival eq. (1) and growth eq. (2) regressions.

We assume that competition kernels $F_{jm}(d)$ are non-negative and decreasing, so that distant plants have less effect than close plants. Otherwise, we let the data dictate the shape of the kernel by fitting a spline model using the methods of Teller et al. (2016). We used data from all historical plots and contemporary control-treatment plots to estimate the competition kernels. Once we had estimated the competitions kernels, we used them to calculate the values of W for each individual, and fit the full survival and growth regressions, which include the interspecific interaction coefficients, ω. All genets in a quadrat were included in calculating W, but plants located within 5 cm of quadrat edges were not used in fitting.

We model recruitment at the quadrat level rather than at the individual genet level because the mapped data do not allow us to determine which recruits were produced by which potential parent plants. We assume that the number of individuals, y, of species j recruiting at time $t + 1$ in the location q follows a negative binomial distribution:

$$y_{jq,t+1} = NegBin(\lambda_{jq,t+1}, \theta), \tag{5}$$

where λ is the mean intensity and θ is the size parameter. In turn, λ depends on the composition of the quadrat in the previous year:

$$\lambda_{jq,t+1} = C'_{jq,t}\exp(\varphi_{jg}^{R} + \gamma_{j,t}^{R} + \langle\omega_{j,t}^{R}, \sqrt{C'_{jq,t}}\rangle), \tag{6}$$

where the superscript R refers to recruitment, $\sqrt{C'_{jq,t}}$ is the 'effective cover' (cm^2) of species j in quadrat q at time t, φ is a group dependent intercept, γ is a random year effect, ω is a vector of coefficients that determine the strength of intra- and interspecific density-dependence. We square root-transformed the effective cover $C'_{jq,t}$ because it produced a

better model fit. Following previous work, we treated year as a random factor allowing

intercepts to vary among years (Adler et al. 2010).

Because plants outside the mapped quadrat could contribute recruits to the focal

quadrat or interact with plants in the focal quadrat, we estimated effective cover as a

mixture of the observed cover, C, in the focal quadrat, q, and the mean cover, $\hat{C}$, across

the spatial location, g, in which the quadrat is located: $C'_{jq,t} = p_j C_{jq,t} + (1 - p_j)\hat{C}_{jg,t}$

where p is a mixing fraction between 0 and 1 that was estimated as part of fitting the

model. In the treatment model for recruitment, a new term is added to the exponential

term on the right hand side of (6), $\boldsymbol{T\chi_j^R}$ where χ describes the effect of each treatment

level on recruitment. Likewise in the climate model this term is replaced by $\boldsymbol{M\xi_j^R}$ where

the ξ gives a set of coefficients for the year and treatment specific soil moisture

covariates in $\boldsymbol{M}$.

We fit all vital rate models using Hamiltonian-Markov Chain Monte Carlo

(HMCMC) simulations in the programs STAN 10.1 and rStan (STAN 2016). Each

model was run for 2,000 iterations and four independent chains with different initial

values for parameters. We discarded the initial 1,000 samples. Convergence was

observed graphically for all parameters, and confirmed by assessing the split $\hat{R}$ statistic

which at convergence is equal to one (STAN 2016).

We fit the treatment models for species survival and growth with and without the

size by treatment interactions in the treatment effect term χ. We then judged whether

including the interaction terms improved model fit by comparing the Watanabe-Aikake

Information Criteria (WAIC) scores of each version of the model and retained the version

with the lower WAIC score (Gelman 2014). WAIC are similar to AIC scores and allow

for comparison of Bayesian models. Lower WAIC scores indicate a better balance of goodness-of-fit and model parsimony. When a treatment model for survival or growth of a species included a size by treatment effect in χ, we also included a size by soil moisture effect in the ξ term in the climate model for that species and vital rate. This allowed us to more directly compare the predictions from the climate model to the effects in the treatment model.

Selecting soil moisture covariates

After generating a time series of predicted daily soil moisture from SOILWAT, we averaged daily soil moisture across spring, summer and fall seasons in each year. We considered each of the three seasonal soil moisture variables at three different time periods relative to the demographic transition from year t to year $t + 1$. Soil moisture in the year between t and $t + 1$ is indicated with a "1" subscript. Soil moisture in the year before t is indicated with a "0" subscript. And soil moisture preceding this year is indicated with a "lag" subscript. For example, for year 2010, $spring_1$ indicates soil moisture in the spring of 2010, $spring_0$ indicates soil moisture during spring of 2009 and $spring_{lag}$ indicate soil moisture during spring 2008.

We wanted to avoid fitting nine soil moisture covariates (three seasons and three lags each) for each species and vital rate, so we used only three soil moisture covariates per species and vital rate. We selected these three by calculating the correlations of each soil moisture variable with the random year effects from the baseline model and then selecting the three soil moisture variables with the strongest correlations with these year effects. This screening technique has been used in previous demographic studies at this

site (Dalgleish et al. 2010) and correlations with climate are often used to screen for

potential climate influence on tree-ring growth in dendrochronology (Wang et al., 2003)

although it has the risk of leaving out important variables. We felt this approach was

justified because we did not make inference on these fitted parameters until after we

validated their ability to predict the out of sample data in the experimental plots.

Predicting cover from individual-based models

  The vital rate regressions allow us to evaluate whether soil moisture and the

experimental treatments have an effect on species performance. But the population

response ultimately depends on the integrated effects of treatment or soil moisture on all

three vital rates. To evaluate whether the climate models could predict the responses of

these species in the drought and irrigation experiment at the overall population level we

used an individual-based model (IBM) to compare observed and predicted changes in

population size from one year to the next.

  To simulate changes in population size, (defined as canopy cover for *A. tripartita*

and as basal cover for the grasses), in each quadrat from year t to year $t + 1$, we initialized

the IBM with the observed genet sizes and locations of the four focal species observed in

year t in each quadrat. For every individual genet in a quadrat, we projected its size and

survival probability in the next year using the growth and survival models and the

appropriate crowding and soil moisture or treatment covariates for that year and quadrat.

Likewise, we projected the number of new recruits in the quadrat in the next year using

the recruitment model. We calculated the expected cover in year $t + 1$ as the total area of

new recruits, plus the sum of the predicted area of each existing plant at time $t + 1$

multiplied by each plant's expected survival probability from time t to $t + 1$.

We generated predictions using 1000 samples from the posterior distributions of each model parameter which allowed us to carry forward all of the uncertainty of the fitted vital rate models into our cover predictions. Because we were interested in comparing model predictions to observations, and were not interested in the effects of demographic stochasticity on populations within each plot, we used the mean predictions from each vital rate model for predictions and did not use the random individual variation in the models (e.g., recruitment is the λ of [6], rather than a random draw from a negative binomial distribution with a mean of λ). After generating predictions for each year from the climate and baseline models, we found the predicted quadrat-level changes in cover as $log(Cover_{t+1}/Cover_t)$.

Quantifying predictive accuracy

We assessed the predictive performance of the climate and baseline models by calculating the mean square error (MSE) between the predicted and observed responses in the experimental data as,

$$MSE = \frac{1}{n}\sum_{i=1}^{n}\left(y_i - E(y_i|\theta)\right)^2, \tag{7}$$

where y_i is the outcome of observation i and $E(y_i|\theta)$ gives the expected outcome given the parameters in the model θ. The MSE is easy to interpret, but is not always appropriate for models fit with non-normal error structures (Gelman et al. 2014). We also considered a more general statistic for prediction accuracy, the log pointwise predictive density (lppd) (Gelman et al. 2014). The lppd for a given model is defined as,

$$lppd = \sum_{i=1}^{n} \log \int p(y_i|\theta)p_{post}(\theta)d\theta, \tag{8}$$

where the integral on the right side gives the probability of observing the outcome *y* at each data point *i* given the full posterior distribution of the parameters in the model $p_{post}(\theta)$. In practice we computed the $\widehat{lppd}$ from the posterior simulations generated by STAN as,

$$\widehat{lppd} = \sum_{i=1}^{n} \log \left(\frac{1}{S} \sum_{s=1}^{S} p(y_i|\theta^S) \right), \tag{9}$$

where the summation of $p(y_i|\theta^S)$ gives the total probability of observing the actual response y_i given the simulated posterior distribution θ^S across the full set of model simulations *S*. The log of this sum is then averaged across the set of all observations *i*. Higher lppd scores indicate that the model better predicts the observations.

In addition, we evaluated whether the climate model predicted treatment effects of similar direction and magnitude to those observed in the experiment. We did this by extracting the soil moisture coefficients contained in ξ for each of the vital rates and then multiplying those by the appropriate soil moisture covariates for each year and treatment level in the experimental data. We then averaged these across all five years within each treatment level to find the average treatment effect predicted by the climate model. We compared these to the posteriors of the treatment parameters, χ, from the treatment model. As a measure of agreement between our predictions and observed response we calculated the correlation between the predicted and observed treatment effects. We considered the effect of climate covariates or treatment effects to be significant when the 95% Bayesian credible intervals on the posterior estimates did not overlap zero.

Results

Effects on soil moisture

Our treatments successfully changed the soil moisture in the experimental plots in the directions expected (Fig. 3.1). Spring spot measurements of soil moisture from all the plots showed that on average the drought plots were roughly 50% drier, while irrigated plots were roughly 40% wetter than ambient conditions (Table 3.2). The continuously recorded soil moisture data also showed treatment effects, but these were weaker on average than the spot measurements and depended on season and recent rainfall (Table 3.3; Fig. 3.2). We saw weaker effects during the spring than during the fall and summer: the drought plots were about 20-30% drier than ambient in the fall and summer but only 7 to 14% drier during the spring, while the irrigated plots were 30% wetter during the fall and summer but only 20-25% wetter during the spring. Treatment differences were slightly larger during rainy periods, especially in the spring (rainfall effect in Table 3.3). We did not find evidence that the drought shelters and the irrigation treatments consistently affected air temperature at 30 cm above the plots.

The SOILWAT soil moisture model predicted average monthly soil volumetric water content of between 10 ml/ml and 15 ml/ml each month, with the month of April being the wettest and the months of July, August and September being the driest on average. Annual variation in seasonal soil moisture for each year was positively correlated with seasonal precipitation and negatively correlated with seasonal temperature. During the course of the experiment, SOILWAT reproduced much of the daily variation observed in soil moisture recorded by our automatic data loggers, but the average soil moisture predicted by SOILWAT was about 5 ml/ml higher than the soil

moisture content observed in the field.

After adjusting the SOILWAT seasonal soil moisture predictions by the treatment effects, we found that the soil moisture predicted in the drought plots was generally below the historical seasonal averages: the summer of 2012 and 2013, the fall of 2013, and the spring and winter of 2014 fell below the 5th percentile limit for drought in the historical period (Fig. 3.3). Soil moisture in our irrigation plots was often above the historical average soil moisture but conditions never exceeded the 90th percentile for soil moisture in the historical period (Fig. 3.3).

Effects on cover and vital rates

The cover of *H. comata* and *P. spicata* fell significantly in the drought plots from 2011 to 2016 (Table 3.4; Fig. 3.4). The cover of *P. secunda* showed a slight decrease in the drought plots and an increase in the irrigated plots but these changes were not significant (Table 3.4). In contrast to the grasses, the cover of *A. tripartita* increased slightly in all three treatments (Fig. 3.4).

Our treatment models fit to the experimental and observational data indicated a variety of treatment effects on the vital rates of each species. Based on the WAIC scores, we retained size by treatment effects in the growth models for *A. tripartita* and *P. secunda*, and the survival model for *P. secunda*. For *A. tripartita* we found significant size by treatment effects of drought: drought had positive effects on plants of average size and smaller (Fig. 3.5, observed effects), but plants larger than the mean size by more than 1.5 standard deviations grew slightly less in the drought treatment than in the controls. *A. tripartita* showed the opposite response in the irrigated plots, (although the irrigation parameters were not significant at the 95% confidence level): irrigation reduced growth

for small plants while irrigation increased growth of plants more than 1.5 standard deviations larger than the mean size. Drought led to a strong (but not significant) decrease in *H. comata* growth, while irrigation had no effect on growth. Like *A. tripartita*, we saw size by treatment effects on *P. secunda* growth, with the negative effects of drought becoming greater for larger plants. *P. secunda* showed the opposite response in the irrigation plots with larger plants showing the largest increase in growth in response to irrigation (although not significant). *P. spicata* growth was relatively unaffected by the drought and irrigation treatments.

Survival of all three grass species decreased in the drought plots (Fig. 3.6, observed effects). And *P. secunda* showed a negative size by drought interaction effect: the survival of larger plants was more negatively affected by drought than that of the smaller plants. *A. tripartita* survival was relatively unaffected by the drought and irrigation treatments.

Recruitment in irrigation plots was significantly lower than in control plots for two grass species *P. secunda* and *P. spicata* (Fig. 3.7, observed effects). However, recruitment was also lower in the drought plots than in the control plots (although not significantly so), indicating that the decrease in the irrigated plots may have not been entirely due to the irrigation. The recruitment data for *A. tripartita* were relatively limited, with only 32 new recruits in total observed in all 30 plots over the course of the five-year experiment and we observed no treatment effects.

Consistent with previous research most of our demographic models estimated strong negative intra-specific crowding effects and weaker negative inter-specific crowding effects on the focal species (Adler et al. 2010, Chu and Adler 2015, Chu et al.

2016, Adler et al. in prep.).

Effects of soil moisture on vital rates

We choose three seasonal soil moisture variables for each species' based on their correlation with the random year effects in the baseline model (Table 3.5). We included size by soil moisture variables for *A. tripartita* and *P. secunda* based on the treatment response we observed in the experiment. All three time lags and all three seasons show up in the selected variables. After fitting the vital rate models with the selected soil moisture variables we observed a trend towards positive soil moisture effects on growth of all three grasses (Fig. 3.8). For *H. comata* the soil moisture of the most recent summer ($summer_1$) had a significantly positive effect while the soil moisture during $summer_0$ and $fall_{lag}$ were also positive but not significant. For *A. tripartita,* $fall_0$ and $summer_0$ had strong negative effects on growth. There were also strong positive size by climate interaction effects for *A. tripartita*: soil moisture had a stronger negative effect on small plants and a positive effect only on the largest plants (Fig. 3.8).

Soil moisture had significant effects on the survival of all four species (Fig. 3.9). As for growth, the grasses showed mainly positive effects while *A. tripartita* showed a significant negative effect of $summer_0$ and a strong negative effect of $spring_0$. For *H. comata* $spring_{lag}$ soil moisture had a significant positive effect while $spring_0$ and $fall_1$ had strong, but not significant, positive effects. *Poa secunda* showed a significant positive effect of the previous $spring_0$ and there was an interaction between this effect and plant size: as plant size increased this effect became more positive. Finally, for *P. spicata* there was a significant positive effect of $spring_{lag}$ soil moisture on survival.

There were only two significant effects of soil moisture on recruitment: $fall_{lag}$ soil moisture had a positive effect on *P. secunda*, and $summer_{lag}$ soil moisture had a negative effect on *P. spicata* recruitment (Fig. 3.10). Soil moisture of $summer_0$ also had a strong negative effect on *P. spicata* recruitment. The intra- and interspecific crowding effects estimated in the climate model were similar to those estimated in the treatment model.

Evaluating the predictions

Adding climate covariates improved some but not all of our vital rate predictions (Table 3.6). The climate models improved overall prediction MSE for growth of *A. tripartita* and growth and survival of *P. secunda* (Table 3.6). In terms of lppd, the climate model outperformed the baseline model in six out of twelve models: for *A. tripartita* growth, *H. comata* recruitment, *P. secunda* growth and survival and *P. spicata* growth and recruitment (Table 3.6). When we look at the predictions for each treatment separately we see that climate covariates improved model predictions more often in the drought treatments than in the control or irrigation treatments (Table C1). For all four species, the climate model outperformed the baseline model for predicting the response of growth to drought in terms of lppd (Table C1). The climate model also outperformed the baseline model for predicting irrigation effects on growth for all species except *H. comata*.

Overall our climate models often predicted the correct direction of the drought and irrigation treatments (Figs 3.5, 3.6, 3.7). In four cases we both observed and predicted treatment effects significantly different from zero based on the 95% Bayesian credible interval around the parameter mean: the drought response of *H. comata* survival

(Fig. 3.6), the drought response of *P. secunda* growth (Fig. 3.5), the irrigation response of *P spicata* and *P. secunda* recruitment (Fig. 3.7). In only one of these cases, for *P. secunda* recruitment, was the predicted effect in the opposite direction from the observed treatment effect (Fig. 3.7). The overall correlation between the predicted and observed treatment effects for all treatments, species and vital rates was r = 0.54, whereas the correlation for the drought treatment effects was r = 0.77 and for the irrigation effects r = 0.46 (Fig. 3.11).

Using the vital rate models for each species we generated one step ahead cover predictions for each quadrat in each year of the experiment. Average cover predicted by the climate and baseline models tended to be lower than the observed cover for *A. tripartita* and *P. secunda* (Fig. 3.12). Considering each treatment and species separately, the predicted population growth rates for *A. tripartita*, *P. secunda* and *P. spicata* were all consistently lower than the observed population growth rates (Figs. 3.13, 3.15, 3.16). The climate models made more accurate predictions (lower MSE) than the baseline models for *P. secunda* and *P. spicata* (Table 3.7). The climate model predictions for these species were also slightly more correlated with the observations than the baseline model predictions (Table 3.7). Considering model performance in each treatment separately, the climate model made better predictions than the baseline model for cover of *A. tripartita*, *P. secunda*, and *P. spicata* in the irrigation treatment, *P. spicata* in the control treatment and *H. comata* in the drought treatment (Fig. 3.14).

Discussion

Our experiment showed that observational data on the response of plant populations to annual climate variation can indeed help us predict the direction of species

responses to experimental climate manipulations (Fig. 3.11). The historical climate-demography correlations helped predict the direction of experimental responses even though adding climate parameters to the demographic models only improved vital rate predictions for half of the models (Table 3.6). This should give us some hope that even when climate effects in demographic models fit to observational data are weak or not significant, they may contain useful qualitative information on the direction of climate effects in the future.

Comparison of experimental and natural climate effects

While previous studies in this system used the observational data to describe the effects of climate on demography and survival, this is the first study to demonstrate effects of climate experimentally. We see many points of similarity between these studies in the responses of the four dominant species to precipitation treatments in the present study (Dalgleish et al. 2010, Adler et al. 2012, Chu et al. 2016). First, in all three previous studies the strongest positive effects of precipitation among the four species are reported for *H. comata*; this matches the negative effects of our drought experiment on this species (Fig. 3.4). This effect is driven by a negative growth and survival response to drought (Figs. 3.5, 3.6). On the other hand, if we had only conducted an irrigation experiment our results may not have shown this consistency with previous work as *H. comata* showed no positive response to irrigation. Previous studies also reported positive effects of precipitation on the other grasses, *P. secunda* and *P. spicata*. Again our results are consistent with this result: drought led to declines in cover of *P. spicata*, (Fig. 3.4), and in the growth and survival of *P. secunda* (Figs. 3.5, 3.6). As for *H. comata,* the magnitudes of drought effects on these grasses were greater than the irrigation effects.

The effects of precipitation on *A. tripartita* are more complicated. Previous research reported negative direct effects of precipitation on this species (Adler et al. 2012, Chu et al. 2016). This effect seems odd because it is hard to imagine why precipitation would have a direct negative effect on a species in this dry ecosystem. The largely positive (but size dependent) effects of drought treatments on *A. tripartita* growth should give us more confidence in the negative effects of precipitation shown in the historical data. It is possible that some of the positive effect on *A. tripartita* growth in our drought plots is the result of reduced grass cover (Fig. 3.12, Chu et al. 2016). However, our growth model includes interspecific crowding and so should take into account any changes in grass abundance that could be driving a positive response from *A. tripartita*. Other studies have shown that saturated soils in the spring are detrimental for big sagebrush (*A. tridentata*) a closely related species (Sturges 1989, Germino and Reinhardt 2014). But soil saturation would conservatively seem to require soils to be above 30 or 40% volumetric water content for several weeks, something that we did not observe (Fig. 3.2). Another possible explanation is that our drought treatments reduced snow cover in the winter and early spring, an effect that has been shown to benefit related sagebrush species in other ecosystems (Perfors et al. 2003).

Overall we were somewhat surprised by the weak effects that reducing water availability by 50% and increasing water availability by 150% had in this arid system. Cross-biome studies of the relationship between precipitation and ANPP generally show that arid systems are highly sensitive to water limitation (Huxman et al. 2004). We have two explanations for the seemingly weak effects of precipitation we observed on demography. First, we measure the size of the perennial bunchgrasses in this system by

their basal cover, which may not have a strong relationship with their annual production. It is likely that we would find larger effects of precipitation on these grasses if we had a more complete measurement of aboveground biomass. Moreover, much of the growth of these species may be going into roots which were unmeasured.

Another explanation for the weak effects of precipitation are that perennial species in this cold desert ecosystems are well adapted to tolerate drought, either through escaping drought by growing early in the year, or by avoiding drought stress later in the year through high water use efficiency (Bazzaz 1979, Franks 2011). Indeed, our soil moisture data generally show a pulse of soil moisture in the spring when many grasses are actively growing (Fig. 3.2). Likewise, *A. tripartita* is more deeply rooted than the grasses and able to continue its growth throughout the growing season by drawing from deeper soil water (Germino and Reinhardt, 2014). The adaptations of native perennial plants in cold deserts could make them less sensitive to water availability than species in a more mesic ecosystem.

Can the past predict the future?

Our second research question was whether we could use long term observational data on species response to precipitation to predict the response of each species to the experiment. Using the IBM, we predicted changes in population size for each year and found that climate model predictions were indeed better than the baseline models for two species: *P. spicata* and *P. secunda* (Table 3.7). Our success in using soil moisture to predict the responses of these species to the climate experiment may be attributed to larger sample size for model training and validation for these species than for *A. tripartita* and *H. comata* (Table 3.1). In the drought treatment, our one step ahead cover

predictions for *H. comata* and *P. secunda* were also better than the baseline model.

Moreover, we found that climate models produced better predictions of species vital rates

for half of the species/vital rate combinations we tested (Table 3.6). This matches Adler

et al. (2013) who reported improved population-level predictions for half of the species

predicted. Likewise, in a within sample cross-validation analysis, Tredennick et al.

(2016) found that including climate covariates improved population level predictions for

two out of four species in a mixed grass prairie in Montana.

We also compared the treatment parameters from the treatment model fit to the

experimental data to the treatment parameters predicted by the climate model fit only to

the observational data (Fig. 3.11). Among all the climate effects we predicted and

observed, there were only four cases where vital rate predictions and observations were

both significantly different from zero (Figs. 3.5, 3.6, 3.7). In three of these cases, we

successfully predicted the direction of the treatment effects. However, for *P. secunda*

recruitment we predicted a positive response of irrigation, but observed a negative

response (Fig. 3.7). From a statistical standpoint this is our arguably our greatest error in

prediction. However, recruitment decreased in both the drought and irrigation plots for *P.*

secunda and also for *P. spicata* (Fig. 3.7). So it is likely the decrease in *P. secunda*

recruitment in the irrigated plots was due to pre-existing differences between the set of

experimental plots and the historical control plots rather than the precipitation treatments

themselves.

The drought effects we observed on the three grasses were often stronger than the

effects we predicted, while the irrigation effects observed were often weaker than

predicted (Figs. 3.5, 3.6, 3.7). In this water limited system, we expected that experimental

irrigation would lead to increased plant performance, but we saw few cases where irrigation benefited any of the plants. A pattern qualitatively similar to this shows up in both natural and experimental data comparing precipitation to ANPP: decreases in grassland ANPP induced by drought are often of greater magnitude than increases in ANPP induced by experimental irrigation or by above average precipitation (Hsu and Adler 2014, Gherardi and Sala 2015). If we had fit our growth and survival models with a non-linear function for soil moisture, perhaps informed by more mechanistic understanding of water limitation on the physiology of these plants, we may have made more accurate predictions of the drought and irrigation effects (Ehrlén et al. 2016).

Conclusion

Our results give us more confidence that observational data can be used to detect and predict the effects of annual soil moisture variation on sagebrush steppe plants. This should encourage more researchers to try and use observational data to predict population response to climate in both experimental and natural settings (Houlahan et al. 2016, Ehrlén et al. 2016). Nevertheless, our success at predicting the short-term response of two out of four species to a simple precipitation manipulation is not likely to impress applied ecologists and policymakers who need accurate predictions for the effects of climate change in large complex systems. Clearly more work is needed to learn how to accurately predict the ecological responses of species to climate change. Towards that goal, perhaps the best way forward is to conduct more tests like this one.

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Tables

TABLE 3.1. Total number of individual genets of each species observed in the observational and experimental datasets. Observational data include all individual genets observed prior to the experiment and represent the data used for model fitting, while the experimental data includes all individuals present in the experimental plots observed from 2011 to 2016 and used for testing model predictions. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.

	ARTR	HECO	POSE	PSSP
observational data	1905	4326	6839	8642
experimental data	168	419	1539	979
Total	2073	4745	8378	9621

TABLE 3.2. Results of linear mixed effects model fit to the spring soil moisture data. The intercept refers to the average soil moisture in the ambient plots. Mean effect and s.e. are shown.

	Model 1
(Intercept)	8.81***
	(1.54)
TreatmentDrought	−3.97***
	(0.45)
TreatmentIrrigation	3.26***
	(0.45)
AIC	3191.87
BIC	3222.92
Log Likelihood	-1588.93
Num. obs.	624
Num. groups: plot	24
Num. groups: PrecipGroup	8
Num. groups: date	5
Var: plot (Intercept)	0.45
Var: PrecipGroup (Intercept)	0.23
Var: date (Intercept)	11.24
Var: Residual	8.90

***$p < 0.001$, **$p < 0.01$, *$p < 0.05$

TABLE 3.3. Parameter estimates from a linear mixed effects model describing average effects of the treatments on daily soil moisture. The intercept coincides with the effects of the drought treatment in the fall. Treatment effects were quantified as the difference in soil moisture between treated plots and ambient controls. Differences are scaled by the s.d. of ambient soil moisture. Mean and s.e. of each parameter estimate are shown.

	Model 1
(Intercept)	−0.57***
	(0.16)
TreatmentIrrigation	1.23***
	(0.03)
rainfallrainy	−0.05
	(0.03)
seasonspring	0.27***
	(0.02)
seasonsummer	0.15***
	(0.02)
seasonwinter	0.25***
	(0.02)
TreatmentIrrigation:rainfallrainy	0.18***
	(0.03)
TreatmentIrrigation:seasonspring	−0.23***
	(0.03)
TreatmentIrrigation:seasonsummer	−0.26***
	(0.03)
TreatmentIrrigation:seasonwinter	−0.33***
	(0.03)
rainfallrainy:seasonspring	−0.23***
	(0.04)
rainfallrainy:seasonsummer	−0.07
	(0.04)
rainfallrainy:seasonwinter	−0.07
	(0.07)
AIC	14581.58
BIC	14695.49
Log Likelihood	-7274.79
Num. obs.	9133
Num. groups: simple_date	1596
Num. groups: PrecipGroup	8
Var: simple_date (Intercept)	0.00
Var: PrecipGroup (Intercept)	0.19
Var: Residual	2.50

***$p < 0.001$, **$p < 0.01$, *$p < 0.05$

TABLE 3.4. Treatment effects on change in cover for each species from start of the experiment to the last year of experiment (2011 to 2016). Intercept gives control effects. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.

ARTR	Estimate	Std.Error	t-value	Pr(>|t|)
(Intercept)	-0.28	0.46	-0.61	0.55
TreatmentDrought	0.94	0.77	1.21	0.24
TreatmentIrrigation	0.89	0.77	1.15	0.27
HECO	Estimate	Std.Error	t-value	Pr(>|t|)
(Intercept)	0.40	0.26	1.54	0.15
TreatmentDrought	-3.00	0.58	-5.18	0.001
TreatmentIrrigation	-0.12	0.5	-0.25	0.81
POSE	Estimate	Std.Error	t-value	Pr(>|t|)
(Intercept)	-0.72	0.46	-1.57	0.13
TreatmentDrought	0.03	0.82	0.03	0.97
TreatmentIrrigation	1.15	0.78	1.47	0.16
PSSP	Estimate	Std.Error	t-value	Pr(>|t|)
(Intercept)	0.02	0.21	0.09	0.93
TreatmentDrought	-0.89	0.38	-2.34	0.03
TreatmentIrrigation	0.15	0.38	0.38	0.70

TABLE 3.5. Selected climate variables for each vital rate model for each species. Correlations and p-values between the chosen variables and the intercept of the baseline model are shown. For ARTR growth and POSE growth and survival, the correlations between the year effects on size and the soil moisture variables are also given. "f" = fall, "su" = summer, "sp" = spring. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.

vital_rate	species	climate variable	Int. cor.	p val.	Size cor.	Size p. val.
growth	ARTR	su.0	-0.49	0.02	0.26	0.26
growth	ARTR	f.0	-0.28	0.23	0.40	0.08
growth	ARTR	sp.1	0.17	0.45	-0.33	0.14
growth	HECO	su.1	0.69	0.00		
growth	HECO	su.0	0.50	0.02		
growth	HECO	f.lag	0.37	0.10		
growth	POSE	f.lag	0.31	0.17	-0.11	0.64
growth	POSE	su.lag	0.29	0.20	-0.20	0.38
growth	POSE	sp.1	0.26	0.25	-0.20	0.38
growth	PSSP	f.lag	0.34	0.13		
growth	PSSP	su.lag	0.25	0.27		
growth	PSSP	f.0	-0.22	0.34		
recruitment	ARTR	su.lag	-0.32	0.16		
recruitment	ARTR	su.0	-0.26	0.25		
recruitment	ARTR	sp.1	0.22	0.34		
recruitment	HECO	su.lag	-0.31	0.18		
recruitment	HECO	su.0	-0.30	0.18		
recruitment	HECO	f.lag	0.19	0.40		
recruitment	POSE	sp.1	0.49	0.02		
recruitment	POSE	f.lag	0.34	0.13		
recruitment	POSE	f.1	0.32	0.16		
recruitment	PSSP	su.lag	-0.52	0.02		
recruitment	PSSP	su.0	-0.48	0.03		
recruitment	PSSP	sp.0	0.30	0.19		
survival	ARTR	su.0	-0.60	0.00		
survival	ARTR	sp.0	-0.41	0.06		
survival	ARTR	su.1	-0.40	0.07		
survival	HECO	sp.0	0.44	0.04		
survival	HECO	sp.lag	0.43	0.05		
survival	HECO	f.1	0.33	0.14		
survival	POSE	sp.0	0.44	0.04	0.22	0.34
survival	POSE	sp.1	0.27	0.23	-0.46	0.04
survival	POSE	f.lag	-0.00	0.99	0.30	0.19
survival	PSSP	sp.0	0.36	0.11		
survival	PSSP	sp.lag	0.34	0.13		
survival	PSSP	su.1	0.26	0.26		

TABLE 3.6. Comparison of model predictions from climate model and baseline model for each species and vital rate. Two prediction scores are reported, MSE and lppd. Lower MSE indicates improved predictions whereas higher lppd indicates improved predictions. Instances where the climate model outperformed the baseline model are marked with "***" in the last column. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.

species	vital_rate	score	climate model	baseline model	diff	improved
ARTR	growth	lppd	-186.08	-189.17	3.09	***
ARTR	growth	MSE	0.55	0.55	-0.00	***
ARTR	recruitment	lppd	-79.05	-77.81	-1.24	
ARTR	recruitment	MSE	169.86	9.47	160.39	
ARTR	survival	lppd	-37.55	-36.42	-1.13	
ARTR	survival	MSE	0.06	0.06	0.00	
HECO	growth	lppd	-475.54	-454.36	-21.18	
HECO	growth	MSE	1.26	1.18	0.09	
HECO	recruitment	lppd	-149.43	-151.60	2.17	***
HECO	recruitment	MSE	288.16	235.57	52.59	
HECO	survival	lppd	-158.99	-147.06	-11.93	
HECO	survival	MSE	0.12	0.11	0.01	
POSE	growth	lppd	-1823.71	-1831.56	7.85	***
POSE	growth	MSE	1.72	1.73	-0.01	***
POSE	recruitment	lppd	-260.05	-257.46	-2.59	
POSE	recruitment	MSE	45.40	37.32	8.08	
POSE	survival	lppd	-698.06	-718.60	20.54	***
POSE	survival	MSE	0.14	0.14	-0.00	***
PSSP	growth	lppd	-1232.93	-1237.92	4.99	***
PSSP	growth	MSE	1.51	1.51	0.00	
PSSP	recruitment	lppd	-271.34	-273.94	2.60	***
PSSP	recruitment	MSE	79.09	42.68	36.41	
PSSP	survival	lppd	-332.47	-307.26	-25.21	
PSSP	survival	MSE	0.11	0.10	0.01	

TABLE 3.7. Mean square error of predicted cover changes and correlations between cover changes predicted and observed. Predictions for the cover changes in the experimental plots were generated wither from the climate or baseline models. Instances where the climate model made better predictions than the baseline model are indicated with the "***" in the last column. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.

species	stat	baseline model	climate model	diff	improved
ARTR	cor	0.48	0.19	-0.29	
ARTR	MSE	0.30	0.30	0.00	
HECO	cor	0.29	0.22	-0.07	
HECO	MSE	0.49	0.57	0.07	
POSE	cor	0.45	0.53	0.07	***
POSE	MSE	0.42	0.41	-0.01	***
PSSP	cor	0.36	0.38	0.03	***
PSSP	MSE	0.39	0.39	-0.01	***

Figures
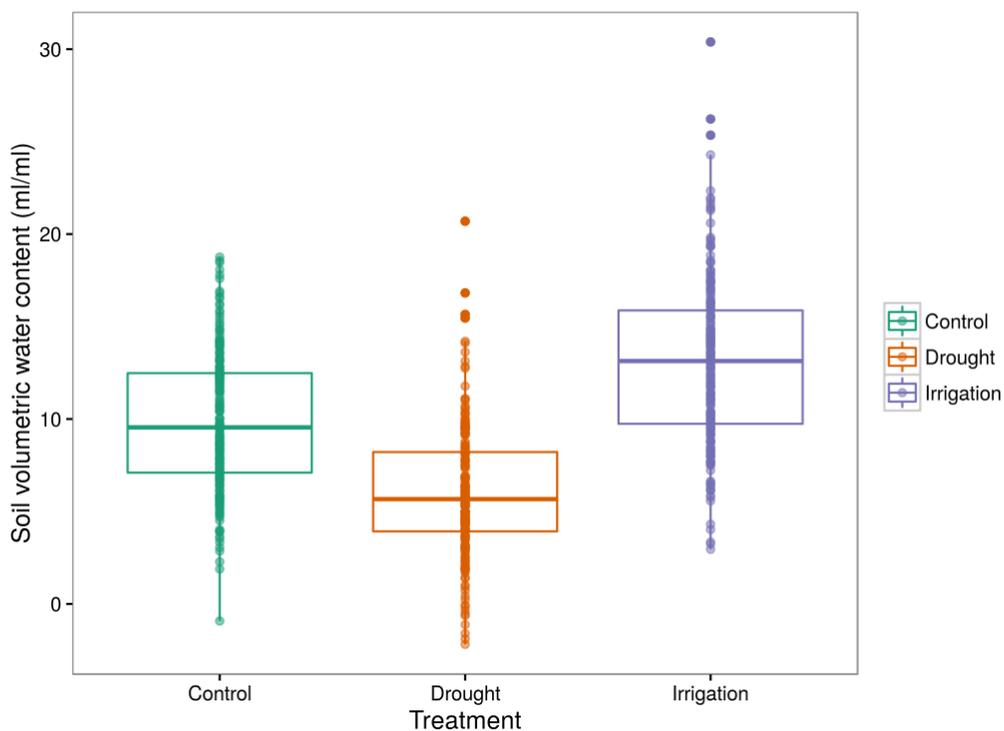
FIG. 3.1. Soil moisture in the upper 5 cm of drought and irrigated plots compared to ambient controls. Soil moisture was measured at six locations around each plot at five different dates during the spring. Box plots show the median soil moisture and the interquartile range. Dots show individual soil moisture measurements. Readings of volumetric soil moisture less than zero were occasionally obtained in very dry soil.
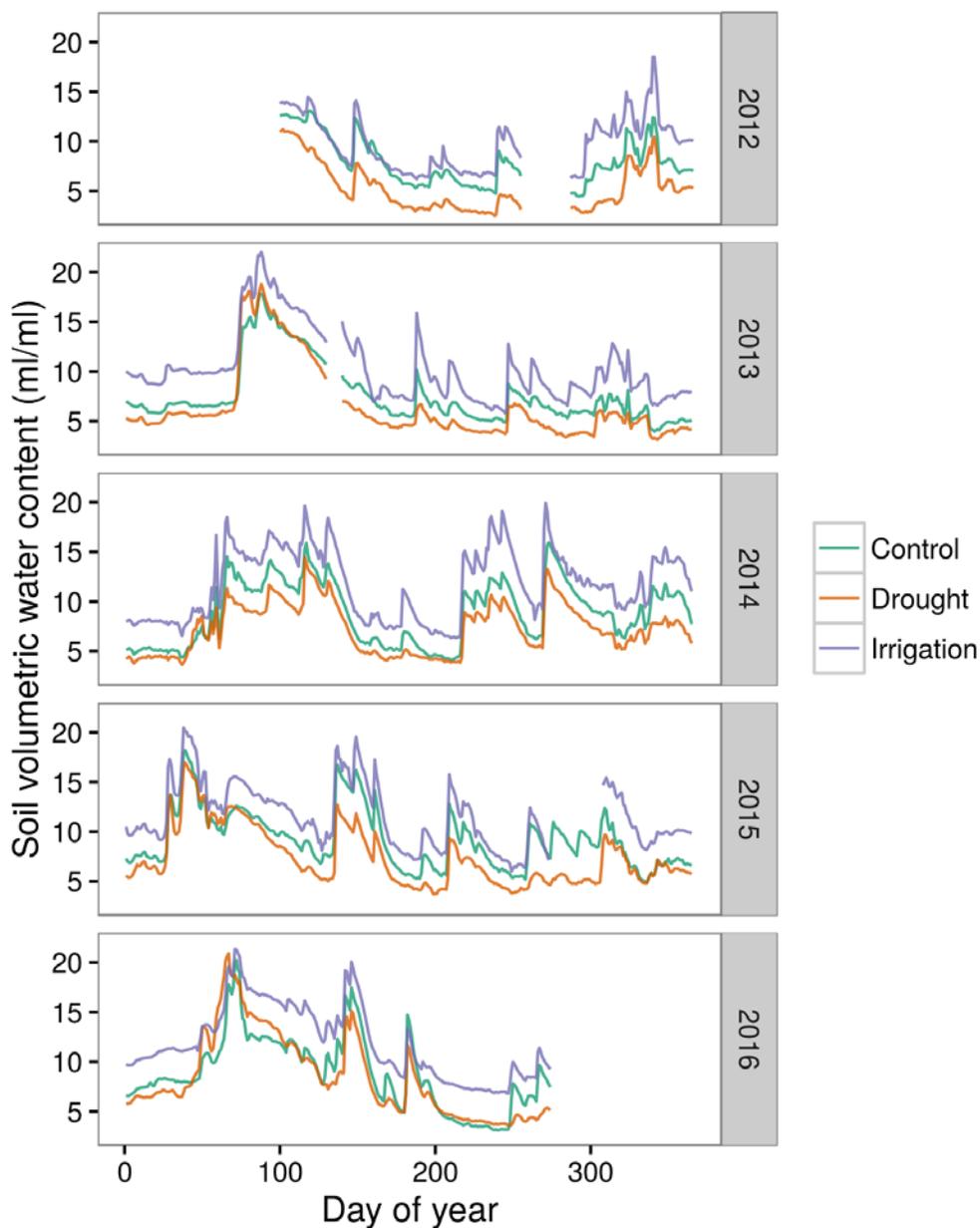
FIG. 3.2. Average soil moisture in the control, drought, and irrigation treatments during each year of the experiment. Soil moisture was monitored in four drought plots, four irrigated plots and four ambient control plots. Two sensors were installed at 5 cm depth at each plot and two at 25 cm and data was logged every 2 hours.
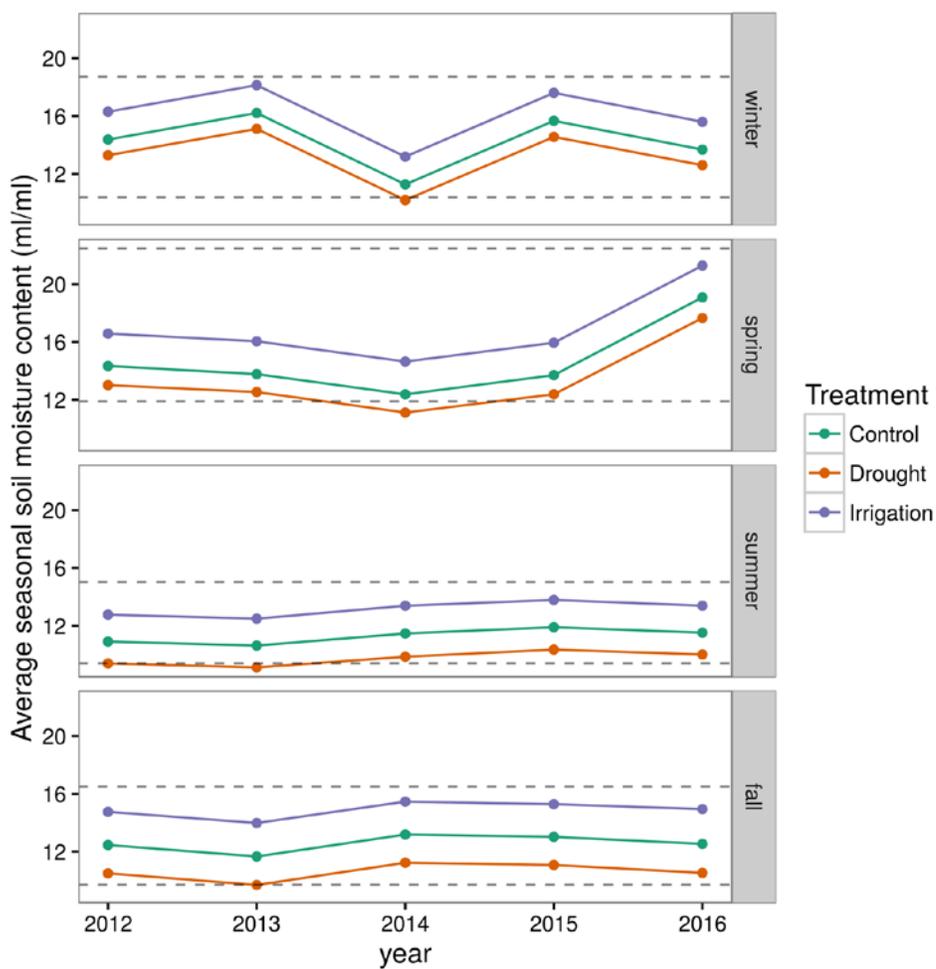
FIG. 3.3. Average seasonal soil moisture in the control, drought, and irrigation treatments during each year of the experiment. The dashed gray lines give the 5th percentile and 95th percentile limits for seasonal soil moisture in the historical record (1929 to 2010).
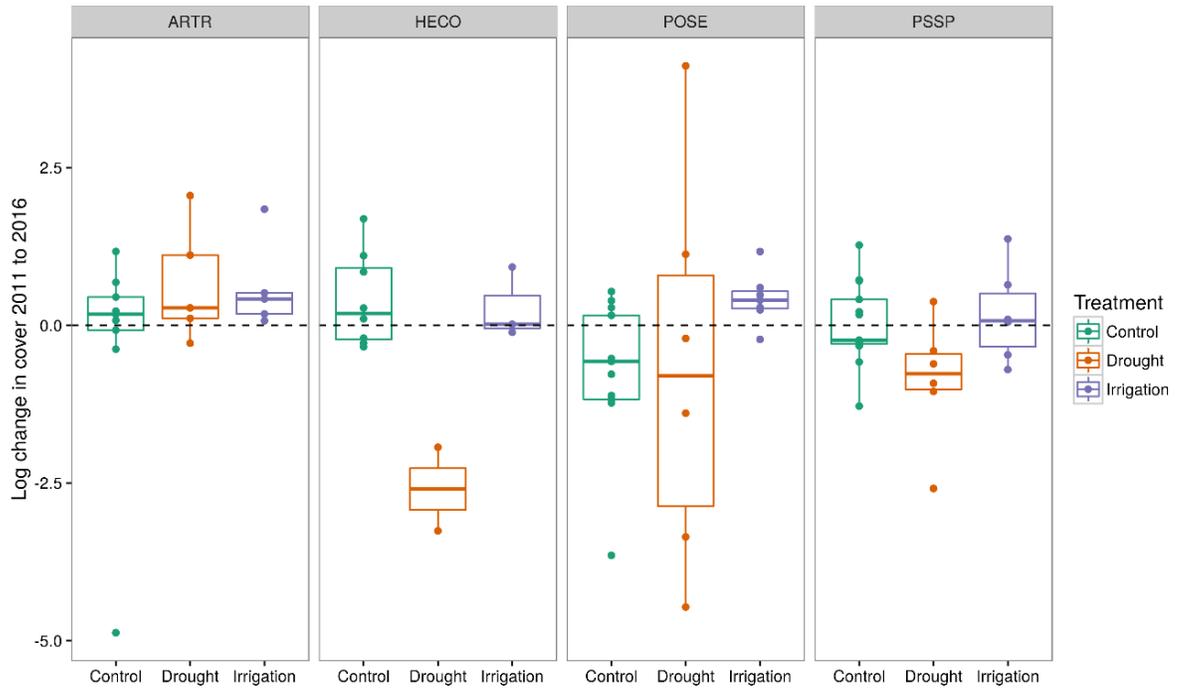
FIG. 3.4. Log change in cover in each of the experimental plots from the pre-treatment monitoring in 2011 to the last year of the experiment in 2016. Box plots show the median cover change and the interquartile range. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.
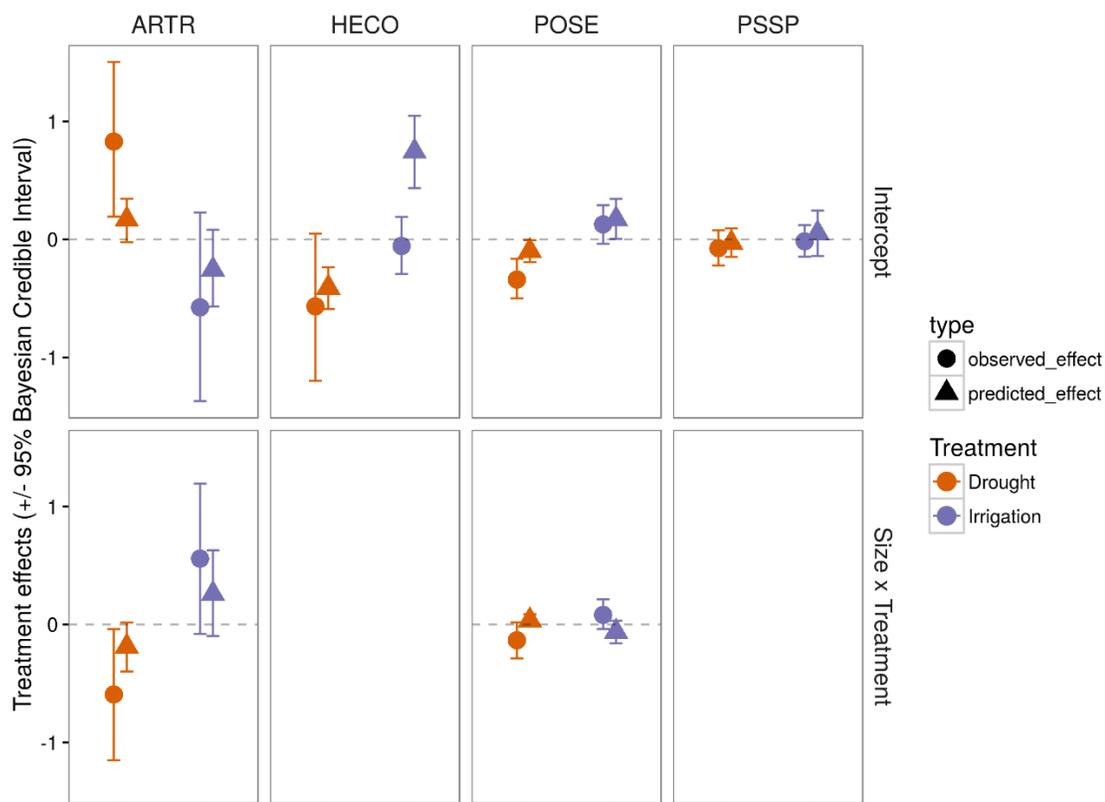
FIG. 3.5. Predicted and observed treatment effects on growth of all four species. We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero. Size by treatment interactions were only fit for *A. tripartita*, and *P. secunda*. Plant size was centered on mean size and scaled by its standard deviation. Observed effects show effects of the experiment taken from the treatment model fitted to all data. Predicted effects show effects predicted by the climate model given the observed effects on soil moisture. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.
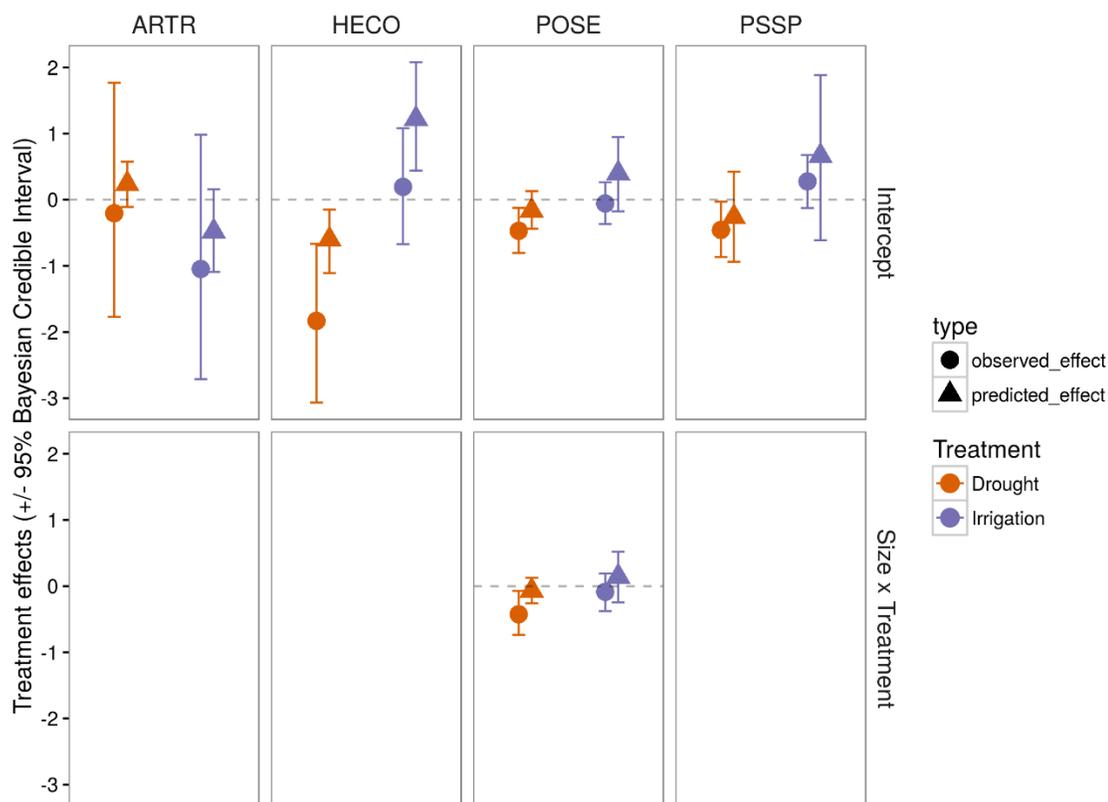
FIG. 3.6. Predicted and observed treatment effects on survival of all four species. We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero. Size by treatment interactions were only fit for *P. secunda*. Plant size was centered on mean size and scaled by its standard deviation. Observed effects show effects of the experiment taken from the treatment model fitted to all data. Predicted effects show effects predicted by the climate model given the observed effects on soil moisture. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.
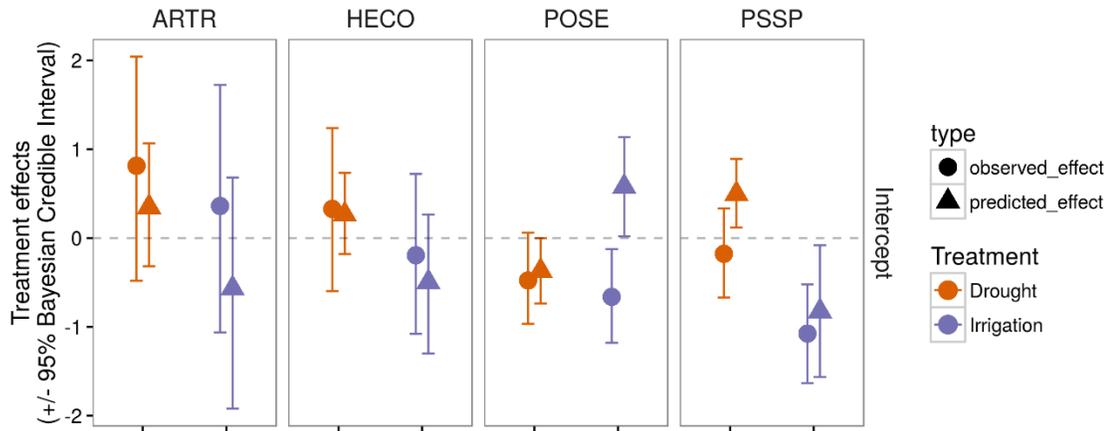
FIG. 3.7. Predicted and observed treatment effects on recruitment of all four species. We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero. Observed effects show effects of the experiment taken from the treatment model fitted to all data. Predicted effects show effects predicted by the climate model given the observed effects on soil moisture. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.
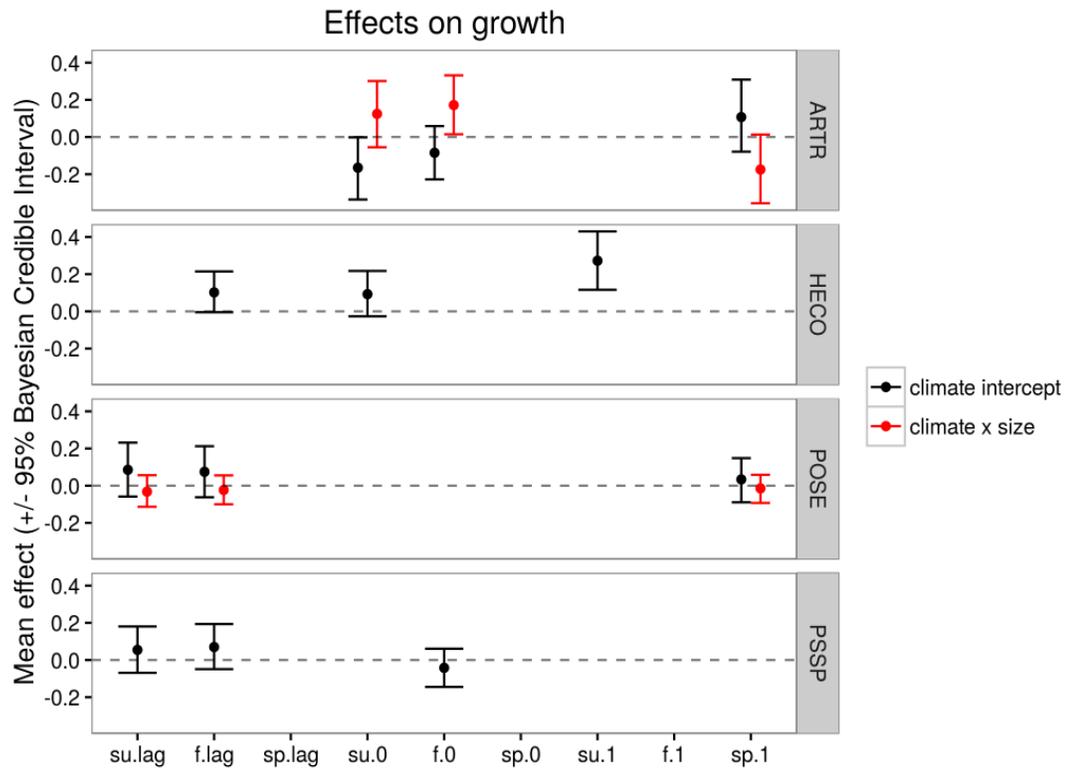
FIG. 3.8. Parameter estimates for the selected seasonal soil moisture covariates on the growth of all four species. Parameters are ordered chronologically from most recent to the current growing season on the right to most distant on the left. Red parameters show size x climate interaction effects. We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.
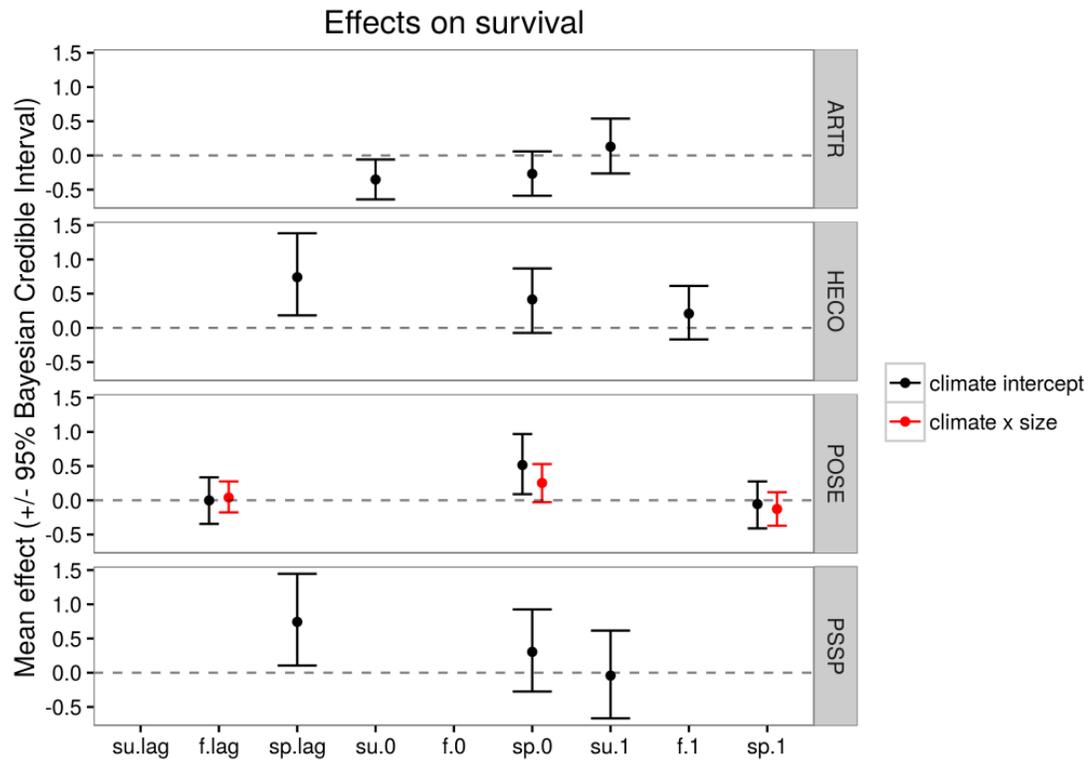
FIG. 3.9. Parameter estimates for the selected seasonal soil moisture covariates on the survival of all four species. Parameters are ordered chronologically from most recent to the current growing season on the right to most distant on the left. Red parameters show size x climate interaction effects. We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.
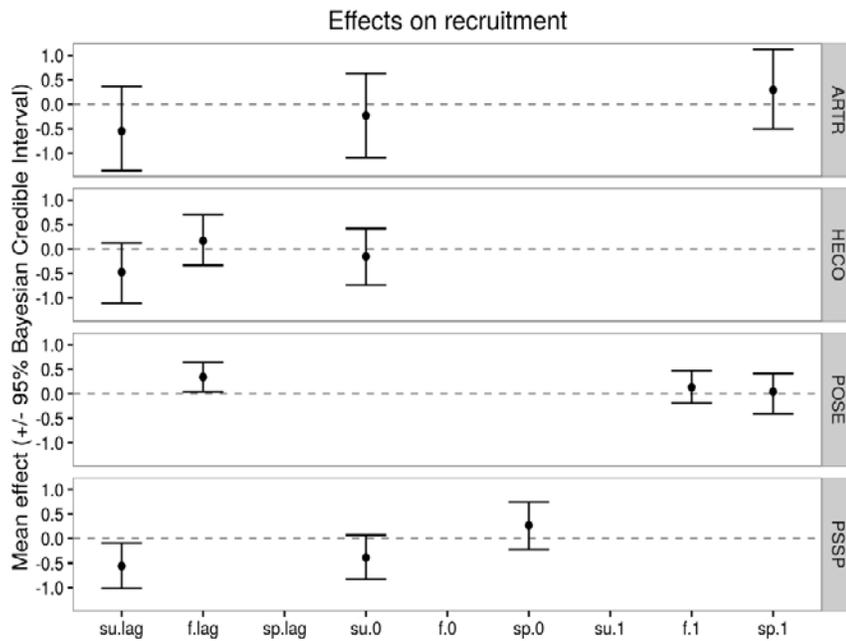
FIG. 3.10. Parameter estimates for the selected seasonal soil moisture covariates on the recruitment of all four species. Parameters are ordered chronologically from most recent to the current growing season on the right to most distant on the left. We assessed a parameter as significant when the 95% Bayesian credible intervals did not overlap zero. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.
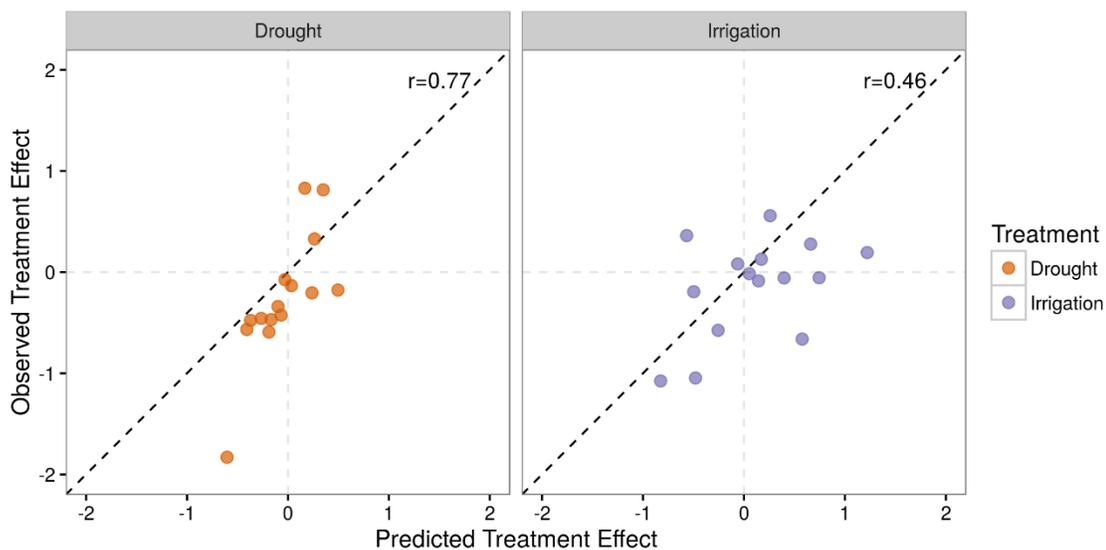
FIG. 3.11. The treatment effects predicted by the climate model compared to the drought effects observed (left side) and irrigation effects observed (right side). Parameters from all species and vital rates are shown together. Observed effects show effects of the experiment taken from the treatment model fitted to all data. Predicted effects show effects predicted by the climate model given the observed effects on soil moisture. The correlation between predicted and observed parameters is given on each panel. Black dashed line shows a 1:1 line.
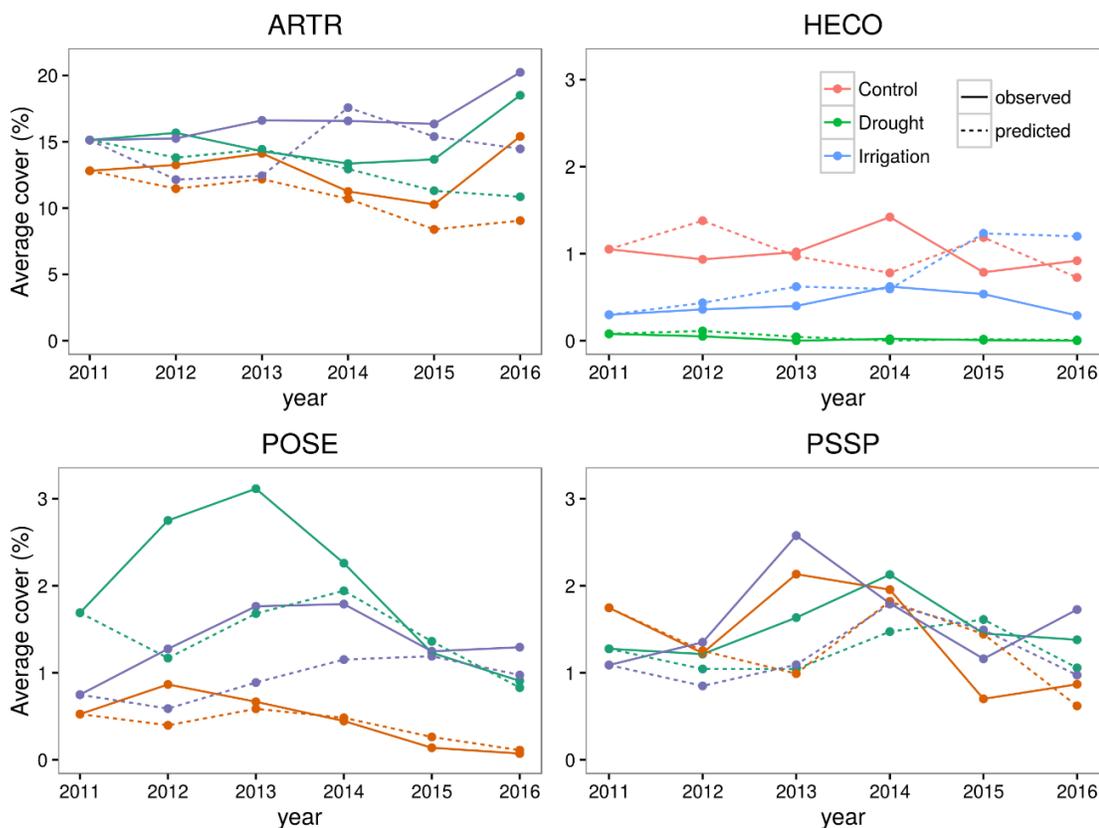
FIG. 3.12. Observed average cover per quadrat in the experimental and control plots (solid lines) and one step ahead cover predictions from the climate model (dashed lines). Cover predictions for each year are generated from the IBM based on the observed distribution of plants in each quadrat in the current year. Quadrat cover was not predicted for the first year of the experiment in 2011. Note the different cover scales for *A. tripartita* and the three grass species. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.
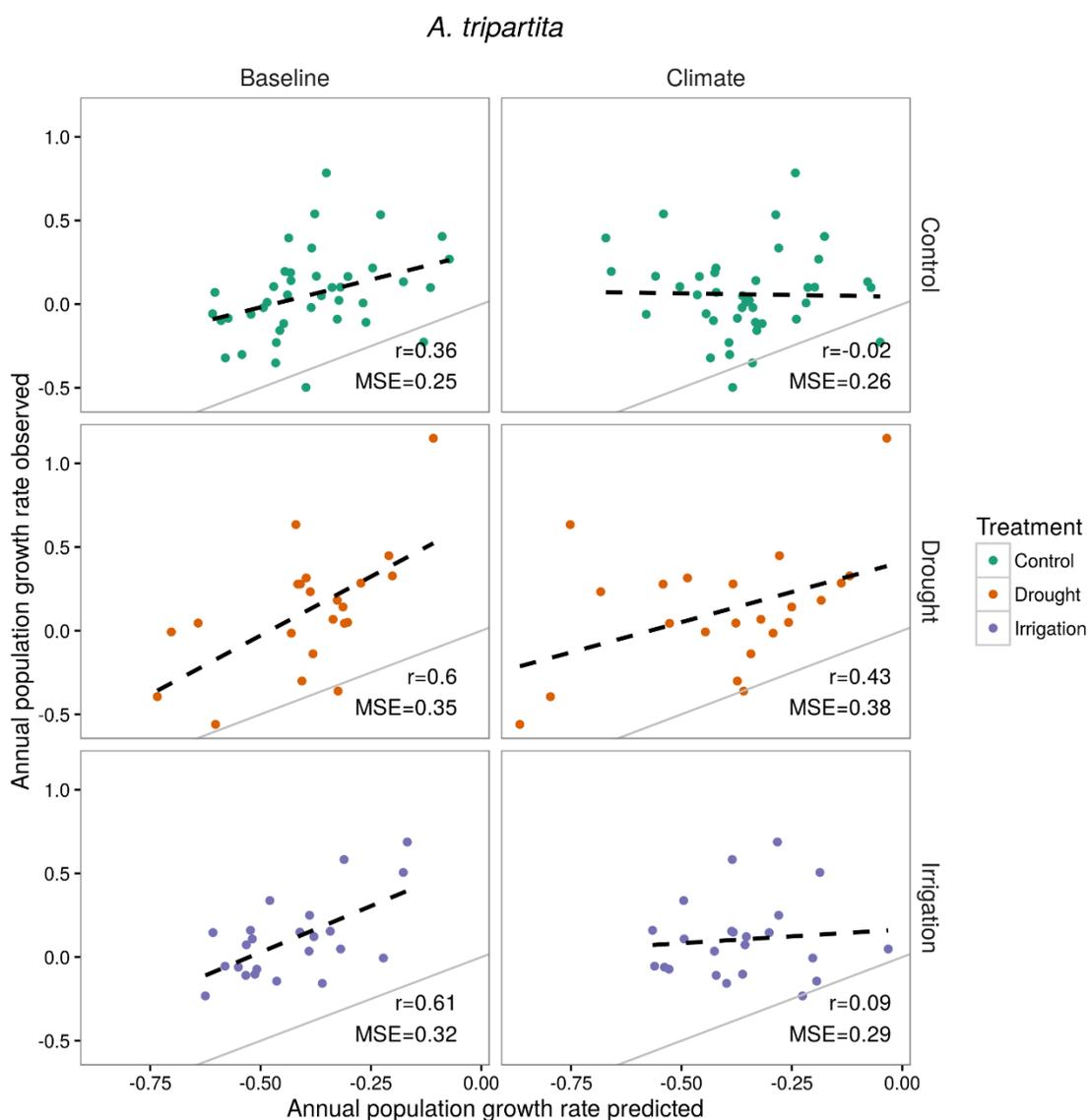
FIG. 3.13. Observed and predicted one step ahead log change in cover of *A. tripartita*. Changes in cover predicted by baseline model (no soil moisture effects) are shown on the left and those predicted by the climate model (including soil moisture effects) are shown on the right. Black dashed lines show the best fit linear regression between predicted and observed growth rates. Gray line shows 1:1 line.
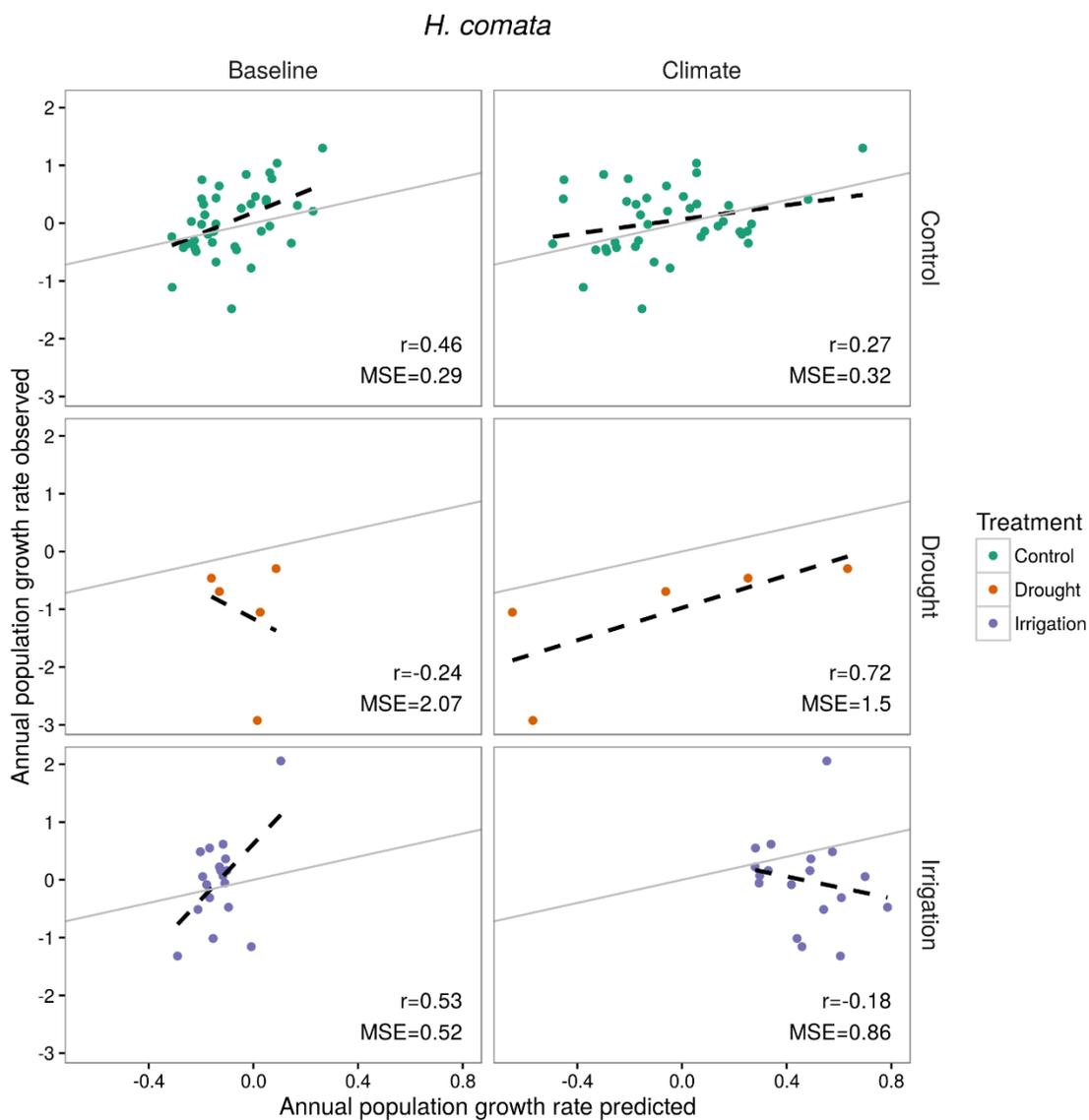
FIG. 3.14. Observed and predicted one step ahead log change in cover of *H. comata*. Changes in cover predicted by the climate model are shown on the left and those predicted by the baseline model are shown on the right. Correlations coefficients between predictions and observations and MSE are shown for each treatment and model. Gray line shows 1:1 line.
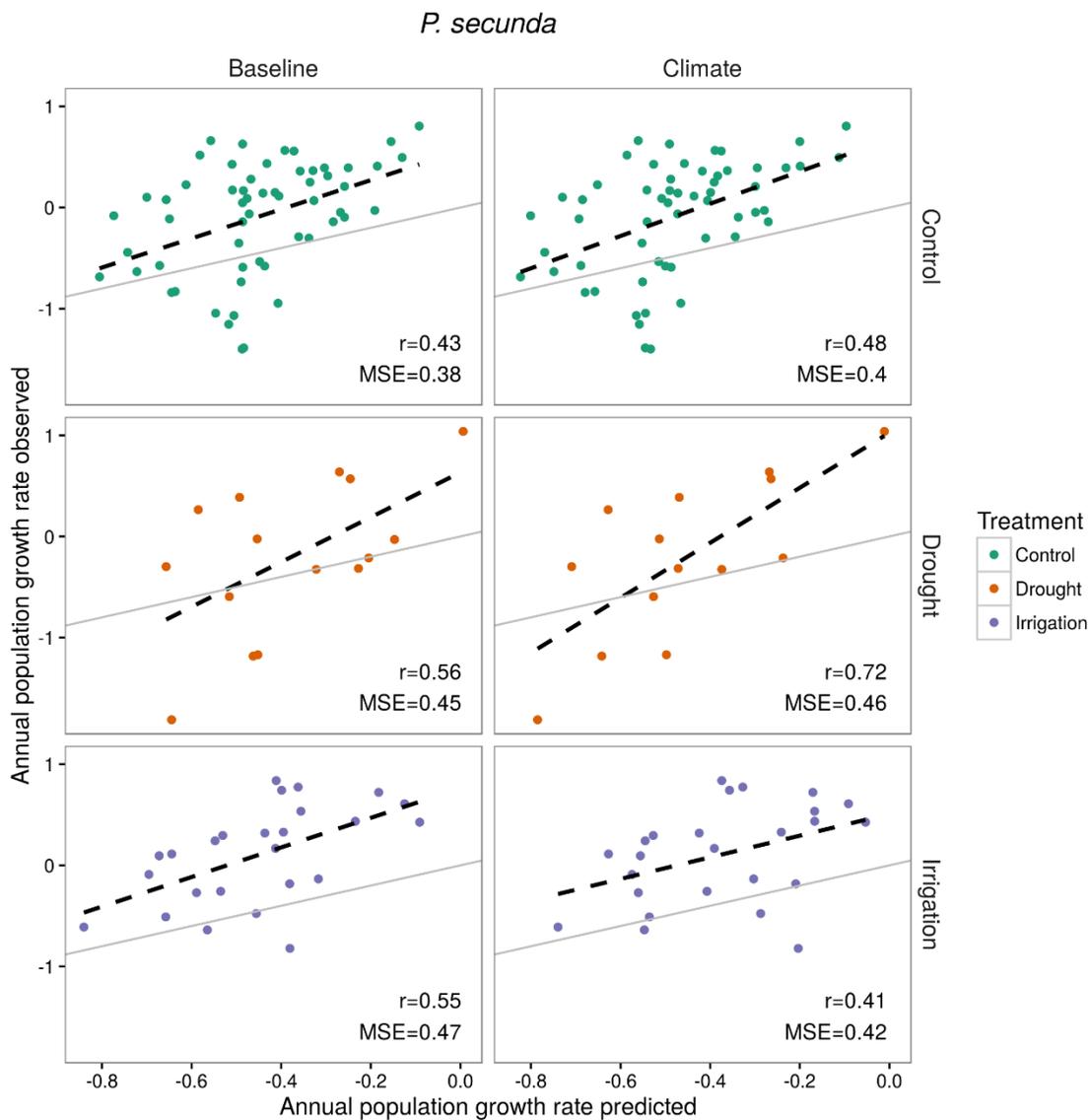
FIG. 3.15. Observed and predicted one step ahead log change in cover of *P. secunda*. Changes in cover predicted by the climate model are shown on the left and those predicted by the baseline model are shown on the right. Correlations coefficients between predictions and observations and MSE are shown for each treatment and model. Gray line shows 1:1 line.
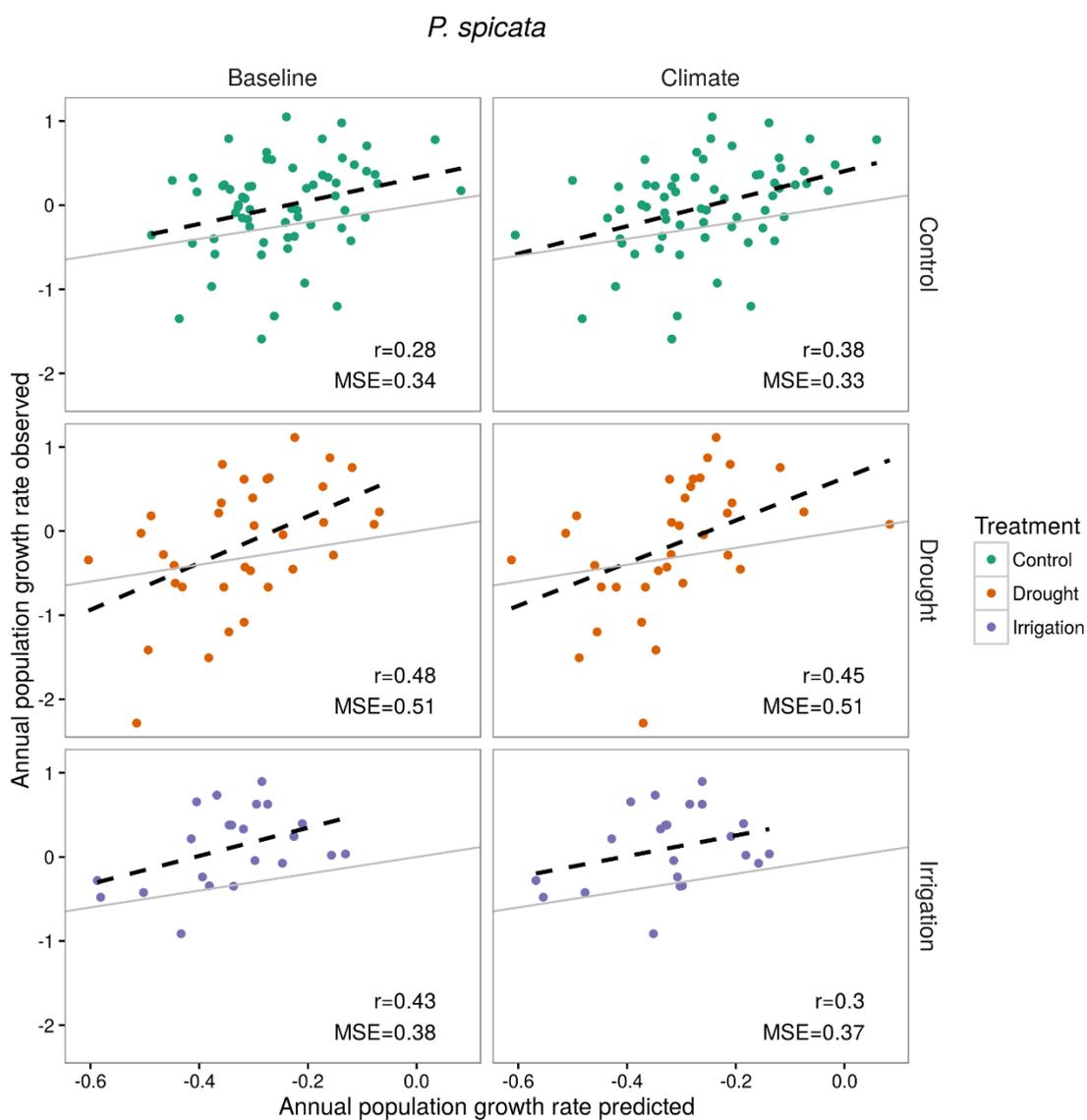
FIG. 3.16. Observed and predicted one step ahead log change in cover of *P. spicata*. Changes in cover predicted by the climate model are shown on the left and those predicted by the baseline model are shown on the right. Correlations coefficients between predictions and observations and MSE are shown for each treatment and model. Gray line shows 1:1 line.

CHAPTER 4

INDIRECT EFFECTS OF ENVIRONMENTAL CHANGE IN RESOURCE

COMPETITION MODELS[1][2]

Abstract

Anthropogenic environmental change can affect species directly by altering

physiological rates or indirectly by changing competitive outcomes. The unknown

strength of competition-mediated indirect effects makes it difficult to predict species

abundances in the face of ongoing environmental change. Theory developed with

phenomenological competition models shows that indirect effects are weak when

coexistence is strongly stabilized, but these models lack a mechanistic link between

environmental change and species performance. To extend existing theory, we examined

the relationship between coexistence and indirect effects in mechanistic resource

competition models. We defined environmental change as a change in resource supply

points and quantified the resulting competition-mediated indirect effects on species

abundances. We found that the magnitude of indirect effects increases in proportion to

niche overlap. However, indirect effects also depend on differences in how competitors

respond to the change in resource supply, an insight hidden in non-mechanistic models.

Our analysis demonstrates the value of using niche overlap to predict the strength of

indirect effects and clarifies the types of indirect effects that global change can have on

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competing species.

Introduction

Anthropogenic environmental change affects species directly but also indirectly by altering interactions with predators, pathogens and competitors (Tylianakis et al. 2008). As a result, competition-mediated indirect effects may alter plant and animal community responses to environmental change (Stacey and Fellowes 2002; Jiang and Morin 2004; Brooker 2006; Tylianakis et al. 2008; Adler et al. 2009; Sletvold et al. 2013). In this paper, we define the effects of environmental change at the level of local population density: the direct effect is the sensitivity of a focal species population to some environmental change while holding other species abundances and interaction effects constant; the net effect is the sensitivity of the focal population to environmental change allowing for other species abundances and interactions to change; and the indirect effect is the difference between the net and direct effects (Adler et al. 2012). More specifically, we can define a competition-mediated indirect effect as the difference between the sensitivity of a focal species to environmental change when the influence of competitors is held constant and the sensitivity of a focal species when the influence of competitors is allowed to change along with the changing environment (fig. 4.1).

Despite the widespread interest in how global change will affect natural communities, only a handful of studies have controlled for both the mechanism of environmental change and the effects of interspecific competition. Experiments in which both the density of competitors and the global change driver are manipulated are ideal for measuring this kind of indirect effect (Jiang and Morin 2004; Adler et al. 2009; Levine et al. 2010; Eskelinen and Harrison 2013), but the effects of competitors and global change

can also be investigated with observational data and statistical and mathematical models

(Lemoine and Böhning-Gaese 2003; Poloczanska et al. 2008; Adler et al. 2012).

Competition mediated-indirect effects range from strong (Eskelinen and Harrison 2013),

to relatively weak (Klanderud 2005; Levine et al. 2010) and can vary depending on the

underlying driver of change (Liancourt et al. 2012). The observed variation in the

strength of competition-mediated indirect effects suggests that improved theory could

help us predict when and where competition is likely to change the net effect of global

change on focal populations.

Adler et al. (2012) linked environmental change and competition-mediated

indirect effects with coexistence theory. The intuition is straightforward: small niche

overlap between competing species implies weak competitive interactions and small

indirect effects of environmental change, while large niche overlap implies strong

competition and large indirect effects. Adler et al. (2012) supported this argument by

analyzing phenomenological competition models in which population growth is limited

by per capita interspecific ($\square_{CF}$, $\square_{FC}$) and intraspecific ($\square_{FF}$, $\square_{CC}$) competition, where the

subscript 'F' refers to a focal species, and 'C' refers to its competitor. Stable coexistence

between competitors requires some form of negative frequency dependence, which

causes a species' growth rate to increase when it is rare, and to decrease when it is

common (Chesson 2000). Adler et al. (2012) used the strength of negative frequency

dependence as a proxy measure for niche overlap: strong negative frequency dependence

should indicate low niche overlap between competitors. In both the theoretical models

and empirical models parameterized with long-term data from a perennial plant

community, they found that the magnitude of indirect effects of climate variation

decreased with increasing negative frequency dependence in a perennial plant community.

Although Adler et al. (2012) links coexistence theory with indirect effects of environmental change, their phenomenological competition framework lacks an explicit connection between species performance and environmental conditions. For example, in the theoretical models Adler et al. (2012) used, it seems unrealistic and arbitrary that hypothetical environmental change affects a species' fecundity but has no effects on other model parameters such as competition coefficients. Models that include the mechanism of competition would provide a more rigorous framework for developing theory about indirect effects and environmental change. In a mechanistic model, a simulated environmental change, such as an increase in resource supply, would simultaneously influence many aspects of performance of both the focal species and its competitor. A second weakness of Adler et al. (2012) is the use of negative frequency dependence as a proxy measure of niche overlap. A more precise measure of niche overlap in terms of phenomenological competition coefficients is given in Chesson (2013 p. 233):

$$Niche\ overlap = \rho,$$

$$\rho = \sqrt{\frac{\alpha_{FC}\alpha_{CF}}{\alpha_{FF}\alpha_{CC}}}$$

(1)

In this definition niche overlap, ρ, is the geometric mean of interspecific interactions divided by the geometric mean of intraspecific interactions. Stable coexistence is possible only if intraspecific competition is greater than interspecific competition, leading to $\rho < 1$.

Our goal is to provide a framework for understanding competition-mediated

indirect effects that will be useful to ecologists working on empirical studies of global change. Our specific objectives are to link phenomenological definitions of niche overlap to parameters in mechanistic resource competition models and to test the prediction that indirect effects between competitors should be greater when niche overlap is large.

General Definition of Competition-Mediated Indirect Effects

As a general example, we start with two functions that give the equilibrium abundances of a focal species (N_F^*) and its competitor (N_C^*):

$$N_F^* = f(S, N_C^*), N_C^* = g(S, N_F^*). \tag{2}$$

We assume that these equilibrium abundances are in some way determined by the shared resources available in the environment, given by S. We are interested in the derivative dN_F^*/dS as a measure of how sensitive the focal species is to a change in the environment. If we assume that both f and g are continuously differentiable functions, we can express their derivatives as a total derivative (Chiang 1984):

$$\frac{dN_F^*}{dS} = \frac{\partial N_F^*}{\partial S} + \frac{\partial N_F^*}{\partial N_C^*}\frac{dN_C^*}{dS}, \frac{dN_C^*}{dS} = \frac{\partial N_C^*}{\partial S} + \frac{\partial N_C^*}{\partial N_F^*}\frac{dN_F^*}{dS}. \tag{3}$$

These equations are immediately useful because they give us the net effects of a change in S as the sum of direct effects and indirect effects. The direct effect is the sensitivity of the focal species to a change in S while holding the competitor's abundance constant at the equilibrium and is given by the partial derivative $\partial N_F^*/\partial S$ above. We can solve for the derivative of the focal species from the equations in (3):

$$\frac{dN_F^*}{dS}\bigg|_{net} = \left(\frac{\partial N_F^*}{\partial S} + \frac{\partial N_F^*}{\partial N_C^*}\frac{\partial N_C^*}{\partial S}\right)\left(1 - \frac{\partial N_C^*}{\partial N_F^*}\frac{\partial N_F^*}{\partial N_C^*}\right)^{-1}. \tag{4}$$

This equation gives us the net sensitivity of the focal species to a change in the resource availability, allowing both the competitor and focal species to respond. We define indirect effects as the net effects minus the direct effects, thus we can solve for indirect effects by subtracting the partial derivative $\partial N_F^*/\partial S$ from the equation above:

$$\frac{dN_F^*}{dS}\bigg|_{indirect} = \frac{dN_F^*}{dS}\bigg|_{net} - \frac{\partial N_F^*}{\partial S}, \tag{5}$$

$$\frac{dN_F^*}{dS}\bigg|_{indirect} = \left(\frac{\partial N_F^*}{\partial S} + \frac{\partial N_F^*}{\partial N_C^*}\frac{\partial N_C^*}{\partial S}\right)\left(1 - \frac{\partial N_C^*}{\partial N_F^*}\frac{\partial N_F^*}{\partial N_C^*}\right)^{-1} - \frac{\partial N_F^*}{\partial S}.$$

We now turn to using more explicit functions to model resource uptake and population growth and also consider the relationship with niche overlap.

Essential Resource Model

For competing plants, accounting for shared abiotic resources—soil nutrients, water and sunlight—is perhaps the most straightforward way to model competition. These resources are often essential: some amount of the resource must be present for the plant to grow and cannot be substituted by another (Tilman 1982). For instance, a non-parasitic plant requires some amount of light in order to photosynthesize; substituting light with other resources—water, CO_2, P—will not mitigate the need for light.

Our two species essential resource competition model follows Tilman (1977; 1982 p. 38). In this model, per-capita growth of the focal species and competitor are determined by the availability of two resources, R_1 and R_2, following a saturating Monod

function:

$$\frac{1}{N_F}\frac{dN_F}{dt} = MIN\left(\frac{r_F R_1}{(R_1 + k_{F1})} - m_F, \frac{r_F R_2}{(R_2 + k_{F2})} - m_F\right),$$

$$\tag{6}$$

$$\frac{1}{N_C}\frac{dN_C}{dt} = MIN\left(\frac{r_C R_1}{(R_1 + k_{C1})} - m_C, \frac{r_C R_2}{(R_2 + k_{C2})} - m_C\right),$$

where r is the maximum growth rate for each species, R is the concentration of each

resource, and m is a resource loss or mortality rate for each species. The k terms

determine the concentration of resource one or two for which growth of each species

equals half the maximum rate. The larger k is the more resource is required for a species

to achieve a positive growth rate. Resources are supplied in proportion to the difference

between an environmental supply point, S, and the current resource concentration, R.

Resources are taken up by each species in proportion to population growth rate and

resource loss/mortality rate (Tilman 1982 p. 46):

$$\frac{dR_1}{dt} = a(S_1 - R_1) - q_{F1}\left(\frac{dN_F}{dt} + m_F N_F\right) - q_{C1}\left(\frac{dN_C}{dt} + m_C N_C\right),$$

$$\tag{7}$$

$$\frac{dR_2}{dt} = a(S_2 - R_2) - q_{F2}\left(\frac{dN_F}{dt} + m_F N_F\right) - q_{C2}\left(\frac{dN_C}{dt} + m_C N_C\right),$$

where a is a resource turnover rate and the q terms (Tilman uses 'c') give the amount of

each resource required for each unit of biomass growth for each species. Each species has

a minimum resource requirement for growth and reproduction to balance mortality and

loss—this resource requirement defines the zero-net growth isoclines (ZNGI) for the

species (Tilman 1982). Coexistence is possible when the ZNGIs cross—meaning that

there is a point where each species is limited by a separate resource (fig. 4.2). This

equilibrium is only stable when each species consumes more of the resource limiting its

own growth than it does of the resource limiting its competitor. For example, in Figure

4.2 the focal species is limited by R_1 and the competitor is limited by R_2, and a stable

equilibrium requires resource consumption and supply rates described by the inequality

(from Tilman 1982, p. 77):

$$\frac{q_{F2}}{q_{F1}} < \frac{S_2 - R_2^*}{S_1 - R_1^*} < \frac{q_{C2}}{q_{C1}}. \tag{8}$$

In other word, the species can only coexist stably when the resource supply point lies

between their resource consumption vectors. Because we are interested in indirect effects

produced by competition, we make the assumption that the conditions for coexistence are

met.

Equilibrium abundances, N_F^* and N_C^*, are reached at resource concentrations R_1^*

and R_2^*. Assuming the focal species is limited by R_1 and the competitor by R_2, we can

solve for the equilibrium abundances, N_F^* and N_C^*, by setting the differential equations in

(7) to zero and setting the resource concentrations to their equilibrium concentrations R_1^*

and R_2^*.

In Appendix D, we show how Chesson's measure of niche overlap, ρ, is related to

the parameters of Tilman's essential resource model. Under the assumption that the focal

species is limited by resource one and the competitor by resource two:

$$\rho = \sqrt{\frac{q_{F2}q_{C1}}{q_{F1}q_{C2}}}, where \frac{q_{F2}}{q_{F1}} < \frac{q_{C2}}{q_{C1}}. \tag{9}$$

The terms q_{F1} and q_{C2} correspond to each species' use of the resource it is most limited

by, and thus determine intraspecific competition effects. As a result, equation (9)

parallels the phenomenological expression for niche overlap in equation (1). If the focal

species uses a very different ratio of resources from its competitor, ρ will be small, while

if it uses a similar ratio of resources, ρ will approach one. Graphing resource

consumption vectors is an intuitive way to assess niche overlap: generally niche overlap

is smaller for a larger angle between species' resource consumption vectors (Petraitis

1989; fig. 4.2) and the greater the area of the parallelogram formed with the resource

consumption vectors as sides (Barabás et al. 2014).

Modeling environmental change

In a mechanistic resource competition model, we can simulate environmental

change as a change in resource supply points, S_1 or S_2. This is a reasonable choice in the

case of direct addition of essential resources such as phosphorous and nitrogen (Jupp and

Spence 1977; Vitousek et al. 1997). It also makes sense when resource supply changes

as an indirect consequence of other types of anthropogenic change. For example, global

warming can increase availability of soil nitrogen (Nadelhoffer et al. 1991), as can

invasion by nitrogen fixing exotic plants (Vitousek and Walker 1989); climate change

can alter water availability (Fensham and Fairfax 2007); forest thinning changes light

availability to understory species (Thomas et al. 1999); and aquatic invasive species can

drive changes in light availability to submerged aquatic plants (Zhu et al. 2006).

For example, if S_1 represents the supply point for nitrogen in the environment, we

can explore the net and indirect effects of anthropogenic nitrogen deposition by

calculating the rate of change in focal species abundance, N_F^*, with respect to S_1,

assuming that other limiting resources such as light are not changing (Dybzinski and

Tilman 2007). Once we solve for N_F^* in the equations above we can then differentiate the

full equation to find the net effect of a change in S_1:

$$\frac{dN_F^*}{dS_1}\bigg|_{net} = \frac{a}{m_F q_{F1}} \left(1 - \frac{q_{C1} q_{F2}}{q_{F1} q_{C2}}\right)^{-1}. \tag{10}$$

Notice that the definition of niche overlap that we derived earlier appears on the right

hand side of the equation above, meaning that we can rewrite (10) as:

$$\frac{dN_F^*}{dS_1}\bigg|_{net} = \frac{\partial N_F^*}{\partial S_1} (1 - \rho^2)^{-1}. \tag{11}$$

The net sensitivity accounts for the fact that the focal species and competitor can respond

to the change in the environment and to each other, achieving new equilibrium

abundances. To find the direct effects we hold competitor abundance constant at its

previous equilibrium and then find the derivative of the focal species abundance with

respect to S_1 at the resource equilibrium:

$$\frac{\partial N_F^*}{\partial S_1}\bigg|_{R_1^*, R_2^*} = \frac{a}{m_F q_{F1}}. \tag{12}$$

Note that in this model of resource competition, at equilibrium each species is

only sensitive to the direct effects of one resource—Liebig's law of the minimum

(Tilman 1982). In this example, the focal species is sensitive only to R_1 and the

competitor only to R_2. We can apply the formula for indirect effects by subtracting the

direct effects from the net effects:

$$\frac{dN_F^*}{dS_1}\bigg|_{indirect} = \frac{\partial N_F^*}{\partial S_1} (1 - \rho^2)^{-1} - \frac{\partial N_F^*}{\partial S_1},$$

$$\tag{13}$$

$$\frac{dN_F^*}{dS_1}\bigg|_{indirect} = \frac{\partial N_F^*}{\partial S_1} \left(\frac{\rho^2}{1 - \rho^2}\right).$$

Equation (13) shows that the indirect effects are proportional to the direct effects

and a second term determined by niche overlap (fig. 4.3). As species become more similar in their resource use, ρ approaches one and the strength of the indirect effect increases. In this case the indirect effect is positive—it amplifies the positive direct effect of the increase in resource supply because we are adding to the resource that is most limiting to the focal species.

Changes in the non-limiting resource

Now consider a change in the supply of the resource that is limiting to the competitor. In our example, a small change in S_2 will not have a direct effect on the focal species, so the net effect must be entirely determined by indirect effects. An increase in S_2 will have a direct positive effect on the competitor and this will reduce the availability of R_1 for the focal species. So we can simply solve for net effects as above:

$$\frac{dN_F^*}{dS_2}\bigg|_{net} = \frac{dN_F^*}{dS_2}\bigg|_{indirect} = \frac{-m_C q_{C1}}{m_F q_{F1}} \frac{a}{m_C q_{C2}} \left(1 - \frac{q_{C1} q_{F2}}{q_{F1} q_{C2}}\right)^{-1}. \tag{14}$$

We can factor out the definition of niche overlap from the first term on the right hand side and rearrange:

$$\frac{dN_F^*}{dS_2}\bigg|_{indirect} = \frac{-a}{m_F q_{F2}} \left(\frac{\rho^2}{1 - \rho^2}\right). \tag{15}$$

The sensitivity to the change in S_2 is similar to the indirect effects of an increase in S_1 seen in equation (13)—it includes a term that increases as niche overlap approaches one and a term describing how the focal species is affected by the changing resource. Note that the indirect effect is negative, an increase in S_2 benefits the competitor at the expense of the focal species (fig. 4.4). The term $a/m_F q_{F2}$ gives sensitivity of the focal species to a change in S_2 in the case that R_2 is limiting. This should not be confused with the partial

derivative $\frac{\partial N_F^*}{\partial S_2}\Big|_{R_1^*,R_2^*}$ which is equal to zero because it is evaluated at the equilibrium where

the focal species is not limited by R_2.

Substitutable Resource Model

The essential resource model may not be appropriate for modeling many

important competitive interactions, including those among animals competing for shared

food resources (Rothhaupt 1988). We extended our analysis to a substitutable resource

competition model following Tilman (1982, p. 270):

$$\frac{1}{N_F}\frac{dN_F}{dt} = r_F \frac{w_{F1}R_1 + w_{F2}R_2 - \tau_F}{k_F + w_{F1}R_1 + w_{F2}R_2 - \tau_F} - D,$$

$$\frac{1}{N_C}\frac{dN_C}{dt} = r_C \frac{w_{C1}R_1 + w_{C2}R_2 - \tau_C}{k_C + w_{C1}R_1 + w_{C2}R_2 - \tau_C} - D,$$

(16)

where R is the concentration of each resource, r is maximum growth rate of each species,

N is the biomass or population of each species, D is a constant mortality rate, k is a half-

saturation constant for each species' use of resources, τ is a minimum amount of total

resource required for growth of each species, and w is a weighting factor that converts the

availability of each resource into its value for each species. Resources are supplied and

consumed according to the equations:

$$\frac{dR_1}{dt} = D(S_1 - R_1) - q_{F1}N_F - q_{C1}N_C,$$

$$\frac{dR_2}{dt} = D(S_2 - R_2) - q_{F2}N_F - q_{C2}N_C,$$

(17)

where S gives the resource supply point of each resource and q gives the amount of each

resource consumed per individual of each species. This model assumes a constant

diffusion of resources (i.e. the animal prey or plant food) to the consumers. Using a

logistic growth function in (17) may be a better way to model biological resources (but see Rothhaupt 1988). Tilman also simplified resource uptake in these equations by assuming that resource uptake is only proportional to consumer abundance: in equation (17), a consumer can continue to draw down resources even when resource availability is infinitesimally small or even negative. This assumption is unrealistic but it should not affect dynamics when considering small changes in resource supply near a positive equilibrium. As in the essential resource model, we will assume that inequality (8) holds: the focal species is limited by R_1 and the competitor is limited by R_2 and the species stably coexist. In Appendix D we show that when these conditions are met niche overlap is defined by the following expression:

$$\rho = \sqrt{\frac{(q_{F1}w_{C1} + q_{F2}w_{C2})(q_{C1}w_{F1} + q_{C2}w_{F2})}{(q_{F1}w_{F1} + q_{F2}w_{F2})(q_{C1}w_{C1} + q_{C2}w_{C2})}} \tag{18}$$

This definition of niche overlap is more complex than the definition for the essential resource model. In this model niche overlap depends not only on the relative resource consumption rates given by the q terms, but also on the relative value of each resource to each species, given by the w terms. Barabás et al. (2014) referred to these two aspects of consumer-resource dynamics as the impact niche, given by the q's, and the sensitivity niche, given by the w's.

In order to define net effects, we first solve for the focal species equilibrium abundance and then differentiate with respect to S_1:

$$\left.\frac{dN_F^*}{dS_1}\right|_{net} = \frac{D}{q_{F1}}\left(1 - \frac{q_{C1}q_{F2}}{q_{C2}q_{F1}}\right)^{-1}. \tag{19}$$

These net effects look much like the net effects in the essential resource model. Note that

the term on the right resembles the definition of niche overlap, except that it does not include the *w* terms.

Next we solve for the direct effects of a change in S_1 on the focal species. The steps for doing this are more complicated than in the essential resource model. When both species are competing for resources, the resource concentration equilibrium (R_1^*, R_2^*) is where their ZNGI's intersect. However, when we change the resource supply point, and hold the competitor's abundance constant at N_2^*, the resource concentration equilibrium shifts slightly along the focal species ZNGI (fig. A1). Solving for the direct effects requires that we first solve for the new focal species equilibrium in light of the changing resource supply point and also the shifted resource equilibrium. Doing this we arrive at this expression for direct effects near the equilibrium:

$$\left.\frac{\partial N_F^*}{\partial S_1}\right|_{R_1^*, R_2^*} = \frac{Dw_{F1}}{q_{F1}w_{F1} + q_{F2}w_{F2}}. \tag{20}$$

The indirect effect is the net effect minus this direct effect:

$$\left.\frac{dN_F^*}{dS_1}\right|_{indirect} = \frac{D}{q_{F1}}\left(1 - \frac{q_{C1}q_{F2}}{q_{C2}q_{F1}}\right)^{-1} - \frac{Dw_{F1}}{q_{F1}w_{F1} + q_{F2}w_{F2}}. \tag{21}$$

This definition of indirect effects does not include the full definition of niche overlap. Specifically, the relative resource values for the competitor (w_{C1}, w_{C2}) found in the niche overlap definition in (18) are not found in this equation. In order to see the relationship with the complete expression for niche overlap, we can rewrite this equation in an unsimplified form that does contain the definition of niche overlap:

$$\left.\frac{dN_F^*}{dS_1}\right|_{indirect} = \left(\frac{\partial N_F^*}{\partial S_1} - \beta\frac{\partial N_C^*}{\partial S_1}\right)\frac{\rho^2}{1 - \rho^2}, \tag{22}$$

$$where\ \beta = \frac{q_{C2}w_{C2} + q_{C1}w_{C1}}{q_{F2}w_{C2} + q_{F1}w_{C1}},$$

$$and\ \frac{\partial N_C^*}{\partial S_1} = \frac{Dw_{C1}}{q_{C2}w_{C2} + q_{C1}w_{C1}}.$$

This formula shows that the size and direction of indirect effects depend not only on niche overlap, but also on the difference in direct effects given by the first term in parenthesis on the right-hand-side of equation (22) (see different lines in Figure 4.5). By comparison, the essential resource model is a special case of the substitutable resource model where one species is insensitive to the direct effects of a change in resource supply. This is seen by setting the partial derivatives that define direct effects on one or the other species in equation (22) to zero and noting the similarity to equations (13) or (15). At the other extreme, if both species respond equally to the change in the resource (scaled by the β term, which is the inverse of the effect of the focal species on the competitor), the indirect effects are equal to zero at all values of niche overlap (line labeled *"0"* in Figure 4.5). We confirmed the analytical results for the essential and substitutable models for a limited range of parameters using simulations in the program R (R Core Team, 2014; see zip file provided as supplementary material online).

Discussion

The uncertain nature of competition-mediated indirect effects limits our ability to make useful predictions about how anthropogenic change will affect populations and communities. Indirect effects may offset or reverse direct effects and appear an unknown time after direct effects have already been observed (Suttle et al. 2007). We hope to reduce some of the mystery surrounding indirect effects by showing how direct and

indirect effects arise in simple mechanistic competition models, and how indirect effect strength can be related to the niche differences that stabilize coexistence between competing species. Consistent with previous work based on phenomenological competition models (Adler et al. 2012), we found that indirect effects were closely related to the stability of coexistence and niche overlap: species that are very similar in their resource requirements are strongly affected by the competition-mediated indirect effects of a change in resource supply points (figs 4.3, 4.4, 4.5). While it is reassuring that our results are consistent with theory developed in non-mechanistic competition models, our analysis goes a step further by using the recently derived definition of niche overlap from Chesson (2013). Moreover, our use of a mechanistic model that explicitly links environmental change with competition provides novel insights about the strength and direction of indirect effects of environmental change.

Our analysis of an essential resource model shows that a change in resource supply can affect a focal species through two separate pathways: if the resource that is most immediately limiting to the focal species at equilibrium is perturbed, then the focal species is affected by a combination of direct and indirect effects (13), and the magnitude of indirect effects increases with the square of niche overlap (fig. 4.3). Alternatively, the focal species can be affected by a change in the supply of the resource that is not immediately limiting to it at equilibrium. In this case, the magnitude of the indirect effect increases with both the niche overlap and the focal species' sensitivity to the changing resource (eq. [15]; fig. 4.4). Indirect effects have their largest magnitude (either positive or negative in sign depending on which resource is perturbed) when niche overlap is high and when the focal species is highly sensitive to the resource that is changing.

Analysis of a substitutable resource model demonstrated that the two distinct modes of indirect effects described above are extremes at either end of a continuum. Indirect effects are strongest when there is a large difference in competing species' direct sensitivities to the change in resource supply and when niche overlap is large (fig. 4.5). In other words, indirect effects require some change in relative fitness between competitors (defined by the difference in direct effects), and this difference is then amplified by the amount of niche overlap. Equation (22) shows that the effect of the focal species on the competitor also matters: when this effect is strong (i.e. small magnitude of β), it decreases the magnitude of the competitor's effect on the focal species.

Competition-mediated indirect effects of a change in resource supply can be summarized as the product of two key components: niche overlap, and the difference between species in direct sensitivities to the change in resource supply (22). In theory, information about direct effects to changes in resource supply should be relatively easy to acquire by studying how species respond to resource manipulation in monoculture (Tilman and Wedin 1991; Adler et al. 2009; Levine et al. 2010). The short-term response of species to an environmental change might also provide information about direct effects (Suttle et al. 2007). Measuring niche overlap is much more data intensive but is possible with a combination of empirical data and models. Chu and Adler (2015) report niche overlap values for 17 pairs of perennial competitors in five different grassland communities and all niche overlap values fell between 0.07 and 0.4. Even in the absence of information about direct effects, these estimates of niche overlap provide information about the maximum magnitude of indirect effects relative to direct effects. Equation (13)

shows that niche overlap needs to be above 0.7 for indirect effect strength to equal direct

effect strength (fig. 4.3); the estimated niche overlap values all fall well below this

threshold, meaning that the magnitude of indirect effects would be much less than the

magnitude of direct effects. While this simple application of our theory implies that

indirect effects might be safely ignored in these communities, it ignores a number of

complications. First, Chu and Adler's niche overlap values are based on a

phenomenological approach and undoubtedly reflect more coexistence mechanisms than

just resource partitioning (Chesson 2000). Second, pairwise niche overlap values may

not be proportional to indirect effects when multiple species are interacting—that is,

indirect effects between two species could depend on changes in the abundance of other

competitors (Levine 1976). Third, our analysis of competitive interactions does not

preclude the possibility of strong indirect effects produced by trophic interactions

(Winder and Schindler 2004; Tylianakis et al. 2008; van der Putten et al. 2010; Barton

and Ives 2013; Ockendon et al. 2014).

We modeled environmental change as an increase or decrease in the resource

supply point. However, there are other ways to model environmental change. We can

categorize changes into three groups depending upon their mechanism. In the first group

are changes to the environment that cause the resource availability to change, but that

leave the species traits that control growth and resource use unchanged. In the second

group are environmental perturbations that cause underlying rates of growth and

mortality to change. For example, higher temperatures might increase mortality or

growth rates (Doak and Morris 2010). Changes in growth or mortality rates will affect

equilibrium resource concentrations and species equilibrium abundances but not niche

overlap. In the third group are environmental changes that affect the amount of resource

taken up per unit of growth, e.g. the q or the w parameters in equations (9) and (18).

Increased atmospheric CO_2 for instance, can increase plant water use efficiency (Lee et

al. 2001; Reich et al. 2001; Ainsworth and Long 2005), and may also reduce light

required for growth (Zotz et al. 2006), while increased temperature may alter nitrogen use

efficiency (An et al. 2005) or water use efficiency (Shaw et al. 2000). Similarly,

temperature can affect the relative rates at which protists consume different species of

bacteria prey, leading to coexistence at some temperatures but competitive exclusion

under others (Jiang and Morin 2004). Unlike environmental changes in the first two

groups, these kinds of changes affect niche overlap between species and make predicting

the outcome of environmental change more difficult. Distinguishing which global

change drivers are likely to affect growth and resource use in the three ways outlined here

should be a useful first step in categorizing competition-mediated indirect effects.

Our conclusions about the size of indirect effects assume that species can coexist

prior to and after anthropogenic change. This assumption is warranted if we are

interested in relatively small environmental changes at a short time-scale when

colonization and extinction of competitors are unlikely. However, environmental change

can rapidly disrupt coexistence in some cases (Jiang and Morin 2004; Stevens et al. 2004;

Suttle et al. 2007). In a resource competition model, coexistence requires that the rate of

resource supply is greater than the minimum amount required for positive population

growth, and also that the ratio of resources supplied falls between the resource use ratios

of the focal species and its competitor (see inequality (8) and fig. 4.2). A sufficient

increase in the supply of one resource can lead to competitive exclusion (fig. 4.1;

Dybzinski and Tilman 2007). Nevertheless, niche overlap still provides important information: the smaller the niche overlap in terms of resource use ratios, the greater the region of coexistence across a gradient of species performance or resource supply (Barabás et al. 2014). Therefore, changes to resource supply should be less likely to lead to exclusion when niche overlap is small. Moreover, resource partitioning is not the only coexistence mechanism; species-specific responses to spatial heterogeneity, temporal heterogeneity and natural enemies may also contribute to coexistence and further decrease niche overlap (Chesson 2000). Our analysis suggests that management that preserves these mechanisms and keeps niche overlap small could help maintain the diversity of plant and animal communities in the face of anthropogenic changes in resource supply.

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Tables

Table 4.1: Symbols used

Variable	Definition
$\dfrac{\partial N_i^*}{\partial S_j}\bigg|_{R_1^*,R_2^*}$	Direct effect of change in supply of resource j on species i evaluated near the resource equilibrium R_1^*, R_2^*
$\dfrac{dN_i^*}{dS_j}\bigg|_{indirect}$	Indirect effects of change in supply of resource j on species i
$\dfrac{dN_i^*}{dS_j}\bigg|_{net}$	Net effect of a change in supply of resource j on species i
a	Resource turnover rate in the essential resource model
D	Constant mortality rate in the substitutable model
k_{ij}	Amount of resource j where population growth rate of species i is half of maximum rate
m	Per capita mortality
N_i	Population density of species i
q_{ij}	Per capita uptake rate of resource j by species i
r	Maximum rate of population growth
R_j	Concentration of resource j
S_j	Resource supply point for resource j
α_{ij}	Per capita competition effects of species j on species i
B	The inverse of the effects of the focal species on the competitor
ρ	Niche overlap
τ_i	The minimum amount of total resource required for growth of species i in the substitutable model.
w_{ij}	A weighting factor that converts the availability of each resource j into its value for each species i in the substitutable model.

Figures
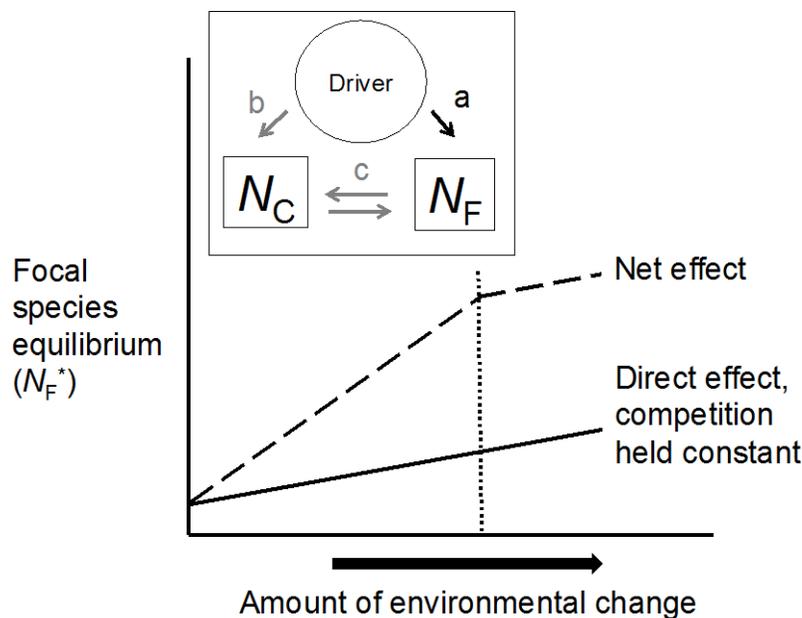
Figure 4.1: The hypothetical change in focal species abundance ($N_F{}^*$) caused by environmental change. When competitive interactions are allowed to change, the focal species abundance increases along with environmental change ("net effect", dashed line). When competitive interactions are held constant at the initial level, the focal species abundance increases less steeply as the environment changes ("direct effect", solid line). The indirect effect is the difference between the slopes of the direct and net effects. In this example the indirect effect amplifies the positive direct effect. To the right of the dotted vertical line the focal species excludes its competitor and there are no competition-mediated indirect effects. Our analysis focuses on indirect effects in the region of parameter space where the focal species and its competitors can stably coexist—left of the dotted line. The inset shows how an environmental driver affects the focal species directly (arrow a) and indirectly by changes in competitive interactions (arrows b and c).
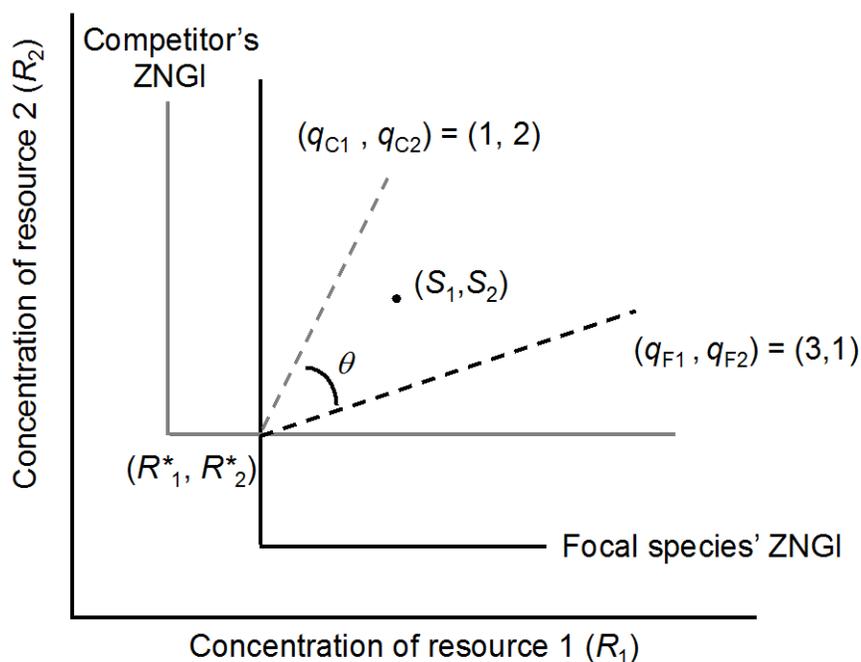
Figure 4.2: A ZNGI plot for two species competing for two essential resources. The resource consumption vectors for the focal species and competitor are given by the values in parentheses and shown with the dashed black and gray lines. Coexistence is possible when the resource supply point (S_1, S_2) falls between the two resource consumption vectors. The niche overlap between species, ρ, will generally decrease as the angle θ between the resource consumption vectors increases. In this example niche overlap would be equal to 0.41 using equation (9).
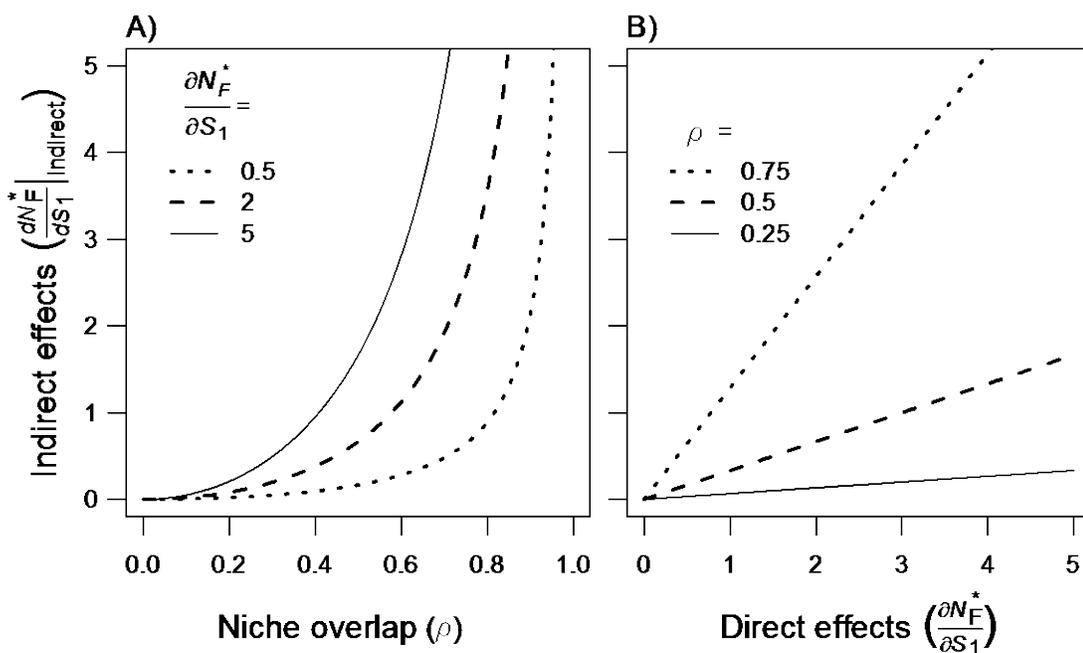
Figure 4.3: Competition-mediated indirect effects on the focal species when there is a change in the supply point of the essential resource (S_1) limiting the focal species. The indirect effects depend on both niche overlap and the direct effect of the change in resource supply point, $(\partial N_F^*/\partial S_1)$. These figures present two different ways of looking at indirect effects: in A) niche overlap is on the x-axis with different lines for three different sensitivities to direct effects. In B) focal sensitivity to direct effects is on the x-axis with different lines for three different values of niche overlap.
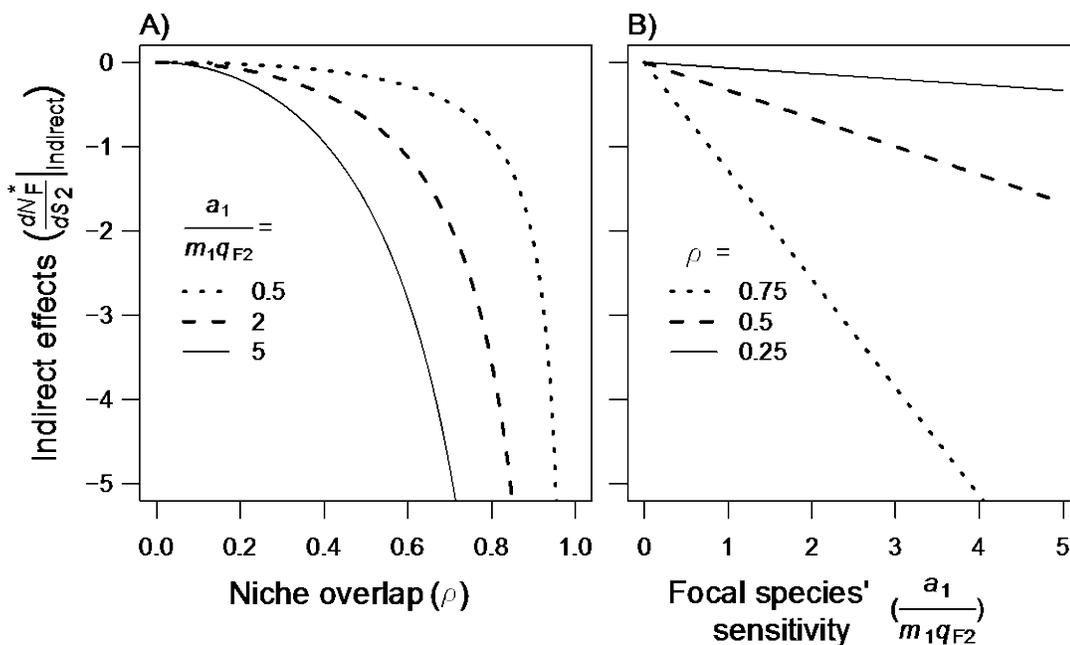
Figure 4.4: Competition-mediated indirect effects on the focal species when there is a change in the supply point for the essential resource limiting to its competitor (S_2). The effects depend on niche overlap (ρ) and the sensitivity of the focal species to the changing resource, $a/m_F q_{F2}$. A) Niche overlap is shown on the x-axis with different lines for three different values of focal species' sensitivity to S_2. B) The focal species' direct sensitivity to S_2 is on the x-axis and different lines are shown for three different values of niche overlap.
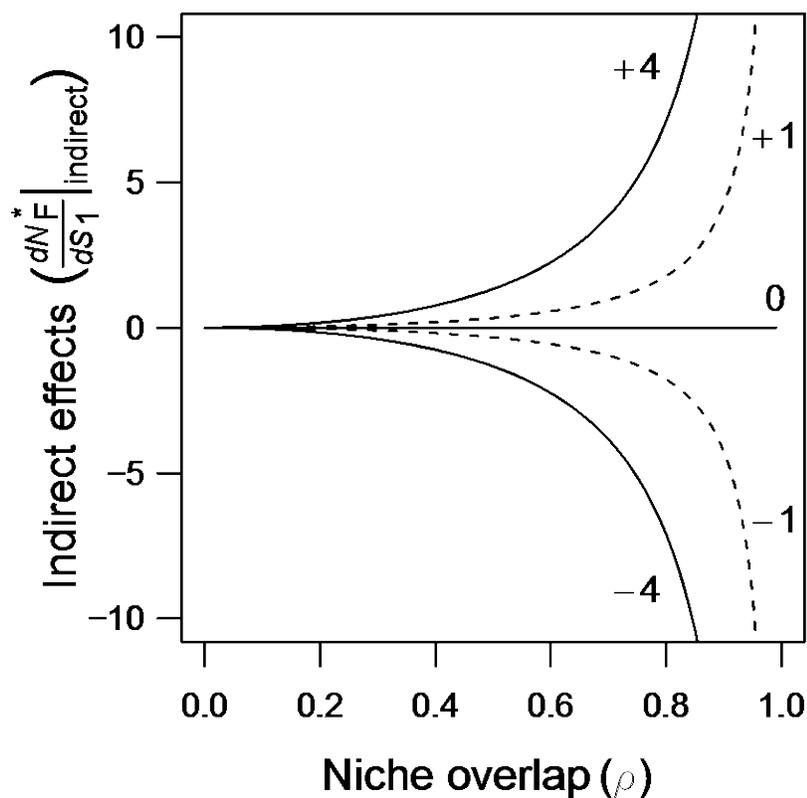
Figure 4.5: Indirect effects of a change in resource supply point in a substitutable resource model. Indirect effects on the focal species increase with niche overlap (ρ), but also depend on each species' direct sensitivity to the change in resource supply (see equation [22]). Numbers next to each line give the difference between the focal species' and competitor's direct sensitivities to a change in resource supply. The indirect effects are positive when the focal species' sensitivity to direct effects is greater than the competitor's, and negative when the focal species' sensitivity is less than the competitor's. All lines are calculated with $\beta = 1$ in equation (22).

CHAPTER 5

CONCLUSION

Our work shows the value of considering population and community responses to climate change across a wide range of scales and with observational data, experiments and theory. Observational, experimental and theoretical studies lead us to a number of conclusions about the future effects of climate change on sagebrush steppe and on plant communities more generally. First we believe climate change may have strong effects on sagebrush steppe, through direct effects of increasing temperature on sagebrush, and effects of changing precipitation on dominant perennial grasses. Second we show that at least for some plant species, long-term observational data and population models can be used to predict the effects of climate change in the future. And third, the indirect effects of climate change among plants of sagebrush steppe are likely to be weak when species respond in similar directions to the effects of climate change and when niche overlap between the species is small.

In a range-wide analysis of big sagebrush population response to climate variation, we showed that sagebrush cover tends to increase in response to warm years in cold sites and decrease in response to warm years in hot sites. This coherent range-wide pattern is consistent with the hypothesis that growing season temperature limits this species' distribution. Based on this response we predict that sagebrush abundance across its range may shift in response to warmer conditions in the future: increasing in abundance in the colder parts of its range and decreasing in abundance in the hotter parts of its range as the climate warms. While similar to the predictions made by species distribution models for sagebrush (Schlaepfer et al. 2012, Still and Richardson 2015), we

arrive at this prediction using a distinct modeling approach and an independent set of data. Our work will be of immediate value to ongoing conservation planning for the Greater Sage-Grouse (*Centrocercus urophasianus*) (Coates et al. 2016).

Working at a much finer spatial and demographic scale, we analyzed the demographic responses of four dominant sagebrush steppe species to natural climate variation in a long term observational dataset. As in our first analysis, we used the temporal patterns in these data to infer the effects of climate change on each species' population and then used this knowledge to predict the species' responses to variation in future precipitation. However, unlike our first analysis, we went an important step further and validated the accuracy of our population-level predictions. We did this by conducting a drought and irrigation experiment and comparing the effects in the experiment to the effects we predicted from the observational data. While ecologists often make predictions about the effects of climate change from observational data, there have been few tests of the accuracy of these predictions (Adler et al. 2013, Houlahan et al. 2016). Our success predicting the population-level response of two species, and the fact the predicted effects of drought and irrigation in our experiment largely matched those observed, should give population ecologists hope that many of the correlations between climate variation and species performance we see in observational data do represent real effects of climate and not spurious correlations (Hilborn 2016).

Obviously any prediction for the future effects of climate change on sagebrush steppe must adequately predict the effects of climate change on its namesake species. Climate change is forecast to have variable and region specific effects on the precipitation regimes of sagebrush ecosystems in the coming decades. Sagebrush ecosystems in the

southern parts of the region are likely to see decreases in winter and spring precipitation and increases in drought, while in the north, winter precipitation may increase, and increased precipitation variability and extremes are likely throughout the region (Garfin et al. 2014, Mote et al. 2014).

Our results help us better understand and predict the future effects these changes in precipitation will have on sagebrush. Despite the arid setting, we did not always find strong positive effects of precipitation on plant performance in our first two analyses. At the regional scale, we hypothesized that sagebrush would show a strong positive response to precipitation in the drier parts of its range and possibly a negative response to precipitation in the wettest parts of its range. This pattern would suggest that range limits of sagebrush distribution across climate gradients represent the limits of the fundamental niche of this species with respect to precipitation (Lee-Yaw et al. 2016). In fact, we saw a different pattern—sagebrush cover actually showed a weak negative response to precipitation in the driest sites and a positive response in the wetter sites. This pattern would seem to indicate that the population abundance of sagebrush in dry parts of its range is not limited by precipitation. In our experimental study, conducted at a relatively cold and dry sagebrush steppe, we also found that sagebrush did not necessarily suffer from decreased precipitation. At this site we confirmed a pattern that we observed in long-term observational data, three-tip sagebrush, a close relative of big sagebrush, showed a positive response to experimentally imposed drought conditions. While three-tip sagebrush and big sagebrush are different species, the similar response of three-tip sagebrush in the experiment should lend credence to the negative effects of precipitation we saw in the multi-site sagebrush cover analysis.

In contrast, our research clearly highlights the important role that temperature may have on sagebrush in this region. We found strong responses of big sagebrush to annual temperature in our multi-site analysis. And while we did not examine the effects of temperature directly in our experimental prediction study, we note that previous analyses from our field site showed strong negative and positive effects of temperature on three-tip sagebrush (Dalgleish et al. 2010, Adler et al. 2012). The contrasting and strong effects of temperature on sagebrush clearly deserve further study.

One factor that ecologists often cite that could lead to errors in our predictions of the effects of climate change is the potential for biotic indirect effects (Suttle et al. 2007). For instance, in the sagebrush steppe we studied, the negative responses of grasses to drought could lead to increased abundance of competitors such as sagebrush. Our third study of indirect effects in competition models does not deny this possibility, but it sheds some light on how and when these indirect effects may be strongest. We show that a measure of competitive coexistence, niche overlap, is intimately related to the strength of competition-mediated indirect effects. Our analysis goes beyond previous investigations of indirect effects by using two mechanistic models of resource competition that allow us to tie environmental change explicitly to direct and indirect effects on species abundance. Our work demonstrates two key insights into indirect effects that we believe will be valuable to theoretical and applied ecologists alike: 1) indirect effects are weak when coexistence is stabilized by low niche overlap; and 2) indirect effects are strongest when species have different direct sensitivities to the driver of environmental change. Recent research suggests that in many plant communities, including the sagebrush steppe, the niche overlap between species is relatively low and therefore the competition-mediated

indirect effects of climate change in these systems may be weak (Chu et al. 2016).

However, the fact that perennial grasses and sagebrush sometimes responded in opposite

directions to the effects of drought in our experiment, should increase the magnitude of

indirect effects between these species. A larger scale climate manipulation experiment

controlling for both competitor density and precipitation could test these hypotheses

(Prevéy et al. 2010, Levine et al. 2010).

Taken together we believe our work shows the value of considering the effects of

climate change at multiple scales and levels of ecological complexity, how quantitative

predictions from observational data can be directly tested with field experiments, and

how theory may help reduce some of the uncertainty in the effects of climate change.

From our work alone we cannot forecast the fate of any plant population or community

but we believe our research will provide a valuable guide for future efforts to predict the

effects of climate change on plant communities.

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APPENDICES

Appendix A: Additional Tables and Figures for "Sagebrush (*Artemisia tridentata*)

Response to Interannual Climate Variation Changes Across

the Species Range"

Table A1. Coefficients from a linear mixed effects model fit to Wyoming sagebrush data (n = 2989). Production indicates the difference between data estimating sagebrush cover (%) and production (g per m^2). Estimates for *a* and *b* correspond to the variables in the Gompertz population model described in eq. 1. LRT and P(χ^2) give the likelihood ratio and p-value of the likelihood ratio test on the climate interaction effects. Climate variables are defined in the main text.

	Estimate	Std. Error	t value	LRT	P(χ^2)	
a	1.86	0.14	12.99			
b	0.07	0.03	2.49			
production	0.53	0.60	0.88			
production:b	0.06	0.14	0.40			
ppt	0.02	0.01	2.44			
ppt_lag	-0.01	0.01	-2.90			
tmax	-0.19	0.11	-1.71			
tmax_lag	0.26	0.37	0.71			
ppt:ppt_avg	-0.08	0.03	-2.39	5.75	0.02	*
ppt_lag:ppt_avg	0.05	0.02	2.66	7.21	0.01	*
tmax:tmax_avg	0.01	0.01	1.77	3.27	0.07	
tmax_lag:tmax_avg	-0.01	0.02	-0.75	0.6	0.44	

Table A2. Coefficients from a linear mixed effects model fit to mountain sagebrush data (n = 871). Production indicates the difference between data estimating sagebrush cover (%) and production (g per m^2). Estimates for a and b correspond to the variables in the Gompertz population model described in eq. 1. LRT and P(χ2) give the likelihood ratio and p-value of the likelihood ratio test on the climate interaction effects. Climate variables are defined in the main text.

	Estimate	Std. Error	t value	LRT	P(χ^2)	
a	1.66	0.34	4.93			
b	-0.06	0.06	-1.01			
production	3.38	2.26	1.50			
production:b	-0.23	0.68	-0.34			
ppt	0.04	0.02	2.23			
ppt_lag	0.02	0.01	1.55			
tmax	0.11	0.29	0.39			
tmax_lag	1.99	0.81	2.47			
ppt:ppt_avg	-0.06	0.04	-1.70	3.15	0.08	
ppt_lag:ppt_avg	-0.02	0.02	-0.97	1.12	0.29	
tmax:tmax_avg	-0.01	0.02	-0.44	0.25	0.62	
tmax_lag:tmax_avg	-0.10	0.05	-2.05	4.67	0.03	*

Table A3. Coefficients from a linear mixed effects model fit to basin big sagebrush data (n = 250). Production indicates the difference between data estimating sagebrush cover (%) and production (g per m2). Estimates for *a* and *b* correspond to the variables in the Gompertz population model described in eq. 1. LRT and P(χ2) give the likelihood ratio and p-value of the likelihood ratio test on the climate interaction effects. Climate variables are defined in the main text.

	Estimate	Std. Error	t value	LRT	P(χ^2)
a	0.35	0.26	1.35		
b	0.48	0.11	4.46		
production	1.16	0.50	2.32		
production:b	-0.20	0.25	-0.81		
ppt	0.01	0.07	0.07		
ppt_lag	-0.02	0.05	-0.36		
tmax	-0.95	0.59	-1.61		
tmax_lag	1.98	2.25	0.88		
ppt:ppt_avg	0.08	0.24	0.32	0.06	0.8
ppt_lag:ppt_avg	0.10	0.17	0.59	0.21	0.65
tmax:tmax_avg	0.05	0.03	1.78	2.95	0.09
tmax_lag:tmax_avg	-0.10	0.12	-0.84	1.03	0.31
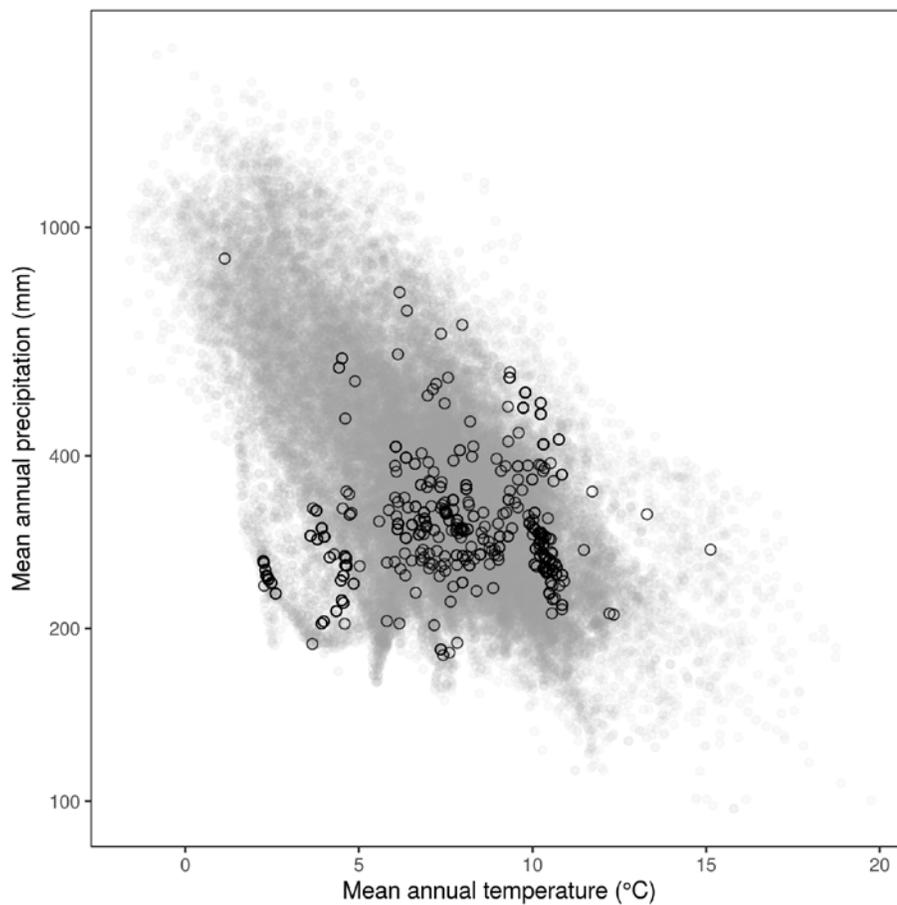
Figure A1. Comparison of range-wide climate niche of sagebrush to multi-year sagebrush monitoring sites. Gray circles show the climate coordinates of locations with sagebrush. Black circles show the climate coordinates for plots with multi-year sagebrush data used in this study. Data for sagebrush occurrence is drawn from the USGS SAGEMAP dataset (http://sagemap.wr.usgs.gov/).
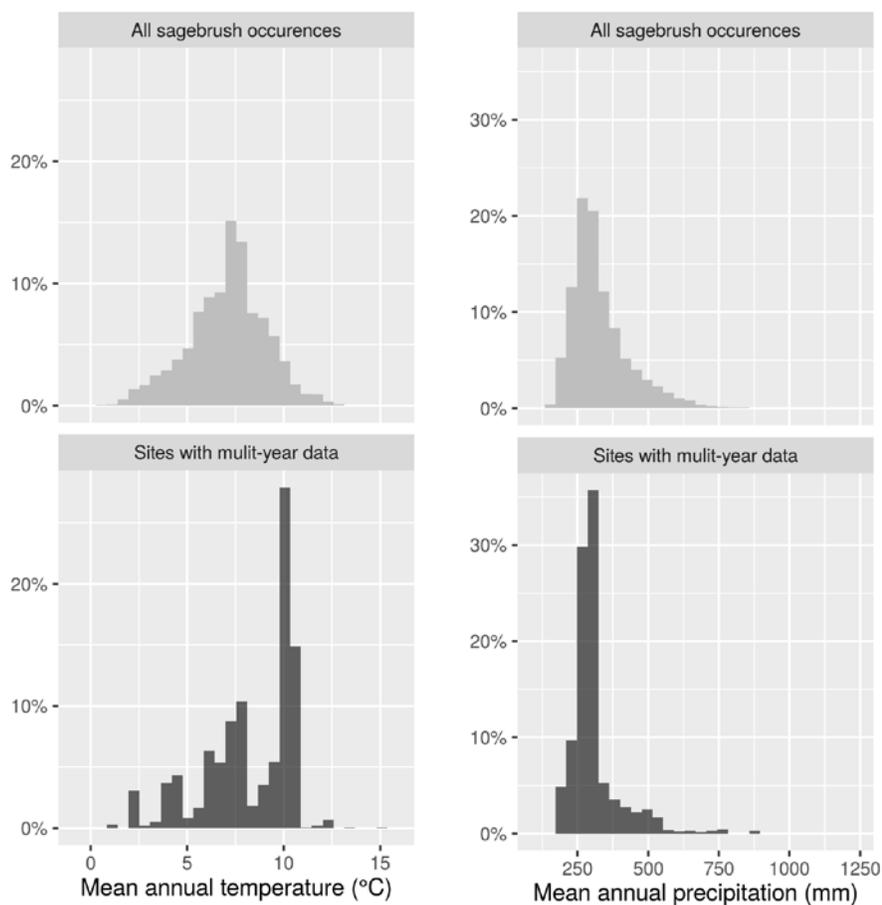
Figure A2. Comparison of range-wide climate niche of sagebrush to multi-year sage-brush monitoring sites. Upper histograms show the frequency of sagebrush dominated areas across mean annual temperature and mean annual precipitation. Lower histograms show the frequency of plots with multi-year sagebrush data used in this study. Data for sagebrush occurrence is drawn from the USGS SAGEMAP dataset (http://sagemap.wr.usgs.gov/).
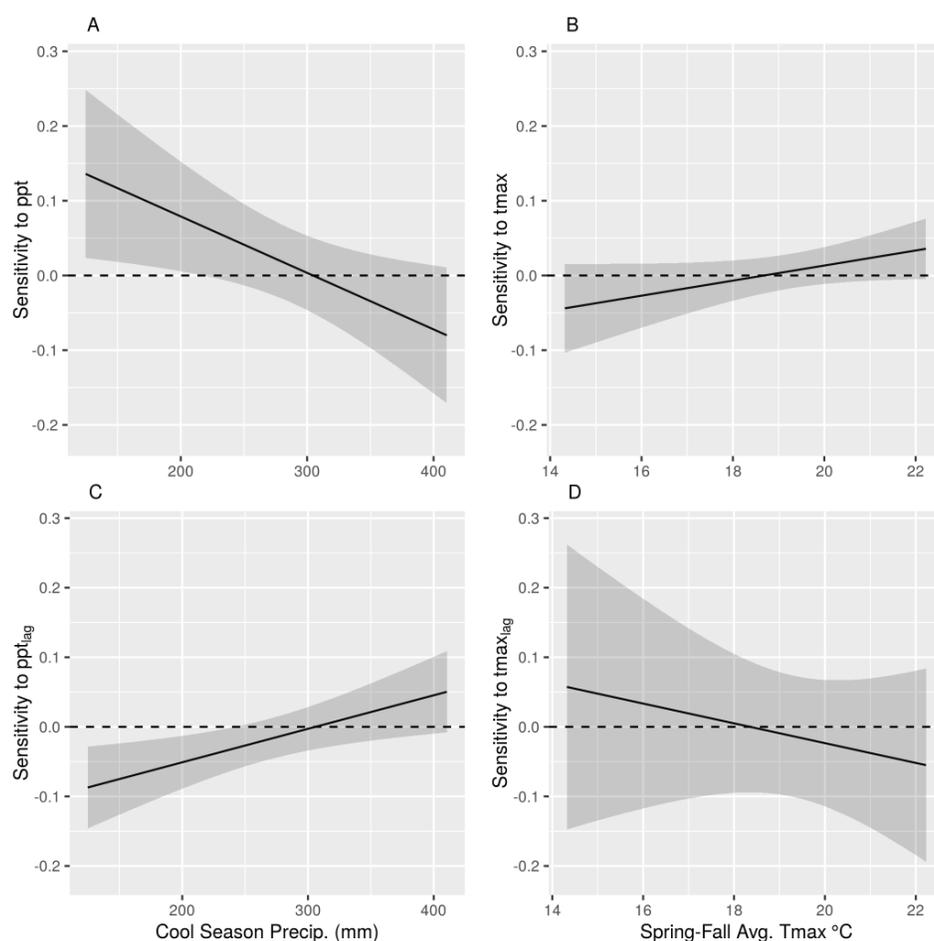
Figure A3. Sensitivity of Wyoming sagebrush abundance to annual climate covariates plotted against average site climate. Sensitivity is defined as the log change in sagebrush abundance produced by a 10 cm increase in precipitation (A, C) or a 1°C increase in temperature (B, D). Effects below zero indicate where above average temperatures or precipitation would decrease population size, while effects above zero indicate where above average annual temperature or precipitation would increase population size. Gray areas show 95% confidence intervals.
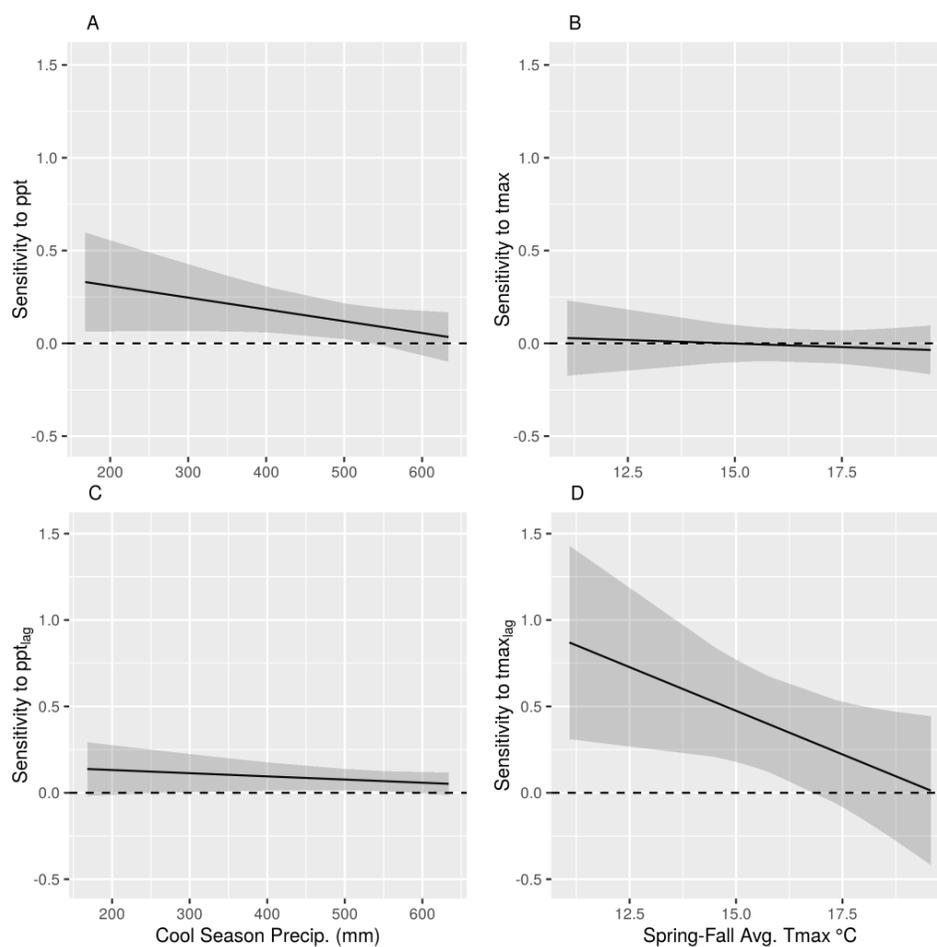
Figure A4. Sensitivity of mountain sagebrush abundance to annual climate covariates plotted against average site climate. Sensitivity is defined as the log change in sagebrush abundance produced by a 10 cm increase in precipitation (A, C) or a 1°C increase in temperature. Effects below zero indicate where above average temperatures or precipitation would decrease population size, while effects above zero indicate where above average annual temperature or precipitation would increase population size. Gray areas show 95% confidence intervals.
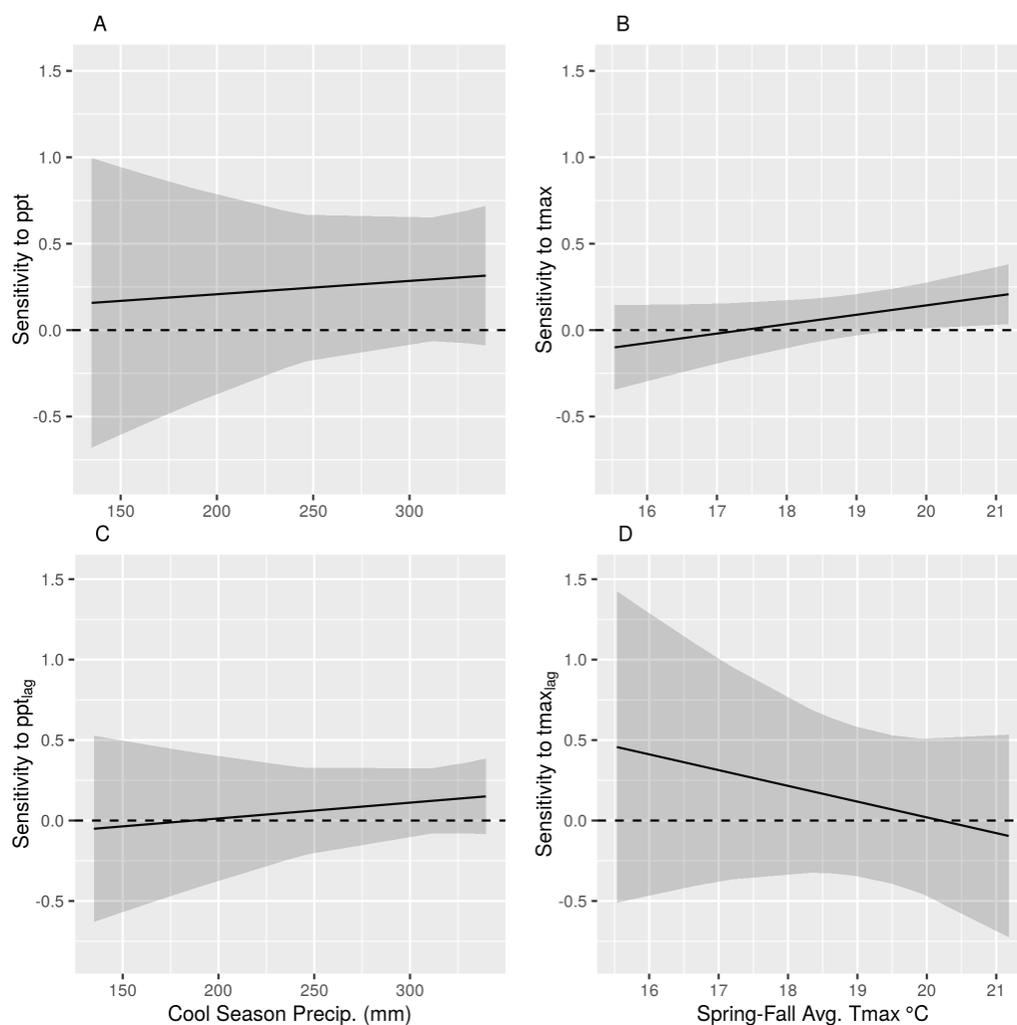
Figure A5. Sensitivity of basin big sagebrush abundance to annual climate covariates plotted against average site climate. Sensitivity is defined as the log change in sagebrush abundance produced by a 10 cm increase in precipitation (A, C) or a 1°C increase in temperature. Effects below zero indicate where above average temperatures or precipitation would decrease population size, while effects above zero indicate where above average annual temperature or precipitation would increase population size. Gray areas show 95% confidence intervals.

Appendix B: Summary of Datasets Used in "Sagebrush (*Artemisia tridentata*)

Response to Interannual Climate Variation Changes Across

the Species Range"

BCD – Vegetation monitoring data from Black Canyon of the Gunnison National Park, Curecanti National Recreation Area, and Dinosaur National Monument. Data were provided by the National Park Service, Northern Colorado Plateau Inventory and Monitoring Network. At each monitoring plot, sagebrush cover is measured using point-intercept along three 50-m transects.

> Witwicki, D., Thomas, H., Weissinger, R., Wight, A., Topp, S., Garman, S. L., and Miller, M. E. 2013. Integrated upland monitoring protocol for the park units in the Northern Colorado Plateau Network. Unpublished protocol, Northern Colorado Plateau Network, Moab, Utah.

CAMPWILLIAMS – Vegetation monitoring at Camp H.G. Williams Utah National Guard training grounds. Sagebrush cover measured by point-intercept at 100 points located along 100-m permanent monitoring transects. Data available by request: contact James Long <james.long@usu.edu>.

> Utah Army National Guard. (2007). *Camp W.G. Williams Integrated Natural Resources Management Plan Update*. Draper, UT: Utah Army National Guard Environmental Resources Management. Retrieved from http://www.ut.ngb.army.mil/environ/Natural%20Resources/Documents/INRMP_AGCW.pdf

> Diersing, V. E., Shaw, R. B., & Tazik, D. J. (1992). US army land condition-trend analysis (LCTA) program. *Environmental Management*, *16*(3), 405–414. http://doi.org/10.1007/BF02400080

FISSER_ARID_LANDS – Rangeland monitoring conducted by Dr. Herbert Fisser of the University of Wyoming from the mid-1950's to the early 1980's at permanent monitoring sites throughout central Wyoming. Data are drawn from tables in reports presented by the Wyoming Agricultural Experiment Station to the Bureau of Land Management. At each permanent plot percent cover of sagebrush is visually estimated in 20 930 cm^2 (1ft^2) subplots located along a 30.5-m (100 ft) transect. Full-text reports are available online in the BLM library: http://www.blm.gov/wo/st/en/info/blm-

library/publications/blm_publications.html

Fisser, H. G. (1962). *Halogeton Research: Arid Land Studies of Grazing Treatments, Ecology, Shrub Improvement and Control, and Moisture Relationships: 1962 Results* (University of Wyoming Agricultural Experiment Station Scientific Report). Laramie, WY: Wyoming Agricultural Experiment Station.

Fisser, H. G. (1965). *Halogeton Research: Arid Land Studies of Grazing Treatments, Ecology, Shrub Improvement and Control, and Moisture Relationships: 1964 Results* (University of Wyoming Agricultural Experiment Station Scientific Report). Laramie, WY: Wyoming Agricultural Experiment Station.

Fisser, H. G. (1966). *Halogeton Research: Arid Land Studies of Grazing Treatments, Ecology, Shrub Improvement and Control, and Moisture Relationships: 1965 Results* (University of Wyoming Agricultural Experiment Station Scientific Report). Laramie, WY: Wyoming Agricultural Experiment Station. Retrieved from https://archive.org/details/halogetonresearc16fiss

Fisser, H. G., Ries, R. E., & Noller, G. L. (1967). *Arid Land Ecology Research: 1966 Results* (University of Wyoming Agricultural Experiment Station Scientific Report No. 41). Laramie, WY: Wyoming Agricultural Experiment Station. Retrieved from https://archive.org/details/aridlandecologyr00fiss

Fisser, H. G., & Noller, G. L. (1967). *Arid Land Ecology Research: Annual Progress Report 1967* (University of Wyoming Agricultural Experiment Station Scientific Report No. 132). Laramie, WY: Wyoming Agricultural Experiment Station.

Fisser, H. G. (1967). *Exclosure Study with Transects of Permanent Plots: 1965-1966 Results* (University of Wyoming Agricultural Experiment Station Scientific Report). Laramie, WY: Wyoming Agricultural Experiment Station.

Fisser, H. G., & Whysong, G. L. (1968). *Arid Land Ecology Research: Annual Progress Report 1968* (University of Wyoming Agricultural Experiment Station Scientific Report No. 178). Laramie, WY: Wyoming Agricultural Experiment Station.

Fisser, H. G., & Whysong, G. L. (1969). *Arid Land Ecology Research: Annual Progress Report 1969* (University of Wyoming Agricultural Experiment Station Scientific Report No. 265). Laramie, WY: Wyoming Agricultural Experiment Station.

Fisser, H. G., & Ries, R. E. (1970). *Arid Land Ecology Research: Annual Progress Report 1970* (University of Wyoming Agricultural Experiment Station Scientific

Report No. 350). Laramie, WY: Wyoming Agricultural Experiment Station.

Fisser, H. G., & Ries, R. E. (1971). *Arid Land Ecology Research: Annual Progress Report 1971* (University of Wyoming Agricultural Experiment Station Scientific Report No. 428). Laramie, WY: Wyoming Agricultural Experiment Station.

Fisser, H. G., & Ries, R. E. (1972). *Arid Land Ecology Research: 1972 Annual Progress Report* (University of Wyoming Agricultural Experiment Station Scientific Report). Laramie, WY: Wyoming Agricultural Experiment Station.

Fisser, H. G. (1974). *Phenology and Production Studies on Semi-Arid Shrub Types: Annual Progress Report: 1973 Results* (University of Wyoming Agricultural Experiment Station Scientific Report No. 607). Laramie, WY: Wyoming Agricultural Experiment Station. Retrieved from https://archive.org/details/phenologyproduct03fiss

Fisser, H. G., & Kleinman, L. H. (1975). *Phenology and Production Studies on Semi-Arid Shrub Types: Annual Progress Report: 1974 Results* (University of Wyoming Agricultural Experiment Station Scientific Report No. 729). Laramie, WY: Wyoming Agricultural Experiment Station. Retrieved from https://archive.org/details/phenologyproduct8977fiss

Fisser, H. G., & Kleinman, L. H. (1976). *Phenology and Production Studies on Semi-Arid Shrub Types: Annual Progress Report: 1975 Results* (University of Wyoming Agricultural Experiment Station Scientific Report No. 831). Laramie, WY: Wyoming Agricultural Experiment Station. Retrieved from https://archive.org/details/phenologyproduct8978fiss

Fisser, H.G., L.W. Young, J.E. Opret, & N.E. Hargis. (1977). *Phenology and Production Studies on Semi-Arid Shrub Types: Annual Progress Report: 1976 Results* (University of Wyoming Agricultural Experiment Station Scientific Report No. 930). Laramie, WY: Wyoming Agricultural Experiment Station. Retrieved from https://archive.org/details/phenologyproduct8979fiss

Fisser, H. G., Young, L. W., Opret, J. E., & Hargis, N. E. (1978). *Phenology and Production Studies on Semi-Arid Shrub Types: Annual Progress Report: 1977 Results* (University of Wyoming Agricultural Experiment Station Scientific Report No. 970). Laramie, WY: Wyoming Agricultural Experiment Station. Retrieved from https://archive.org/details/phenologyproduct8980fiss

Fisser, H. G., Young, L. W., Spaeth, K. E., & Hargis, N. E. (1979). *Phenology and Production Studies on Semi-Arid Shrub Types: Annual Progress Report: 1978 Results* (University of Wyoming Agricultural Experiment Station Scientific Report

No. 985). Laramie, WY: Wyoming Agricultural Experiment Station. Retrieved from https://archive.org/details/phenologyproduct8981fiss

Fisser, H. G., Owens, M. K., Waugh, W. J., Hargis, N. E., & Uhlich, J. (1980). *Phenology and Production Studies on Semi-Arid Shrub Types: Annual Progress Report: 1979 Results* (University of Wyoming Agricultural Experiment Station Scientific Report No. 1044). Laramie, WY: Wyoming Agricultural Experiment Station. Retrieved from https://archive.org/details/phenologyproduct8982fiss

Fisser, H. G. (1981). *Phenology and Production Studies on Semi-Arid Shrub Types: Annual Progress Report: 1980 Results* (University of Wyoming Agricultural Experiment Station Scientific Report No. 1172). Laramie, WY: Wyoming Agricultural Experiment Station. Retrieved from https://archive.org/details/phenologyproduct8983fiss

Fisser, H. G., Deboodt, T. L., Kinucan, R. J., Mulholland, J. L., & Dean, S. K. (1981). *Phenology and Production Studies on Semi-Arid Shrub Types: Annual Progress Report: 1981 Results* (University of Wyoming Agricultural Experiment Station Scientific Report No. 1200). Laramie, WY: Wyoming Agricultural Experiment Station.

Fisser, H. G. (1982). *Phenology and Production Studies on Semi-Arid Shrub Types: Annual Progress Report: 1982 Results* (University of Wyoming Agricultural Experiment Station Scientific Report). Laramie, WY: Wyoming Agricultural Experiment Station.

FISSER_BLACK_THUNDER – Reports presented by the Wyoming Agricultural Experiment Station to the Atlantic-Richfield Mining company on vegetation cover from 22 monitoring sites in eastern Wyoming shortgrass steppe habitat. This represents the eastern most study site in my database. Estimates of shrub cover at each monitoring are from 15 900 cm^2 permanently marked subplots located along three 30.5-m (100 ft) long transects per site. Percent cover of sagebrush is estimated in each subplot with a point-intercept frame. Production data is also reported from estimated aboveground biomass production for shrubs from 20 1 x 2 m quadrats spaced a few meters apart within permanent exclosures at each site.

Fisser, H. G., Lymbery, G., & Taha, F. K. (1975). *Herbage Structure, Production and Phenology on Black Thunder: 1974 Annual Progress Report* (University of Wyoming Agricultural Experiment Station Scientific Report No. 662). Laramie,

WY: Wyoming Agricultural Experiment Station.

Fisser, H. G., Cox, J., & Taha, F. K. (1976). *Herbage Structure, Production and Phenology on Black Thunder: Annual Progress Report 1975 Results* (University of Wyoming Agricultural Experiment Station Scientific Report No. 779). Laramie, WY: Wyoming Agricultural Experiment Station.

Fisser, H. G., Cox, J., & Taha, F. K. (1977). *Herbage Structure, Production and Phenology on Black Thunder: Annual Progress Report 1975 Results* (University of Wyoming Agricultural Experiment Station Scientific Report No. 832). Laramie, WY: Wyoming Agricultural Experiment Station.

Fisser, H. G., Cox, J., Mecke, M., & Taha, F. K. (1977). *Herbage Structure, Production and Phenology on Black Thunder: Annual Progress Report 1977 Results* (University of Wyoming Agricultural Experiment Station Scientific Report No. 856). Laramie, WY: Wyoming Agricultural Experiment Station.

FISSER_GRAZING_SYSTEMS – Rangeland monitoring conducted by Dr. Herbert Fisser of the University of Wyoming at permanent monitoring sites throughout central Wyoming. Data are drawn from reports presented by the Wyoming Agricultural Experiment Station presented to the Bureau of Land Management. At each permanent plot, percent cover of sagebrush is visually estimated in 20 930 cm^2 (1ft^2) permanent subplots located along a 30.5-m (100 ft) long transect. Full-text reports are available online in the BLM library: http://www.blm.gov/wo/st/en/info/blm-library/publications/blm_publications.html

Fisser, H. G., & Gibbens, R. P. (1968). *Influence of Grazing Management Systems on Vegetation and Wildlife Habitat : [Grazing Systems Research] : Annual Report of Progress, July 1967 - July 1968* (University of Wyoming Agricultural Experiment Station Scientific Report No. 102). Laramie, WY: Wyoming Agricultural Experiment Station. Retrieved from https://archive.org/details/influenceofgrazi19gibb

Fisser, H. G., Gibbens, R. P., & May, M. (1969). *Influence of Grazing Management Systems on Vegetation and Wildlife Habitat : [Grazing Systems Research] : Annual Report of Progress, July 1968 - July 1969* (University of Wyoming Agricultural Experiment Station Scientific Report No. 179). Laramie, WY: Wyoming Agricultural Experiment Station. Retrieved from https://archive.org/details/influenceofgrazigibb

Fisser, H. G., & Gibbens, R. P. (1970). *Influence of Grazing Management Systems on Vegetation and Wildlife Habitat : [Grazing Systems Research] : Annual Report of Progress, July 1969 - July 1970* (University of Wyoming Agricultural Experiment Station Scientific Report No. 241). Laramie, WY: Wyoming Agricultural Experiment Station.

Fisser, H. G., & Gibbens, R. P. (1971). *Influence of Grazing Management Systems on Vegetation and Wildlife Habitat : [Grazing Systems Research] : Annual Report of Progress, July 1970 - July 1971* (University of Wyoming Agricultural Experiment Station Scientific Report No. 336). Laramie, WY: Wyoming Agricultural Experiment Station. Retrieved from https://archive.org/details/influenceofgrazi2 0gibb

Fisser, H. G., & Gibbens, R. P. (1972). *Influence of Grazing Management Systems on Vegetation and Wildlife Habitat : [Grazing Systems Research] : Annual Report of Progress, July 1971 - July 1972* (University of Wyoming Agricultural Experiment Station Scientific Report No. 414). Laramie, WY: Wyoming Agricultural Experiment Station.

Fisser, H. G., Gerhart, W. E., & Rodgers, D. E. (1983). *Influence of Grazing Management Systems on Vegetation and Wildlife Habitat : [Grazing Systems Research] : 1975 and 1979 Results and Long-Term Summary* (University of Wyoming Agricultural Experiment Station Scientific Report No. 1047). Laramie, WY: Wyoming Agricultural Experiment Station. Retrieved from https://archive .org/details/influencesofgrazfiss_1

GERMINO – Data from a sagebrush planting and restoration project at Idaho National Laboratory in southeastern Idaho. Sagebrush cover is reported from three 8 x 8 m study plots with planted sagebrush. Sagebrush cover is reported on each plot using point-intercept method or from a point-intercept method applied to high resolution aerial photos of each plot.

Germino, M. J., & Reinhardt, K. (2014). Desert shrub responses to experimental modification of precipitation seasonality and soil depth: relationship to the two-layer hypothesis and ecohydrological niche. *Journal of Ecology*, *102*(4), 989–997. http://doi.org/10.1111/1365-2745.12266

GRCAMEVE – Vegetation monitoring data from Grand Canyon and Mese Verde National Parks. Data were provided by the National Park Service, Southern Colorado Plateau Inventory and Monitoring Network. At each monitoring plot, sagebrush cover is visually estimated in 15 10 m^2 subplots.

DeCoster, J. K., Lauver, C. L., Miller, M. E., Norris, J. R., Snyder, A. E. C., Swan, M. C., Thomas, L. P. & Witwicki, D. L. (2012). *Integrated Upland Monitoring Protocol for the Southern Colorado Plateau Network* (Natural Resource Report NPS/SCPN/NRR No. 2012/577). Fort Collins, CO: National Park Service.

MILLSUT – Results from a long-term field study conducted by Neil West and students at a sagebrush site in central Utah. Sagebrush cover data are reported from point-intercept monitoring along transects in three 20 m x 20 m plots located in unburned areas.

Hosten, P. E., & West, N. E. (1994). *Cheatgrass dynamics following wildfire on a sagebrush semidesert site in central Utah* (General Technical Report INT-GTR No. 313) (pp. 56–62). Ogden, UT: Department of Agriculture, Forest Service, Intermountain Research Station. Retrieved from http://agris.fao.org/agris-search/search.do?recordID=US9569239

Hosten, P.E. (1995). *Assessing the Relative Utility of Models of Vegetation Dynamics for the Management of Sagebrush Steppe Rangelands* (Doctoral dissertation). Utah State University, Logan, UT. Retrieved from http://digitalcommons.usu.edu/etd/1128

West, N. E., & Yorks, T. P. (2002). Vegetation Responses following Wildfire on Grazed and Ungrazed Sagebrush Semi-Desert. *Journal of Range Management*, *55*(2), 171–181. http://doi.org/10.2307/400335

MTHOME – Mountain Home Air Force Base in southern Idaho. Data are from rare plant monitoring reports conducted for the Mountain Home Air Force Base. Sagebrush cover is measured by line-intercept method on 100-m permanent transects at each site.

CH2MHILL. (2000). *Task 1: Slick Spot Identification: Enhanced Training in Idaho Juniper Butte Range* (Report Prepared for United States Air Force Environmental Management 366 CES/CEVA Mountain Home Air Force Base, ID). Boise, ID.

CH2MHILL. (2001). *Task 1: Slick Spot Identification and Lepidium papilliferum Survey: Enhanced Training in Idaho Juniper Butte Range* (Report Prepared for

United States Air Force Environmental Management 366 CES/CEVA Mountain Home Air Force Base, ID). Boise, ID.

CH2MHILL. (2002). *Slick Spot Peppergrass (Lepidium papilliferum) Survey: Enhanced Training in Idaho Juniper Butte Range* (Report Prepared for United States Air Force Environmental Management 366 CES/CEVA Mountain Home Air Force Base, ID). Boise, ID.

CH2MHILL. (2003). *Slick Spot Peppergrass (Lepidium papilliferum) Survey: Enhanced Training in Idaho Juniper Butte Range and Saylor Creek Range* (Report Prepared for United States Air Force Environmental Management 366 CES/CEVA Mountain Home Air Force Base, ID). Boise, ID.

CH2MHILL. (2005a). *Slick Spot Peppergrass (Lepidium papilliferum) Permanent Monitoring Plots 2004: Enhanced Training in Idaho Juniper Butte Range* (Report Prepared for United States Air Force Environmental Management 366 CES/CEVA Mountain Home Air Force Base, ID). Boise, ID.

CH2MHILL. (2005b). *Slick Spot Peppergrass (Lepidium papilliferum) Permanent Monitoring Plots 2005: Juniper Butte Range* (Report Prepared for United States Air Force Environmental Management 366 CES/CEVA Mountain Home Air Force Base, ID). Boise, ID.

CH2MHILL. (2006). *Slick Spot Peppergrass (Lepidium papilliferum) Permanent Monitoring Plots 2005: Juniper Butte Range* (Report Prepared for United States Air Force Environmental Management 366 CES/CEVA Mountain Home Air Force Base, ID). Boise, ID.

CH2MHILL. (2007). *Slick Spot Peppergrass (Lepidium papilliferum) Permanent Monitoring Plots 2005: Juniper Butte Range* (Report Prepared for United States Air Force Environmental Management 366 CES/CEVA Mountain Home Air Force Base, ID). Boise, ID.

CH2MHILL. (2008). *Slick Spot Peppergrass (Lepidium papilliferum) Permanent Monitoring Plots 2005: Juniper Butte Range* (Report Prepared for United States Air Force Environmental Management 366 CES/CEVA Mountain Home Air Force Base, ID). Boise, ID.

CH2MHILL. (2009). *Slick Spot Peppergrass (Lepidium papilliferum) Permanent Monitoring Plots 2005: Juniper Butte Range* (Report Prepared for United States Air Force Environmental Management 366 CES/CEVA Mountain Home Air Force Base, ID). Boise, ID.

CH2MHILL. (2010). *Slick Spot Peppergrass (Lepidium papilliferum) Permanent Monitoring Plots 2005: Juniper Butte Range* (Report Prepared for United States Air Force Environmental Management 366 CES/CEVA Mountain Home Air Force Base, ID). Boise, ID.

CH2MHILL. (2011). *Slick Spot Peppergrass (Lepidium papilliferum) Permanent Monitoring Plots 2005: Juniper Butte Range* (Report Prepared for United States Air Force Environmental Management 366 CES/CEVA Mountain Home Air Force Base, ID). Boise, ID.

CH2MHILL. (2012). *Slick Spot Peppergrass (Lepidium papilliferum) Permanent Monitoring Plots 2005: Juniper Butte Range* (Report Prepared for United States Air Force Environmental Management 366 CES/CEVA Mountain Home Air Force Base, ID). Boise, ID.

CH2MHILL. (2013). *Slick Spot Peppergrass (Lepidium papilliferum) Permanent Monitoring Plots 2005: Juniper Butte Range* (Report Prepared for United States Air Force Environmental Management 366 CES/CEVA Mountain Home Air Force Base, ID). Boise, ID.

Blake, S. (2015). *2014 Slickspot Peppergrass (Lepidium papilliferum) Monitoring Permanent Transects* (Report Prepared for United States Air Force Environmental Management 366 CES/CEVA Mountain Home Air Force Base, ID). Burbank, WA: United States Fish and Wildlife Service, Land Management Research and Demonstration Program.

MUNSON – Data from national park service monitoring at Canyonlands, Dinosaur, Hovenweep and Natural Bridges National Monuments in the Colorado Plateau. Sagebrush cover is reported from visual estimates of cover in 100 0.5 x 0.5 m permanent subplots located along two 100-m transects at each site.

Munson, S. M., J. Belnap, C. D. Schelz, M. Moran, and T. W. Carolin. 2011. On the brink of change: plant responses to climate on the Colorado Plateau. Ecosphere 2(6): art68. doi:10.1890/ES11-00059.1

Schelz, C. D., M. Moran, and R. Alward. 2002. Vegetation long-term monitoring, 1989-2002, Canyonlands, Arches, Natural Bridges National Parks, Southeast Utah Group. Southeast Utah Group Headquarters, Moab, Utah, USA.

OCTC – Vegetation monitoring at Orchard Combat Training Center Idaho Army National Guard training grounds near Boise, Idaho. Sagebrush cover measured by point-intercept at 100 points located along 100 m permanent monitoring transects. Data available by request. Contact the USGS Forest and Rangeland Ecosystem Science Center, 970 Lusk Street, Boise, ID 83706. Phone: 208-426-5200.

Diersing, V. E., Shaw, R. B., & Tazik, D. J. (1992). US army land condition-trend analysis (LCTA) program. *Environmental Management*, *16*(3), 405–414. http://doi.org/10.1007/BF02400080

PARKERMT – Results from Utah State University study examining effects of sagebrush management treatments on wildlife habitat on Parker Mountain in central Utah. Cover data are from 40.5 ha plots monitored for shrub cover by line-intercept method at five 20-m long permanent transects per plot. Data provided by Dave Dahlgren and Terry Messmer <terry.messmer@usu.edu>.

Dahlgren, David K., Renee Chi, and Terry A. Messmer. 2006. "Greater Sage-Grouse Response to Sagebrush Management in Utah." *Wildlife Society Bulletin* 34 (4): 975–85. doi:10.2193/0091-7648(2006)34[975:GSRTSM]2.0.CO;2.

PASSEY – Results from monitoring of sagebrush production in relict sagebrush steppe habitats in southeastern Idaho and northern Utah. Sagebrush annual aboveground production is estimated on 20 randomly located 0.89 m^2 plots at each site. Three plots per site were harvested and weighed each year to calibrate production estimates.

Passey, H. B., Hugie, V. K., & Ball, D. E. (1982). *Relationships Between Soil, Plant Community, and Climate on Rangelands of the Intermountain West* (Technical Bulletin No. 1669). United States Department of Agiculture. Retrieved from http://naldc.nal.usda.gov/download/CAT83777885/PDF

REYNOLDS – Sagebrush cover from Reynolds Creek Experimental Watershed in southwestern Idaho. Sagebrush cover was estimated in permanent plots using point-intercept on seven 60-m transects.

Hanson, C. L., Morris, R. P., & Wight, J. R. (1983). Using Precipitation to Predict Range Herbage Production in Southwestern Idaho. *Journal of Range Management*,

36(6), 766–770. http://doi.org/10.2307/3898205

Hanson, C. L., Johnson, C. W., Wight, J. R., Schumaker, G. A., & Coon, D. L. (1997). *Forage Production, Botanical Composition, and Ground Cover as Affected by Excluding Grazing in Southwest Idaho* (Northwest Watershed Research Center Technical Bulletin No. 94-1). Boise, ID: United States Department of Agriculture, Agricultural Research Service.

RMBL – Rocky Mountain Biological Laboratory climate change experiment. Sagebrush aboveground biomass production in five permanent control plots was estimated without harvesting by comparing sagebrush cover to harvested aboveround biomass in separate calibration plots.

Harte, J., Saleska, S. R., & Levy, C. (2015). Convergent ecosystem responses to 23-year ambient and manipulated warming link advancing snowmelt and shrub encroachment to transient and long-term climate–soil carbon feedback. *Global Change Biology*, *21*(6), 2349–2356. http://doi.org/10.1111/gcb.12831

SAGEMAP – USGS sagebrush fire recovery study at sites in Idaho, Nevada, Oregon and Utah. Sagebrush cover was measured at each site on three 50-m transects using point-intercept. Data available online: http://sagemap.wr.usgs.gov/ESR_Chrono.aspx

Knutson, K. C., Pyke, D. A., Wirth, T. A., Arkle, R. S., Pilliod, D. S., Brooks, M. L., Chambers, J. C., & Grace, J. B. (2014). Long-term effects of seeding after wildfire on vegetation in Great Basin shrubland ecosystems. *Journal of Applied Ecology*, *51*(5), 1414–1424. http://doi.org/10.1111/1365-2664.12309

SAGESTEP – Data from control plots of the Sagebrush Steppe Treatment Evaluation Project. Cover data represent an average of sagebrush cover in control subplots determined by point-intercept technique on five 30-m transects.

McIver, J. D., Brunson, M., Bunting, S. C., Chambers, J., Devoe, N., Doescher, P., Grace, J., Johnson, D., Knick, S., Miller, R., Pellant, M., Pierson, F., Pyke, D., Rollins, K., Roundy, B., Schupp, E., Tausch, R., & Turner, D. (2010). *The Sagebrush Steppe Treatment Evaluation Project (SageSTEP): a test of state-and-transition theory*. Retrieved from http://www.treesearch.fs.fed.us/pubs/34893

SEOR – Sagebrush cover data come from 50 x 80 m permanent monitoring plots located on sagebrush dominated range in southeastern Oregon. Sagebrush cover in each monitoring plot is determined by line-intercept method on five 50-m transects. Data provided by Jon Bates and Kirk Davies, Range Scientists, USDA-Agricultural Research Service, Eastern Oregon Agricultural Research Center, Burns OR. Contact: <jon.bates@oregonstate.edu>.

WYQB – Repeated measurement from permanent plots in sagebrush communities in SW Wyoming (Homer et al. 2013). Sagebrush cover at each plot was determined from visual estimates of cover in 14 1 m^2 subplots located on two 30-m transects. Data available by request, contact Collin Homer, <homer@usgs.gov>.

Homer, C. G., Meyer, D. K., Aldridge, C. L., & Schell, S. J. (2013). Detecting annual and seasonal changes in a sagebrush ecosystem with remote sensing-derived continuous fields. *Journal of Applied Remote Sensing*, *7*(1), 073508–073508. http://doi.org/10.1117/1.JRS.7.073508

Appendix C: Additional Table for "Can Observational Data Predict Population

Response to Climate Change Experiments?"

Table C. Comparison of model predictions from climate model and baseline model for each species and vital rate and treatment. Two prediction scores are reported, MSE and lppd. Lower MSE indicates improved predictions whereas higher lppd indicates improved predictions. Instances where the climate model outperformed the baseline model are marked with "***" in the last column. ARTR = *A. tripartita*, HECO = *H. comata*, POSE = *P. secunda*, PSSP = *P. spicata*.

	species	vital_rate	Treatment	score	climate model	baseline model	diff	improved
1	ARTR	growth	Control	lppd	-107.53	-108.40	0.87	***
2	ARTR	growth	Control	MSE	0.57	0.56	0.01	
3	ARTR	growth	Drought	lppd	-39.71	-40.01	0.30	***
4	ARTR	growth	Drought	MSE	0.53	0.49	0.03	
5	ARTR	growth	Irrigation	lppd	-38.85	-40.75	1.91	***
6	ARTR	growth	Irrigation	MSE	0.50	0.57	-0.07	***
7	ARTR	recruitment	Control	lppd	-32.61	-31.05	-1.56	
8	ARTR	recruitment	Control	MSE	61.88	10.59	51.29	
9	ARTR	recruitment	Drought	lppd	-28.93	-26.52	-2.41	
10	ARTR	recruitment	Drought	MSE	523.95	11.62	512.33	
11	ARTR	recruitment	Irrigation	lppd	-17.51	-20.24	2.73	***
12	ARTR	recruitment	Irrigation	MSE	4.72	5.34	-0.62	***
13	ARTR	survival	Control	lppd	-24.19	-23.06	-1.13	
14	ARTR	survival	Control	MSE	0.07	0.07	0.00	
15	ARTR	survival	Drought	lppd	-5.48	-5.34	-0.13	
16	ARTR	survival	Drought	MSE	0.04	0.04	-0.00	***
17	ARTR	survival	Irrigation	lppd	-7.88	-8.01	0.13	***
18	ARTR	survival	Irrigation	MSE	0.06	0.06	-0.00	***
19	HECO	growth	Control	lppd	-377.77	-369.46	-8.31	
20	HECO	growth	Control	MSE	1.11	1.09	0.02	
21	HECO	growth	Drought	lppd	-8.74	-10.97	2.23	***
22	HECO	growth	Drought	MSE	3.12	4.35	-1.23	***
23	HECO	growth	Irrigation	lppd	-89.03	-73.93	-15.10	
24	HECO	growth	Irrigation	MSE	2.02	1.47	0.55	
25	HECO	recruitment	Control	lppd	-93.35	-93.47	0.12	***

	species	vital_rate	Treatment	score	climate model	baseline model	diff	improved
26	HECO	recruitment	Control	MSE	613.41	499.11	114.29	
27	HECO	recruitment	Drought	lppd	-25.39	-27.56	2.17	***
28	HECO	recruitment	Drought	MSE	1.94	2.33	-0.38	***
29	HECO	recruitment	Irrigation	lppd	-30.69	-30.56	-0.12	
30	HECO	recruitment	Irrigation	MSE	5.21	7.62	-2.41	***
31	HECO	survival	Control	lppd	-124.59	-112.70	-11.90	
32	HECO	survival	Control	MSE	0.12	0.11	0.01	
33	HECO	survival	Drought	lppd	-17.89	-20.82	2.93	***
34	HECO	survival	Drought	MSE	0.22	0.26	-0.05	***
35	HECO	survival	Irrigation	lppd	-16.51	-13.54	-2.97	
36	HECO	survival	Irrigation	MSE	0.09	0.07	0.02	
37	POSE	growth	Control	lppd	-1117.20	-1117.29	0.08	***
38	POSE	growth	Control	MSE	1.50	1.51	-0.00	***
39	POSE	growth	Drought	lppd	-254.17	-257.32	3.16	***
40	POSE	growth	Drought	MSE	2.66	2.69	-0.03	***
41	POSE	growth	Irrigation	lppd	-452.34	-456.95	4.61	***
42	POSE	growth	Irrigation	MSE	1.87	1.90	-0.03	***
43	POSE	recruitment	Control	lppd	-127.64	-128.73	1.09	***
44	POSE	recruitment	Control	MSE	35.20	44.82	-9.61	***
45	POSE	recruitment	Drought	lppd	-60.34	-63.15	2.80	***
46	POSE	recruitment	Drought	MSE	23.60	33.88	-10.28	***
47	POSE	recruitment	Irrigation	lppd	-72.06	-65.58	-6.48	
48	POSE	recruitment	Irrigation	MSE	85.04	27.63	57.41	
49	POSE	survival	Control	lppd	-366.49	-380.49	14.00	***
50	POSE	survival	Control	MSE	0.12	0.12	-0.00	***
51	POSE	survival	Drought	lppd	-175.29	-187.88	12.59	***
52	POSE	survival	Drought	MSE	0.21	0.22	-0.01	***
53	POSE	survival	Irrigation	lppd	-156.28	-150.23	-6.05	
54	POSE	survival	Irrigation	MSE	0.13	0.13	0.00	
55	PSSP	growth	Control	lppd	-627.07	-625.63	-1.44	
56	PSSP	growth	Control	MSE	1.38	1.36	0.02	
57	PSSP	growth	Drought	lppd	-292.90	-297.61	4.71	***
58	PSSP	growth	Drought	MSE	1.82	1.85	-0.03	***
59	PSSP	growth	Irrigation	lppd	-312.96	-314.67	1.71	***
60	PSSP	growth	Irrigation	MSE	1.51	1.51	-0.00	***
61	PSSP	recruitment	Control	lppd	-123.81	-125.23	1.42	***

	species	vital_rate	Treatment	score	climate model	baseline model	diff	improved
62	PSSP	recruitment	Control	MSE	30.59	34.79	-4.20	***
63	PSSP	recruitment	Drought	lppd	-87.34	-86.58	-0.77	
64	PSSP	recruitment	Drought	MSE	222.16	54.58	167.58	
65	PSSP	recruitment	Irrigation	lppd	-60.18	-62.12	1.94	***
66	PSSP	recruitment	Irrigation	MSE	20.90	44.57	-23.67	***
67	PSSP	survival	Control	lppd	-148.69	-140.15	-8.54	
68	PSSP	survival	Control	MSE	0.10	0.09	0.01	
69	PSSP	survival	Drought	lppd	-83.26	-78.09	-5.17	
70	PSSP	survival	Drought	MSE	0.11	0.11	0.01	
71	PSSP	survival	Irrigation	lppd	-100.52	-89.02	-11.50	
72	PSSP	survival	Irrigation	MSE	0.13	0.11	0.01	

Appendix D: Steps for Defining Niche Overlap for "Indirect Effects of

Environmental Change in Resource Competition Models"

I.   Niche overlap in the essential resource model:

Chesson (2013) defines niche overlap (eq. 1 in main text) in terms of

phenomenological competition coefficients from a two species Lotka-Volterra

competition model:

$$\frac{dN_F}{dt} = rN_F(1 - \alpha_{FF}N_F - \alpha_{FC}N_C),$$

(D1)

$$\frac{dN_C}{dt} = rN_C(1 - \alpha_{CF}N_F - \alpha_{CC}N_C).$$

Here we use Chesson's definition to quantify niche overlap in Tilman's essential resource

competition model. To do this, we translate the essential resource model into a Lotka-

Volterra competition model. Tilman accomplishes this by rearranging the equilibrium

equations for the resource models and finding their algebraic equivalence with a Lotka-

Volterra model (Tilman 1982, pp. 190-204). More recently, Meszéna et al. (2006)

showed that a mechanistic resource competition model can be translated into a Lotka-

Volterra model by linearization of the inter- and intra-specific density dependences at the

competitive equilibrium. The linear density dependence of the growth rate of species *i* to

the abundance of species *j* at equilibrium is equivalent to the competition coefficients α_{ij}

in a Lotka-Volterra model. This provides a valid approximation of a Lotka-Volterra

model near the local equilibrium and when resource dynamics are slow relative to

population dynamics (Barabás et al. 2013; Meszéna et al. 2006).

In a resource competition model, the growth rate of each species is determined by a vector of sensitivities to each resource, while the impact that a species has on the amount of resources available is determined by a vector of per capita consumption rates. Meszéna et al. (2006) calls these two vectors the sensitivity niche and the impact niche respectively. The competitive effect of species j on species i at equilibrium is the scalar product of the sensitivity niche of species i and the impact niche of species j. Thus, if we can calculate the sensitivity of each species' growth rate to each resource at equilibrium and the per capita impact that each species has on the depletion of each resource we can calculate the Lotka-Volterra equivalents for the resource competition models (see Meszéna et al. (2006) p. 76 for a relevant example).

If we rewrite the resource dependent growth rate of the focal species from equation (6) in main text as,

$$f_F(R_1, R_2) = \frac{1}{N_F}\frac{dN_F}{dt} = \text{MIN}\left(\frac{r_F R_1}{(R_1 + k_{F1})} - m_F, \frac{r_F R_2}{(R_2 + k_{F2})} - m_F\right), \qquad \text{(D2)}$$

then the components of the sensitivity vector describing how resource availabilities affect the focal species are $(\partial f_F/\partial R_1, \partial f_F/\partial R_2)$. Note that we are concerned with the equilibrium where the focal species is only limited by resource one, therefore the sensitivity to resource two is zero (i.e. $\partial f_F/\partial R_2 = 0$). Likewise, we can define the sensitivity of the competitor and note that at equilibrium its sensitivity to resource one will be zero.

The impact vector for the focal species is defined by how much it depletes resources one and two and is given by setting the equations in (7) to zero and rearranging,

$$I_1 = (S_1 - R_1^*) = \frac{q_{F1}m_F}{a}N_F + \frac{q_{C1}m_C}{a}N_C, \tag{D3}$$

$$I_2 = (S_2 - R_2^*) = \frac{q_{F2}m_F}{a}N_F + \frac{q_{C2}m_C}{a}N_C.$$

where I_1 and I_2 are introduced to indicate the amount of resource depletion (Meszéna et al. 2006). The components of the impact vectors for each species are then given by the following,

$$\frac{\partial I_1}{\partial N_F} = \frac{q_{F1}m_F}{a}, \qquad \frac{\partial I_2}{\partial N_F} = \frac{q_{F2}m_F}{a}, \tag{D4}$$

$$\frac{\partial I_1}{\partial N_C} = \frac{q_{C1}m_C}{a}, \qquad \frac{\partial I_2}{\partial N_C} = \frac{q_{C2}m_C}{a}.$$

The competition coefficients are the products of the resource sensitivities and the per capita impact on the resources,

$$\alpha_{FF} = \frac{q_{F1}m_F}{a}\frac{\partial f_F}{\partial R_1}, \alpha_{FC} = \frac{q_{C1}m_C}{a}\frac{\partial f_F}{\partial R_1}, \alpha_{CF} = \frac{q_{F2}m_F}{a}\frac{\partial f_C}{\partial R_2}, \alpha_{CC}$$

$$= \frac{q_{C2}m_C}{a}\frac{\partial f_C}{\partial R_2} \tag{D5}$$

Note that only one resource for each species appears in the above definitions because in this model each species is only sensitive to one resource at equilibrium. When we substitute the mechanistic definitions of the competition coefficients from equation (D5) into Chesson's definition of niche overlap (Chesson 2013), all the parameters cancel out except for the q's , which define resource consumption rates,

$$\rho = \sqrt{\frac{\alpha_{CF}\alpha_{FC}}{\alpha_{FF}\alpha_{CC}}} = \sqrt{\frac{q_{F2}\,q_{C1}}{q_{F1}q_{C2}}}, \qquad where \;\; \frac{q_{F2}}{q_{F1}} < \frac{q_{C2}}{q_{C1}}. \tag{D6}$$

II.   _Niche overlap in the substitutable resource model:_

We also derive the Lotka-Volterra competition parameters for a substitutable resource competition model by linearizing the dynamics near the equilibrium (see also Tilman 1982, pp. 270-272). In the substitutable model species are everywhere sensitive to both resources one and two. So the sensitivity niche vector for the focal species will be the partial derivatives of (16) with respect to each resource,

$$\frac{\partial f_F}{\partial R_1} = w_{F1}y, \qquad \frac{\partial f_F}{\partial R_2} = w_{F2}y, \tag{D7}$$

$$where \; y = \frac{r_F k_F}{(w_{F1}R_1 + w_{F2}R_2 + k_F - \tau_F)^2}$$

The partial derivatives defining the impact niche vectors for the focal species and competitor are found from equations in (17),

$$\frac{\partial I_1}{\partial N_F} = \frac{q_{F1}}{D}, \qquad \frac{\partial I_2}{\partial N_F} = \frac{q_{F2}}{D}, \tag{D8}$$

$$\frac{\partial I_1}{\partial N_C} = \frac{q_{C1}}{D}, \qquad \frac{\partial I_2}{\partial N_C} = \frac{q_{C2}}{D}.$$

The scalar product of the sensitivity vectors and the impact vectors give the competition coefficients. For the focal species for example,

$$\alpha_{FF} = (q_{F1}w_{F1} + q_{F2}w_{F2})\frac{y}{D}, \qquad \alpha_{FC} = (q_{C1}w_{F1} + q_{C2}w_{F2})\frac{y}{D}. \tag{D9}$$

The same steps can be followed to calculate the competition coefficients for the competitor. These can then be used to define niche overlap for the substitutable model. Note that all the terms but the _q's_ and _w's_ cancel out giving the following,

$$\rho = \sqrt{\frac{(q_{F1}w_{C1} + q_{F2}w_{C2})(q_{C1}w_{F1} + q_{C2}w_{F2})}{(q_{F1}w_{F1} + q_{F2}w_{F2})(q_{C1}w_{C1} + q_{C2}w_{C2})}}. \tag{D10}$$
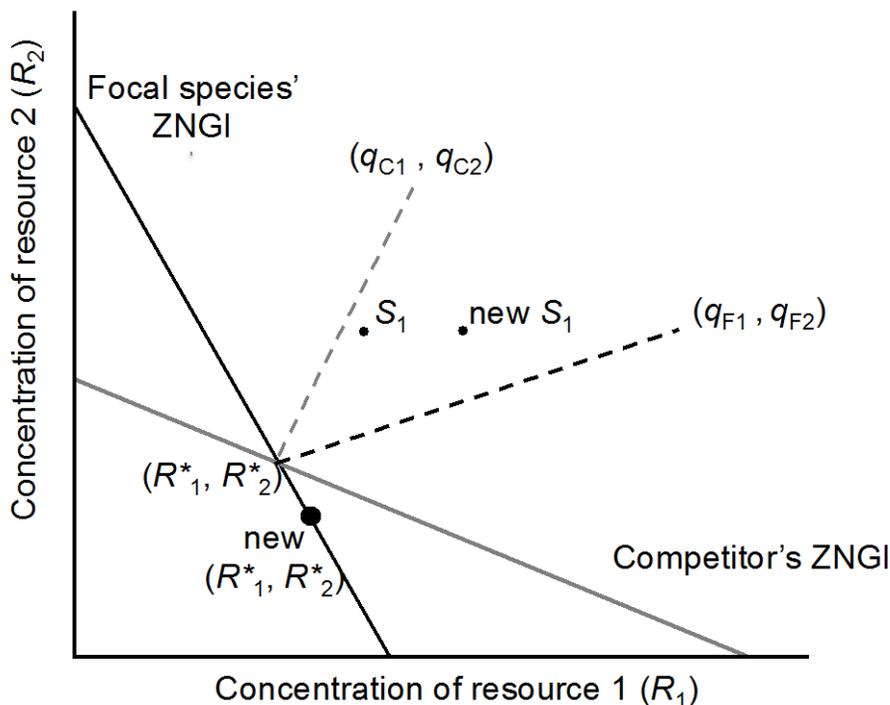
Figure D: A ZNGI plot for two species competing for two substitutable resources. The resource consumption vectors for the focal species and competitor are given by the values in parenthesis and shown with the dashed black and gray lines. Coexistence is possible when the resource supply point (S_1, S_2) falls between the two resource consumption vectors. The equilibrium resource concentration is found at R_1^*, R_2^*. However, when defining direct effects on the focal species, the resource supply point is shifted (new S_1) but the competitor's abundance is held constant; in this case the equilibrium resource concentration will shift slightly along the focal species ZNGI (new R_1^*, R_2^*). This shift needs to be taken into account when solving for focal species' direct sensitivity to a change in the resource environment.

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PEER-REVIEWED PUBLICATIONS

Chu, C., A. R. Kleinhesselink, K. M. Havstad, M. P. McClaran, D. P. Peters, L. T. Vermeire, H. Wei, and P. B. Adler. 2016. Direct effects dominate responses to climate perturbations in grassland plant communities. Nature Communications 7. DOI:10.1038/ncomms11766.

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- 2013   Utah State University Ecology Center Research Support Award ($3000).

- 2011   NSF Graduate Research Fellowship

- 2011   Quinney Wildland Resources PhD Fellowship

- 2010   Sigma Xi Grants in Aid of Research

- 2010   Emmy Lou Driscoll Memorial Scholarship, Sonoma State University

- 2010   John and Delores Headley Scholarship, Sonoma State University

- 2010   Ralph Bushnell Memorial Scholarship, Sonoma State University

- 2009   California Native Plant Society Scholarship, Milo Baker Chapter

RELEVANT COURSEWORK AND WORKSHOPS

- Bayesian Data Analysis. Utah State University. Fall 2014. Using R and JAGS.

- Introduction to Integral Projection Models. Ecological Society of America Meeting. August 2014.

- Software Carpentry. Utah State University. March 23-24, 2013. Programming and databases.

- Computer Programming for Biologists. Utah State University. Fall 2012. Python for programming and SQLite for managing data.

- Bayesian Modeling for Ecologists: An Introduction. Utah State University, March 2012.

ANALYSIS AND DATA MANAGEMENT SKILLS

- R for simulation modeling, statistical modeling, spatial analysis and visualization.

- SQLite for databases management.

- JAGS and Stan for constructing and fitting Bayesian models.

REFERENCES

- Dr. Peter Adler, Associate Professor, Department of Wildland Resources, Utah State University, 5230 Old Main Hill, Logan UT 84322. (435)-797-1021. peter.adler@usu.edu

- Dr. Hall Cushman, Professor, Department of Biology, Sonoma State University, Rohnert Park, CA 94928. (707)-664-2142. cushman@sonoma.edu

- Dr. David Koons, Associate Professor, Department of Wildland Resources, Utah State University, 5230 Old Main Hill, Logan UT 84322. (435)-797-8670. david.koons@usu.edu

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