THE INFLUENCE OF CLIMATE AND SPECIES COMPOSITION ON THE POPULATION DYNAMICS OF TEN PRAIRIE FORBS

Peter B. Adler[1,3] and Janneke HilleRisLambers[2]

[1]*Department of Wildland Resources and the Ecology Center, Utah State University, Logan, Utah 84322-5230 USA*
[2]*Biology Department, University of Washington, Seattle, Washington 98195-1800 USA*

Abstract. Understanding the relative roles of climate and species interactions in regulating population dynamics, one of the oldest challenges in ecology, is now a prerequisite for predicting species responses to climate change. A lack of case studies limits our ability to generalize about the factors that have regulated populations in the past and will be important in the future. Here, we take a first step toward identifying the drivers of plant population dynamics by studying the influence of climate and species interactions on the recruitment and survival of ten forb species from a Kansas (USA) prairie. Combining a long-term demographic data set with a Bayesian hierarchical-modeling approach, we fit models in which annual survival and recruitment rates are driven by precipitation, temperature, and species composition. Although the effects of these covariates differed among species, three general patterns emerged. First, climate had a greater influence than species composition on historical population dynamics. Second, forecasted increases in mean temperatures are likely to impact the population growth of these species more than future changes in precipitation or composition. Third, the significant effects of both climate and species composition on recruitment suggest that range expansions will be particularly difficult to forecast. Based on these patterns, we recommend field experiments to evaluate the ability of plant species to recruit at expanding range margins under warmer temperatures.

Key words: biotic vs. abiotic; climate change; density dependence; mixed-grass prairie, Kansas, USA; population dynamics; recruitment; survival.

INTRODUCTION

A recurring debate in ecology concerns the importance of density-dependent vs. density-independent factors in driving population dynamics. Hixon et al. (2002) trace the first round of the debate back to 1902, but the most heated exchange occurred in the 1950s, when Andrewartha and Birch (1954) made a case for the regulation of population dynamics by abiotic factors, while Nicholson (1954) defended the view that interactions between individuals control population abundances. Most ecologists today recognize the importance of both biotic and abiotic processes and ask "What is the relative contribution of biotic interactions and environmental variables to population dynamics?" (e.g., Coulson et al. 2001, Ibañez et al. 2007).

Answering this question is of paramount importance for predicting how plant and animal populations will respond to climate change. Populations could respond either directly to changes in climate variables or indirectly if shifts in climate alter community composition and species interactions (Fig. 1). In some cases, the indirect effects mediated by species interactions may influence population dynamics more than the direct

effects of climate change (Dormann et al. 2004, Suttle et al. 2007). Species interactions may be especially important in the short term if long life spans or slow migration rates of dominant species cause changes in community composition to lag behind changes in climate.

Unfortunately, despite more than a century of research, we still cannot generalize about the relative role of biotic and abiotic factors in regulating populations. Because of the difficulties of addressing this topic with either experiments (Dunnett and Grime 1999, Callaway et al. 2002, Klanderud and Totland 2005) or observational data and models (Stenseth et al. 1999, Coulson et al. 2001), most studies have focused on single species. We will need to accumulate many more species-specific case studies before we can answer important questions such as, How does the relative importance of climate and species interactions vary across environmental gradients and taxonomic groups? or, Do species interactions have different effects on survival, growth, and recruitment?

Along with generalizations about the relative importance of biotic and abiotic factors, we also should seek to identify which abiotic factors are most important for different kinds of species. This task is complicated because climate variables can affect populations through many pathways. For example, precipitation and temperature interact to determine soil moisture, a key resource for plant growth. But those same variables may

also be involved in cueing phenology and germination (Baskin and Baskin 2001, Menzel et al. 2001), potentially important drivers of population growth. Such "nonresource environmental effects" (Grace 2001) may lead to surprising effects of climate variability on plant communities (Adler and Levine 2007). Regardless of the underlying mechanisms, if patterns in the influence of climate variables or in the relative importance of biotic and abiotic drivers are correlated with species life history traits (e.g., Jiguet et al. 2007), then we may be able to forecast the effect of climate change on species even when little information is available.

Here we take a first step towards identifying general patterns in plant population regulation by studying the influence of climate and species interactions on the dynamics of 10 forb species from a Kansas (USA) prairie. Combining a unique long-term data set with a Bayesian hierarchical approach, we fit a series of population models to address both a retrospective and a prospective question (Caswell 2000). First, we compare the amount of historical variability in plant population dynamics that is explained by climate variables vs. community composition variables. Next, we identify the climate and composition covariates most likely to influence population growth in the future. Based on the results of these analyses, we speculate about the effects of global change on the distribution and abundance of prairie forbs and make recommendations for research to improve future forecasts.

METHODS

Study site and data-set description

The study site is located two miles west of Hays, Kansas, USA (38.8° N, 99.3° W), in native southern mixed-grass prairie. Mean annual precipitation is 580 mm, with 80% falling April through September. Mean annual temperature is 12°C. Gradients in soil type produce distinct plant communities (Albertson and Tomanek 1965), ranging from a shortgrass community on level uplands to communities dominated by taller bluestem species on hill slopes and in swales.

In the early 1930s researchers from Fort Hays State University established more than 50 permanent 1-m^2 quadrats in these plant communities. Every summer until 1972, with few exceptions, they used pantographs (Hill 1920) to map the basal cover (the area of a plant in contact with the soil surface) of all plants in each of the quadrats (Albertson and Tomanek 1965). Most of the quadrats were located inside livestock exclosures, although 15 of the shortgrass quadrats did receive light to moderate spring and summer grazing. The original maps have been digitized and the data and metadata are available in tabular or spatial formats along with monthly precipitation and temperature data (Adler et al. 2007). The unique combination of long temporal extent and fine spatial resolution makes it possible to analyze the fate of individual plants as mediated by
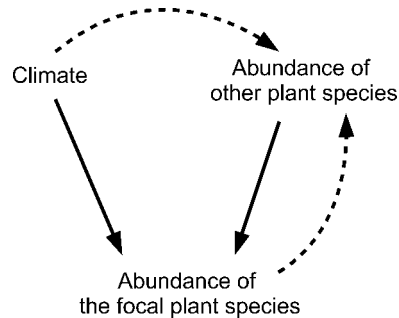

Fig. 1. Conceptual model of the effects of climate and species interactions on the abundance of a focal species. Climate can influence the focal species directly (the solid arrow) or indirectly, through its effects on other plants species (the broken arrow). Our analysis compares the relative strength of the two solid arrows, ignoring the broken arrows and other factors that may influence the abundance of plant species such as herbivory and disturbance.

climate and interactions with intra- and interspecific neighbors (e.g., Adler et al. 2006).

The data set spans a period of climatic extremes. It includes the Great Drought of the 1930s when precipitation was below normal and temperature above normal for almost a decade, the wettest year on record at Hays (1951), and another severe drought in the 1950s when the driest year on record occurred (Fig. 2a, b). This climate variability caused large changes in the abundance of the dominant perennial grasses (Albertson and Tomanek 1965) (Fig. 2c). The goal of our analysis was to tease apart the influences of these climatic and compositional fluctuations on forb population dynamics.

We analyzed the dynamics of 10 forb species (Table 1) that were common enough in the data set to provide sufficient sample size for model fitting. The densities of all 10 species fluctuated considerably over the period of record. Despite their apparent taxonomic and functional similarity (Table 1), their dynamics varied: four species increased in density with time (Fig. 3a), three species reached their highest densities in the middle portion of the time series (Fig. 3b), and three species peaked early in the time series (Fig. 3c). Although perennial forbs contribute only a fraction of the biomass in the grass-dominated communities at Hays, they represent much of the species diversity (Adler 2004). Because their densities are low, the forbs may be more vulnerable to future changes in climate than the dominant grasses.

Modeling approach

Our analysis involved five steps. First, we classified each individual plant in each quadrat map as a survivor or a new recruit. This gave us a record of survival and recruitment across 35 year-to-year transitions. Second, we fit a series of survival models incorporating climate and species composition covariates. Next, we fit a series of recruitment models incorporating the same covari-
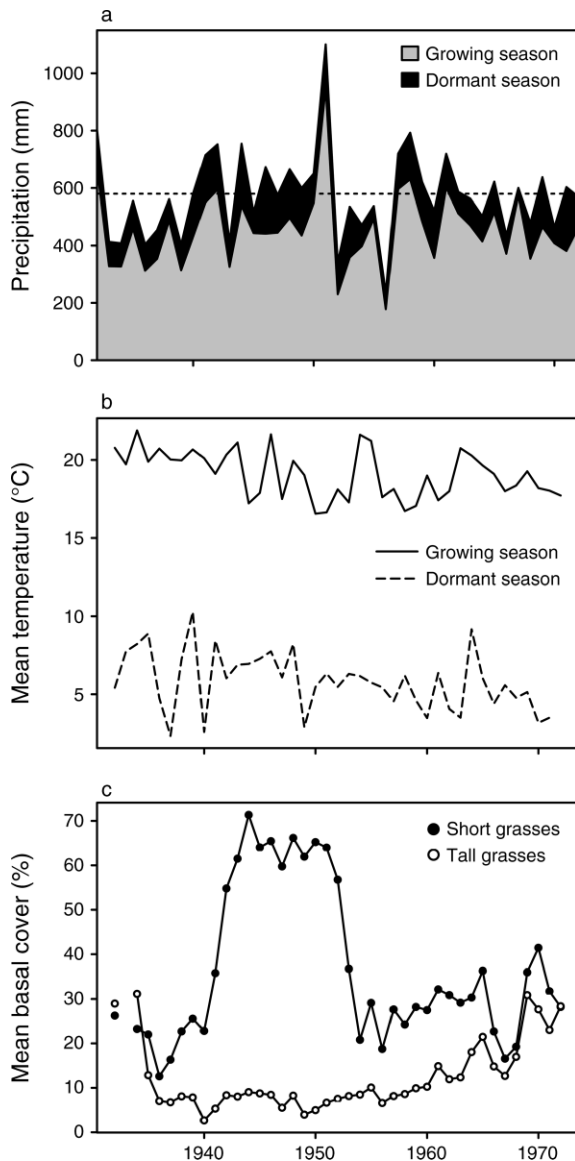
Fig. 2. Values of the climate and composition covariates used to model survival and recruitment rates, 1932–1972. The dashed line in panel (a) shows mean annual precipitation. The composition variables are the combined basal cover of short grasses and tall grasses. The only significant linear trends are in dormant season temperature ($P = 0.047$) and tall grass cover ($P = 0.015$).

ates. Fourth, we used model comparisons to determine the relative roles of climate and composition in explaining historical variation in population densities, our retrospective research objective. Finally, using the survival and recruitment models that incorporated all covariates, we conducted a perturbation analysis to answer our prospective question about population responses to future changes in the covariates. The remainder of the *Methods* describes each of these steps in detail.

We used the same short list of climate and composition covariates for all species. We took this approach to facilitate cross-species comparisons, and because model selection is not straightforward when using Bayesian hierarchical models. Based on previous work (Adler et al. 2006, Adler and Levine 2007), we chose five climate covariates that we expected could have strong influences on all species through their effects on either soil moisture or physiological cues: growing season precipitation (April–September), dormant-season precipitation (the October–March period preceding the growing season), annual precipitation in the previous year, mean growing-season temperature, and mean dormant-season temperature. Precipitation is measured in millimeters (mm) and temperature in degrees Celsius (°C). We chose three composition covariates: the density of conspecifics, the basal cover of the short C_4 grasses (*Bouteloua gracilis* and *Buchloë dactyloides*), and the basal cover of taller C_4 grasses (primarily *Andropogon gerardii*, *Schizachyrium scoparium*, and *Bouteloua curtipendula*). Basal cover is measured as square centimeters (cm^2). We included conspecific density since density dependence is often important in regulating population growth, and chose the short grasses and tall grasses to represent interspecific interactions since these are the two most common functional groups at the site. Other species and functional groups, such as annuals and C_3 grasses, were not abundant enough for reliable parameterization.

Tracking survivors and recruits

For perennial plants, population density (N) depends on survival (S) and recruitment (R) rates:

$$N_{t+1} = SN_t + RN_t. \qquad (1)$$

Although it would be possible to use statistical models to determine the effects of climate variables and neighborhood composition on total population density, we chose to analyze survival and recruitment separately, since climate and composition covariates may impact these life stages differently.

We used a computer program to identify survivors and recruits based on their spatial coordinates (Lauenroth and Adler, *in press*). Because quadrats in the Hays data set were mapped using basal, not canopy, cover, the single-stemmed forb species appear as points, not polygons, and are described by density (number of stems per square meter, stems/m^2). The tracking program uses two basic rules. First, a "new recruit" is defined as an individual that appears in a location >5 cm from any conspecific in the previous year. We chose 5 cm as the critical distance after considering both mapping error and the potential for vegetative growth (Fair et al. 1999). Second, a "survivor" is an individual <5 cm from the location of a conspecific in the previous year. If more than one individual was present in the neighborhood in the previous year, the current year's plant inherits the identity of the closest "parent," and only one individual inherits that identity. This last contingency means that

TABLE 1. The 10 study species (all are perennial forbs native to Kansas, USA).

Species	Family	Species code	Functional group	Sample size†	No. quadrats‡	Maximum life span (yr)§
Cirsium undulatum	Asteraceae	ciun	C_3	632	25	9
Echinacea angustifolia	Asteraceae	ecan	C_3	417	7	11
Hedyotis nigricans	Rubiaceae	heni	C_3	731	17	7
Lesquerella ovalifolia	Brassicaceae	leov	C_3	941	6	14
Paronychia jamesii	Caryophyllaceae	paja	C_3	1064	8	15
Psoralea tenuiflora	Fabaceae	pste	legume	3478	44	11
Ratibida columnifera	Asteraceae	raco	C_3	844	31	3
Solidago mollis	Asteraceae	somo	C_3	2144	21	11
Sphaeralcea coccinea	Malvaceae	spco	C_3	971	29	6
Thelesperma megapotamicum	Asteraceae	them	C_3	608	14	7

† The number of stems occurring in the data set.
‡ The number of quadrats in which each species occurred.
§ From Lauenroth and Adler (*in press*).

the program tracks individual plants, not whole genets. Most forbs in this study can reproduce vegetatively, but our focus was on year-to-year changes in density. Therefore, we classified all new stems as recruits, regardless of the mode of reproduction.

Survival models

For each species, we assume that the survival (1) or mortality (0) of individual i of age a in quadrat j from year $k - 1$ to k (s_{iajk}) is a Bernoulli process with an underlying survival probability of $\hat{s}_{iajk}$:

$$s_{iajk} \sim \text{Bernoulli}(\hat{s}_{iajk}). \qquad (2)$$

In our "basic survival model," we assume that the survival probability is linked by the logit function to age-dependent average survival, μ_{sa}, a quadrat random effect, q_{sj}, and an individual random effect, z_{si}:

$$\text{logit}(\hat{s}_{iajk}) = \mu_{sa} + q_{sj} + z_{si}. \qquad (3)$$

We included two age classes in the average survival term, with $a = 1$ for one-year-old plants and $a = 2$ for older plants. Survival of these forb species is low enough that few individual plants exceed two year life spans, and survival probability does not vary strongly with age after the first two years (Lauenroth and Adler, *in press*). The quadrat random effect explains spatial variation in survival among quadrats, probably caused by differences in soil depth. We assume that the quadrat random effects are normally distributed with a mean of 0 and a variance parameter describing quadrat-to-quadrat variation:

$$q_{sj} \sim \mathcal{N}(0, \sigma_{sq}). \qquad (4)$$

We included the individual random effect to recognize that multiple observations on an individual surviving many years are not independent (for individuals that die after their first year, we set the random effect equal to 0). For individuals surviving more than one year, we assume the random effects are normally distributed with a mean of 0 and a fitted variance parameter:

$$z_{si} \sim \mathcal{N}(0, \sigma_{sz}). \qquad (5)$$

Note that none of the terms in this basic model can explain year-to-year variation in survival probability.

The "climate model" builds on the basic model by adding the five climate (CL) covariates described above (see *Modeling approach*):

$$\text{logit}(\hat{s}_{iajk}) = \mu_{sa} + q_{sj} + z_{si} + \mathbf{X}_{\text{CL}k}\boldsymbol{\beta}_{s\text{CL}} \qquad (6)$$

where $\mathbf{X}_{\text{CL}k}$ is the vector of climate covariates in year k and $\boldsymbol{\beta}_{s\text{CL}}$ is the vector of coefficients relating the climate covariates to survival probability. In this model, interannual variability in survival can be explained by climatic variation.

The "composition model" builds on the basic model by adding three species composition (CO) covariates that vary among individual plants and among years (see *Modeling approach*, above). These covariates are quantified in the 10 cm radius neighborhoods surrounding each individual plant. We write this model as follows:

$$\text{logit}(\hat{s}_{iajk}) = \mu_{sa} + q_{sj} + z_{si} + \mathbf{X}_{s\text{CO}ik-1}\boldsymbol{\beta}_{s\text{CO}} \qquad (7)$$

where $\mathbf{X}_{s\text{CO}ik-1}$ is the vector of composition covariates for plant i in year $k - 1$ and $\boldsymbol{\beta}_{s\text{CO}}$ is the vector of coefficients relating the composition covariates to survival probability. These coefficients can have negative (competition) or positive (facilitative) effects on survival. In this model, interannual variability in survival can be explained by interannual variation in species composition.

Finally, the "full model" includes the elements of the basic model as well as the climate and composition effects together:

$$\text{logit}(\hat{s}_{iajk}) = \mu_{sa} + q_{sj} + z_{si} + \mathbf{X}_{\text{CL}k}\boldsymbol{\beta}_{s\text{CL}} + \mathbf{X}_{s\text{CO}ik-1}\boldsymbol{\beta}_{s\text{CO}}. \qquad (8)$$

Here, interannual variability in survival can be explained by both climate and composition covariates.

We gave all parameters diffuse priors. Mean survival probabilities for the two age classes were drawn from a normal distribution with a mean of zero and a variance of 1000:

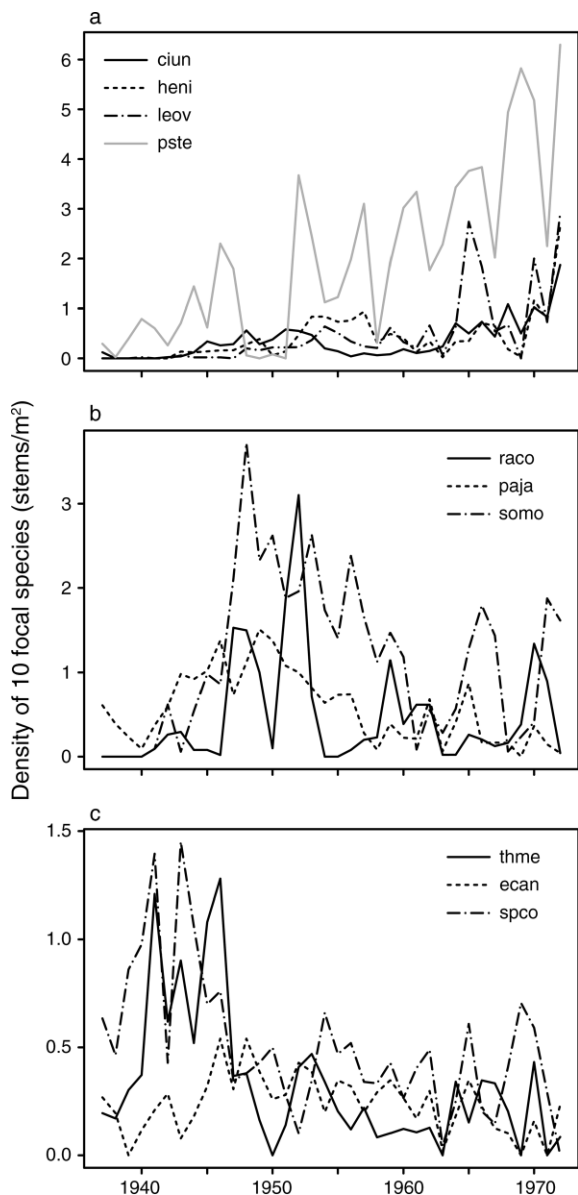$$\mu_{sa} \sim \mathcal{N}(0, 1000). \qquad (9)$$

FIG. 3. Observed mean densities per square meter of the 10 focal species from 1937 to 1972. Means were calculated across all 1-m^2 quadrats, so the densities are low for species with a restricted distribution (*Lesquerella ovalifolia* occurred in just six quadrats while *Psoralea tenuiflora* occurred in 44 quadrats). For definitions of species codes, see Table 1.

The priors for each of the five climate and three composition coefficients were also drawn from independent normal distributions, with mean 0 and variance of 1000:

$$\beta_{sCL(i)} \sim \mathcal{N}(0, 1000) \qquad i = 1{:}5 \qquad (10)$$

$$\beta_{sCO(i)} \sim \mathcal{N}_3(0, 1000) \qquad i = 1{:}3. \qquad (11)$$

The variances for the quadrat and individual random effects were drawn from inverse gamma distributions, which is the conjugate prior for variance parameters

(Clark 2007: Appendix G):

$$\sigma_{sq} \sim \text{IG}(0.5, 0.5) \qquad (12)$$

$$\sigma_{sz} \sim \text{IG}(0.5, 0.5). \qquad (13)$$

We fit the model using Markov chain Monte Carlo (MCMC) implemented in WinBUGS 1.4 (Lunn et al. 2000). We used a hierarchical Bayesian approach because we wished to include quadrat and individual random effects and acknowledge sampling error in response variables as well as covariates (in the case of parents in recruitment models). Achieving these goals was impossible using classical statistics (Ellison 2004, Clark 2005). For each of the 10 species and four models, we ran three chains and chose initial values to represent different portions of parameter space. We checked convergence using the Gelman-Rubin diagnostics (Brooks and Gelman 1998). Means and 95% credible intervals of parameters of interest are estimated by averaging samples from the MCMC runs after equilibrium is reached. The credibility interval limits are the 2.5 and 97.5 percentiles of the posterior distribution. Along with the parameter estimates, we also calculated MCMC estimates of the predicted survival probability for each plant.

Recruitment models

In contrast to the survival model, which applies to individual plants, our data only allow us to observe the process of recruitment at the quadrat level; we do not know which parents produced the recruits we observed. We assume that for each species the observed number of recruits in quadrat j and year k (r_{jk}) is distributed as a Poisson with mean $\hat{r}_{jk}$:

$$r_{jk} \sim \text{Poisson}(\hat{r}_{jk}). \qquad (14)$$

We assume that mean recruit density depends on the number of parents in the previous year contributing to recruitment in that quadrat (p_{jk-1}) and the quadrat and year-specific fecundity of those parents (f_{jk-1}):

$$\hat{r}_{jk} = f_{jk-1} p_{jk-1}. \qquad (15)$$

The number of individuals of each species observed in quadrat j and year k is only an approximate measure of the number of parents contributing recruits to that quadrat the following year. Recruits may also come from plants located outside the quadrat or seeds in the seed bank. To allow for these unobserved contributions, we assume the the observed number of parents is a Poisson realization of a latent "true parents" variable, $\hat{p}$:

$$p_{jk} \sim \text{Poisson}(\hat{p}_{jk}). \qquad (16)$$

Our process model for the latent variable $\hat{p}$ is simple, with mean, quadrat-specific and year-specific parameters for each species:

$$\log(\hat{p}_{jk}) = \mu_p + q_{pj} + y_{pk}. \qquad (17)$$

Our data do not make it possible to separate the many different processes that contribute to recruitment.

Therefore, our fecundity term f_{jk-1} does not simply describe seed production per individual, but rather the per capita production of recruits, incorporating seed production, germination, establishment and seedling survival between the time when potential parents are censused and the following year when new recruits are observed. In the "basic recruitment model," we assume that this overall recruitment rate depends only on a mean fecundity, μ_r, and quadrat random effects, q_{rj}:

$$\log(f_{jk}) = \mu_r + q_{rj}. \qquad (18)$$

We fit these parameters on a log-scale to ensure that per capita recruit production is always positive.

The quadrat random effect in per capita recruit production is normally distributed with a mean of 0 and a variance parameter describing quadrat-to-quadrat variation:

$$q_{rj} \sim \mathcal{N}(0, \sigma_{rj}). \qquad (19)$$

While the basic recruitment model assumes that the per capita recruitment rate is constant from year to year, the "climate recruitment model" explains interannual variability in the recruitment rate as a function of the same five climate variables we used in the survival climate model:

$$\log(f_{jk}) = \mu_r + q_{rj} + \mathbf{X}_{CLk}\boldsymbol{\beta}_{rCLk} \qquad (20)$$

where $\mathbf{X}_{CLk}$ is the vector of climate covariates for year k, and $\boldsymbol{\beta}_{rCL}$ is the vector of coefficients relating the climate variables to the recruitment rate.

The "composition recruitment model" assumes that the recruitment rate varies as a function of the density of conspecific parents in the quadrat, and the basal cover of the short grasses and taller C_4 grasses in the quadrat:

$$\log(f_{jk}) = \mu_r + q_{rj} + \mathbf{X}_{rCLk-1}\boldsymbol{\beta}_{rCO} \qquad (21)$$

where $\mathbf{X}_{rCOk-1}$ is the vector of the covariates in year $k - 1$ (the r subscript emphasizes that these quadrat-level covariates differ from the individual plant composition covariates in the survival model), and $\boldsymbol{\beta}_{rCO}$ is the vector of coefficients.

As for survival, the "full recruitment model" includes all elements of the basic model in addition to the climate and composition covariates:

$$\log(f_{jk}) = \mu_r + q_{rj} + \mathbf{X}_{CLk}\boldsymbol{\beta}_{rCLk} + \mathbf{X}_{rCOk-1}\boldsymbol{\beta}_{rCO}. \qquad (22)$$

We assigned the following diffuse priors:

$$\mu_r \sim \mathcal{N}(0, 100) \qquad (23)$$

$$\beta_{sCL(i)} \sim \mathcal{N}(0, 100) \qquad i = 1{:}5 \qquad (24)$$

$$\beta_{sCO(i)} \sim \mathcal{N}(0, 100) \qquad i = 1{:}3 \qquad (25)$$

$$\sigma_{rq} \sim \mathrm{IG}(0.5, 0.5) \qquad (26)$$

$$\mu_p \sim \mathcal{N}(0, 10) \qquad (27)$$

$$q_{pj} \sim \mathcal{N}(0, 10) \qquad (28)$$

$$q_{yk} \sim \mathcal{N}(0, 10). \qquad (29)$$

The prior variances are lower than for survival because the recruitment rate is fit on a log scale, so small effects can cause large differences in predicted recruitment. We used slightly more informative priors for the parameters that predict the latent variable $\hat{p}$ so that the predicted values of parents would not differ greatly from observed values. We fit the recruitment models using the same MCMC approach described for the survival models.

Retrospective analysis

The goal of the retrospective analysis was to describe the relative influence of the climate and composition variables on the historical population dynamics of each species. We used two approaches, the first based on model selection and the second on a partitioning of deviance.

Deviance information criterion (DIC; Spiegelhalter et al. 2002) is similar to model selection criterion such as the Akaike information criterion (AIC), except that it is designed for hierarchical models fit using MCMC methods. Like AIC, it balances model fit and parsimony. We used DIC to compare the basic, climate, composition, and full versions of the survival and recruitment models for each species. If DIC indicated that the full model was superior, we concluded that both climate and composition covariates were important for explaining variation in the survival or recruitment rates. But if the climate model was superior, for example, we concluded that the climate covariates were more effective than the composition covariates in explaining interannual variation in the vital rate of interest.

With linear models, the coefficient of determination, R^2, can be used to partition the variance explained by different groups of covariates—the climate and composition variables in our case (Legendre and Legendre 1998). If J is the R^2 of the climate model, K the R^2 of the composition model, and L the R^2 of the full model, then $M = J + K - L$, where M is the overlap of J and K, or the amount of variance explained by both the climate or composition variables (presumably due to correlations among the covariates). The portion of variance uniquely explained by the climate variables is $J - M$, and the portion uniquely explained by the composition variables is $K - M$.

Applying this approach to our models is complicated by their nonlinear link functions, the inclusion of random effects and (in the case of the recruitment model) the presence of two likelihoods (both recruits and their parents are stochastic). Fortunately, Zheng (2000) provides a goodness-of-fit measure called D, the proportional reduction in deviance, which is appropriate for generalized linear models with random effects:

$$D = 1 - \frac{\mathrm{dev_I}}{\mathrm{dev_N}} \qquad (30)$$

where $\mathrm{dev_I}$ is the deviance of the model of interest and $\mathrm{dev_N}$ is the deviance of the null model. We used the basic survival and recruitment models as our null models, meaning that the random effects were included. We then calculated D for the climate, composition, and full

models, giving the proportional reduction in deviance compared to the basic model. Finally, we used the variance-partitioning approach described above, substituting the values of D for R^2, to calculate the unique portion of deviance explained by the climate and composition covariates.

We calculated deviance for the survival and recruitment models using the means of the predicted values drawn from the MCMC simulations and assuming Bernoulli and Poisson distributions, respectively. The log-likelihood used in this calculation of deviance is only one piece of the full posterior used in the model fitting. In other words, the deviances and proportional reductions in deviance are not appropriate for comparing or evaluating the fits of the hierarchical models. Instead, we use them only to compare the relative influence of climate and composition on historical variation in survival and recruitment rates. We extended the approach to total population density by summing the predicted number of survivors and recruits for each quadrat in each year and then comparing the predicted number of individuals in each quadrat (resulting from both survival and recruitment) with the observed densities to calculate deviance, assuming a Poisson distribution for the counts.

Prospective analysis

Evaluating how future changes in explanatory variables will impact population dynamics cannot be done with a retrospective approach, which is sensitive to the distribution of the covariates in the observed record. To evaluate potential impacts of changes in the covariates, we therefore conducted a perturbation analysis, using the invasion exponent (the log of the low-density growth rate) as a measure of population performance (Caswell and Takada 2004). We use the invasion exponent instead of equilibrium population growth rates (often used in linear matrix models) because our models contain density-dependent, nonlinear processes. The invasion exponent represents the trajectory of the population at low density: values >0 indicate that the population can increase from low abundance and persist, while values ≤ 0 suggest the population will go extinct.

To estimate the invasion exponent for each species, we initialized a population with a single one-year-old plant. We then calculated the survival probability for this plant and the expected number of recruits it should produce using the full model. To incorporate parameter uncertainty, we estimated survival and recruitment 1000 times, each time drawing parameters from the posterior distribution (all values were drawn from one randomly selected iteration of the MCMC sequence to preserve correlations among parameters). Population growth means and 95% predictive intervals were then estimated by summing the 1000 values of survival and recruitment. We first performed these calculations of the invasion exponent for each species using the historical means of the climate and composition covariates. We then

calculated a series of new invasion exponents assuming proportional increases in the value of each covariate. We increased the three precipitation variables 10% above their respective means, but increased the growing-season and dormant-season temperature variables by 1.2°C, which is 10% of the mean annual temperature (otherwise the change in the dormant-season temperature, with a mean near 3°C, would have been very small). For each species, we increased short grass and tall grass cover by 10% of their observed means from the quadrats in which each species occurred. We used the same values of these covariates for calculating both survival and recruitment. The 10% increases in climate and composition variables fall within the observed ranges of variability for all the covariates.

RESULTS

Parameter estimates for all four survival and recruitment models and all 10 species converged, based on the Gelman-Rubin diagnostics (all $\hat{r} < 1.1$). Mean parameter values and 95% credible intervals from the full survival and recruitment models are shown in Appendix A. The precipitation and temperature covariates had different effects on different species (Appendix A). We found no clear patterns in the direction of these climate effects. Conspecific density had no significant effect on survival for any species but had a significant negative effect on recruitment for 5 of the 10 species (Appendix A). Grass cover had both positive and negative effects. For some species, grass cover had opposite effects on survival and recruitment rates. For example, for both *Hedyotis nigricans* and *Psoralea tenuiflora*, basal cover of short grasses and taller grasses had significant negative effects on survival and significant positive effects on recruitment. Across all 10 species, we observed 12 significant composition effects on recruitment, and 8 effects were positive (Appendix A). In contrast, for survival three of the five significant effects were negative. The models only explained a portion of the spatial and temporal variability in population density (Appendix B), highlighting the importance of unobserved processes and the strength of stochasticity at fine scales.

For 2 of the 10 species, the basic survival model outperformed models with covariates, based on comparisons of DIC (deviance information criterion) (Table 2). For four species, the climate survival model had the lowest DIC, and for the remaining four species the full survival model, containing climate and composition covariates, had the lowest DIC. The composition survival model was never selected. For recruitment, the full model was selected for 9 out of 10 species, while the composition model had the lowest DIC for one species (Table 2). The climate recruitment model was never selected.

In our analysis of proportional reductions in deviance, we found that composition covariates never reduced deviance in survival more than 2.5%, while the climate variables explained up to 9% of deviance in survival (Fig. 4a). However, for most species, the deviance explained

TABLE 2. Model comparison based on deviance information criteria (DIC; lower values of DIC indicate a superior model).

	Survival models				Recruitment models			
Species	Basic	Climate	Competition	Full	Basic	Climate	Competition	Full
Cirsium undulatum	**423.1**	428.9	424.3	430.2	2651.4	2641.9	2652.1	**2639.7**
Echinacea angustifolia	**445.3**	450.7	448.6	453.9	1342.1	1341.0	**1322.3**	1322.5
Hedyotis nigricans	641.3	638.4	636.6	**632.3**	2052.4	2023.1	2043.8	**2010.7**
Lesquerella ovalifolia	769.7	**756.0**	769.6	757.1	1260.4	1223.8	1192.7	**1154.0**
Paronychia jamesii	1080.8	**1073.3**	1083.7	1076.5	2036.2	2022.4	2022.2	**2009.0**
Psoralea tenuiflora	2076.6	2057.4	2072.9	**2051.9**	8320.8	8198.5	8225.1	**8089.3**
Ratibida columnifera	697.2	637.9	686.5	**636.9**	3672.0	3486.2	3640.8	**3483.8**
Solidago mollis	1801.4	1799.3	1797.9	**1796.7**	6719.2	6681.1	6672.7	**6636.0**
Sphaeralcea coccinea	857.2	**833.2**	856.5	837.4	4491.8	4491.2	4407.7	**4398.8**
Thelesperma megapotamicum	431.5	**425.5**	435.0	429.0	1980.5	1968.5	1957.8	**1936.1**

Notes: For each species, the best survival and recruitment models are shown in bold. The "Basic" models contain only random effects, the "Climate" models incorporate climatic covariates, the "Composition" models add information on the basal cover of short grasses and tall grasses, and the "Full" models include both climate and composition variables.

was very low. The pattern was different for recruitment and population density. Composition covariates reduced up to 6% of deviance in recruitment and, for four species, composition reduced deviance more than did climate (Fig. 4b). On the other hand, climate reduced deviance (up to 12%) more than composition for six species. Deviance in overall population density closely followed the recruitment patterns, with climate producing larger reductions in deviance but composition exerting a stronger effect on four species (Fig. 4c). The reduction in deviance that could not be assigned to either climate and composition covariates due to co-linearity was never more than 3%. In fact, this overlap was often slightly negative, suggesting that the explanatory power of these variables increased when both sets were included.

The perturbation analysis showed that, for every species, a 10% increase in growing-season and/or dormant-season temperature would have stronger impacts on population performance than proportional changes in precipitation or species composition (Fig. 5).

Four of the 10 species responded more to dormant-season temperature than growing-season temperature. In almost every case, changes in overall population growth were driven far more by responses at the recruitment stage than at the survival stage (Fig. 5). The direction of the covariate effects varied dramatically among species. Surprisingly, increases in growing-season precipitation reduced population growth for four species. The predicted mean invasion exponents were well below 0 for *Paronychia jamesii*, *Ratibida columnifera*, and *Sphaeralcea coccinea*, indicating a trajectory to local extinction. These species were all at low abundance at the end of the period of record, and two of the three showed decreasing trends with time (Fig. 3).

DISCUSSION

Three general patterns emerged from our analyses. First, climate had a stronger influence than composition on historical population dynamics. Second, our models
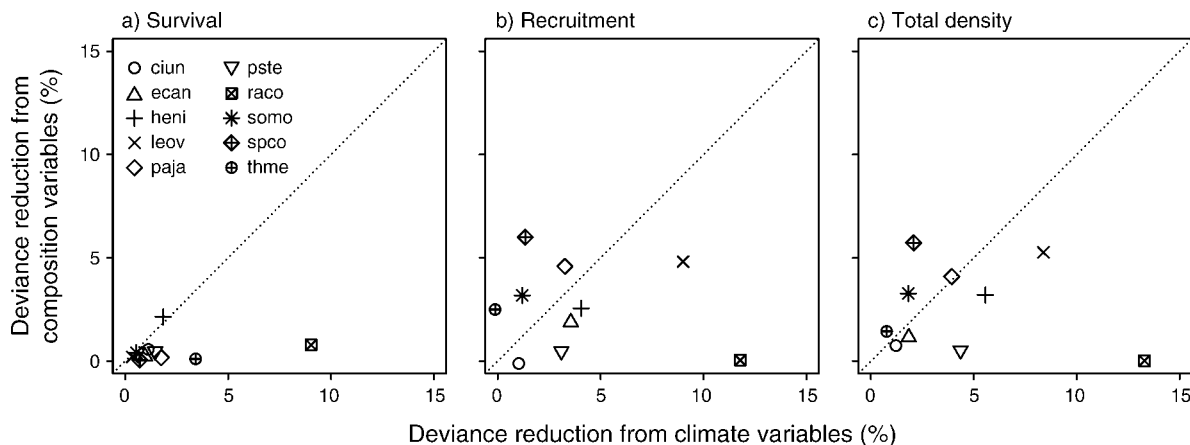

FIG. 4. Percentage reductions in deviance. Points show percentage reductions in deviance, relative to the basic models, by models that include climate and composition variables (the basal cover of short grasses and tall grasses). Species above the dotted 1:1 lines are more influenced by composition covariates than climate covariates, whereas species below the 1:1 lines are more influenced by climate covariates. Separate results are shown for (a) the survival model, (b) the recruitment model, and (c) overall population density, which combines survival and recruitment. Species codes are defined in Table 1.
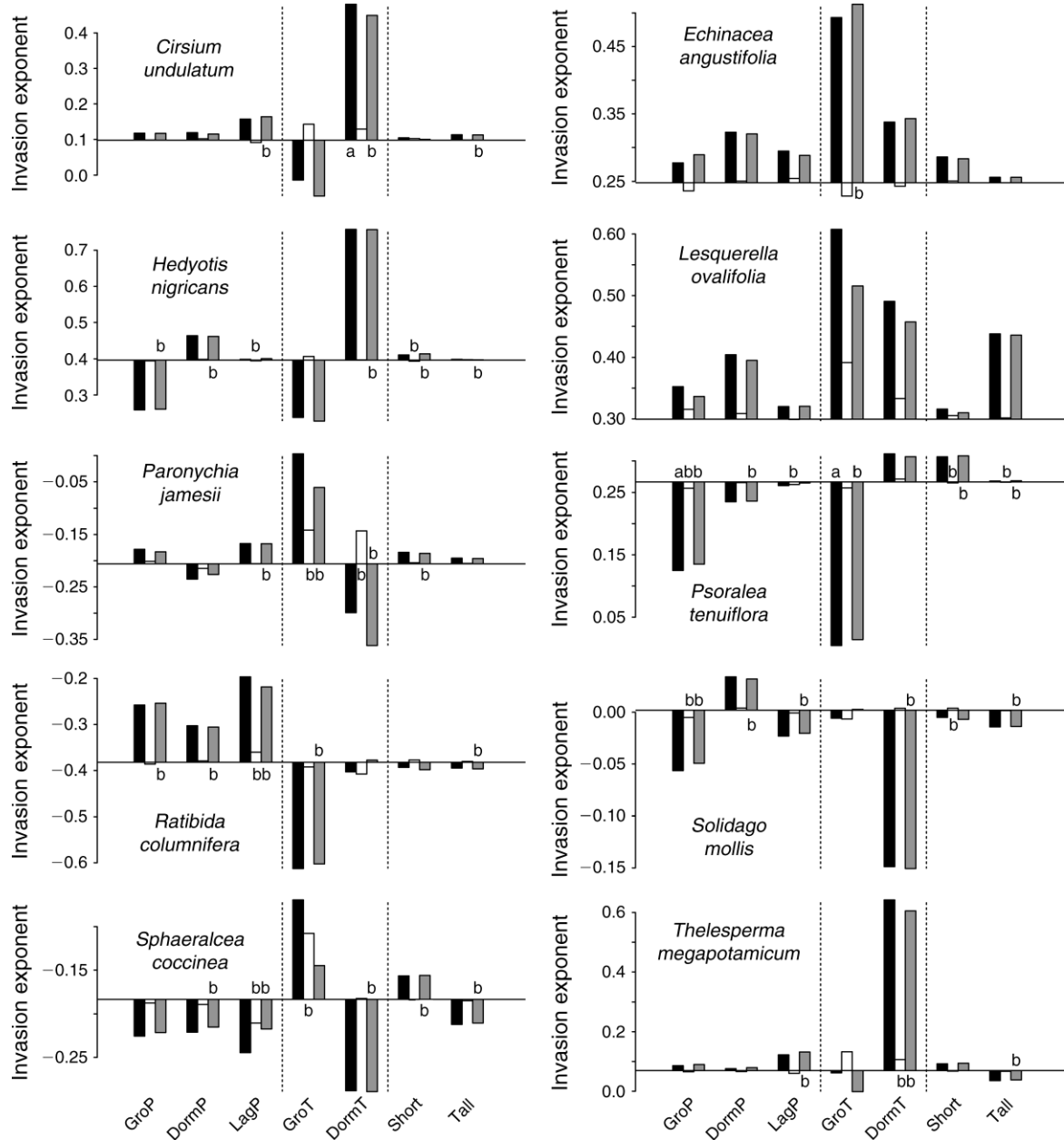
FIG. 5. Predicted changes in the invasion exponent (the log of the low-density population growth rate) in response to a 10% increase in each of the covariates. The solid bars show the predicted invasion exponents as deviations from the historical mean, and the white and gray bars show the relative contributions of changes in survival and recruitment, respectively. Lowercase letter code: "a" indicates that the 95% prediction interval on the invasion exponent does not overlap the historical mean; "b" indicates the survival and recruitment coefficients with 95% credible intervals that do not overlap zero. The vertical dotted lines help visually separate the types of variables. The climate variables are growing-season precipitation (GroP), dormant-season precipitation (DormP), annual precipitation in the previous year (LagP), growing-season temperature (GroT), and dormant-season temperature (DormT). Both temperature variables were increased by 10% of the mean annual temperature. The composition variables shown are the combined basal cover of the short grasses ("Short") and tall grasses ("Tall").

predict that the large increases in mean temperatures forecast for the region are likely to impact the population growth rates of the diverse forb species in mixed-grass prairies. Third, the significant effects of both climate and composition at the recruitment stage

imply that range expansions will be difficult to predict. However, our correlative models only explained a small portion of historical variability in population dynamics, despite the fine spatial resolution and long temporal extent of our data set. Therefore, these patterns should

not be viewed as conclusions but rather as hypotheses to guide future research and improve forecasts of how climate change will impact plant populations.

The importance of climate in historical dynamics

Our results indicate that climate played a more important role than composition in driving the population dynamics of prairie forbs over three decades in the last century. For 6 of the 10 species (Fig. 4), climate covariates reduced model deviance more than composition covariates (although for 3 species neither set of covariates had much explanatory power). In addition, climate covariates reduced deviance >5% for three species, whereas composition only reduced deviance >5% for one species (Fig. 4c). These findings are consistent with previous studies showing that weather had stronger effects than species interactions on plant communities (Fowler 1986, Sacchi and Price 1992).

Despite the importance of climate, composition sometimes played a significant role due to its influence on recruitment. At the recruitment stage, the best model included composition for every species, whereas composition covariates were included for only 5 of the 10 species at the survival stage (Table 2). This result implies that interactions with the dominant grasses have stronger effects on seedlings than on established plants. While these interactions were often positive at the recruitment stage, negative interactions were more common at the survival stage, implying that competition may overwhelm facilitation as plants mature (reviewed by Callaway and Walker [1997]).

Our models do not shed light on the mechanisms causing these responses. We speculate that positive interactions arise due to higher soil moisture under plant canopies, whereas negative interactions may involve competition for water in deeper soil layers. The water-limited nature of these subhumid grasslands supports this hypothesis. However, some species that were positively correlated with grass cover, such as *P. tenuiflora*, responded negatively to growing-season precipitation, complicating the argument for water limitation as the critical factor. Perhaps higher precipitation in some months correlates with greater light limitation, fungal growth, or herbivore pressure, or the balance between facilitation and competition shifts with precipitation, an interaction that our models did not include. Definitive answers to these questions will require field experiments.

Global warming and the structure of mixed-grass prairie communities

Our prospective analysis illustrates that small changes in mean temperatures, during both growing and dormant seasons, could have larger effects on population growth rates than proportional changes in mean precipitation or species composition. Furthermore, increases in temperature are expected with a high degree of confidence while regional forecasts for future changes in precipitation remain extremely uncertain (Christensen et al. 2007), and we know even less about how community composition will change. In fact, mean temperatures in Kansas (USA) are expected to rise more than 3°C (Christensen et al. 2007), much higher than the 1.2°C increase we used in the perturbation analysis. The sensitivity of our models to temperature combined with the likelihood of large increases in temperature suggests that warming will have significant impacts on the distributions and relative abundances of these prairie forb species.

Although our results indicate that warming is likely to affect most species, the direction of the effect varies. For example, six species responded positively to increases in dormant season temperature and four species responded negatively. It may seem surprising that 10 apparently similar prairie forbs could respond so differently to one environmental signal. Typical functional-type classifications would lump most, if not all, of our 10 species in one group (e.g., Hille Ris Lambers et al. 2004). However, temperature can influence plant populations through many different mechanisms. High temperatures affect water balance by increasing evaporative demand, but could also affect phenology (Menzel et al. 2001) and cue germination (Baskin and Baskin 2001, Crawley 2004). The potential for temperature to influence these different processes changes seasonally. In the summer growing season, when temperatures are high, effects on water balance should be strong. In the dormant season, when evaporative demand is low, temperature should have more important effects on phenology and germination. Because most of our species were sensitive to dormant-season temperatures, these latter mechanisms deserve further attention.

Whether future changes in precipitation or species composition will also significantly influence forb populations depends on how much these covariates change. Large changes in precipitation and species composition are certainly possible (e.g., Seager et al. 2007). The Hays data set (Kansas, USA) demonstrates that the basal cover of the dominant grasses can vary 50% over decadal periods. Over the spatial scale of whole species ranges, both precipitation and species composition can vary much more. However, current predictions in central North America predict <10% changes in precipitation (Christensen et al. 2007, Zhang et al. 2007). With so much current uncertainty, clear predictions will not be possible until precipitation forecasts improve and responses of dominant species are better understood.

Range expansions will be difficult to predict

Our results also suggest that the magnitude and rate of geographic range shifts in response to global warming will be difficult to forecast. Composition had a considerable influence on the historical recruitment dynamics of many species. Furthermore, future changes in both climate and composition will affect overall

population growth primarily through the response of recruitment, rather than survival (Fig. 5). In other words, the effects of climate and composition on population dynamics will depend on age structure (Hampe and Petit 2005). At expanding range margins, age structure is dominated by young individuals and population growth depends on recruitment, the stage at which our forbs were most influenced by composition. In addition, as species move into new habitats, they will encounter dramatic changes in species composition. Currently, we cannot predict the direction of these potentially strong novel interactions. The bottom line is that the ability of species to extend their ranges in response to global warming may not be well predicted by temperature increases alone. In contrast, our survival models sometimes performed best without composition covariates and survival rates were relatively unresponsive to changes in mean temperature and precipitation, suggesting that dynamics at the contracting margin of species ranges may be easier to predict.

Future directions

Long-term data sets provide an opportunity to forecast the future effects of climate change based on historical responses to climate variability. To complement this correlative approach, we need a better understanding of the mechanistic relationships between climate and plant demography. In our statistical models, we used the same set of climate and composition covariates for all 10 focal species because we had little species-specific information. This may explain why climate and composition covariates only explained a small portion of interannual variability in vital rates at the quadrat scale (also see Ibañez et al. 2007). Knowledge of how temperature, precipitation, and plant cover combine to influence resource availability and physiological cues will aid model development, and may also explain why the 10 focal species in this study, despite belonging to one functional group, responded so differently to temporal variability in climate and composition.

The patterns we have described should help guide the design of new experiments aimed at forecasting changes in the abundance and distribution of plant species. Our analyses demonstrate that future changes in mean temperatures, especially in the dormant season, are likely to have strong effects on the population growth rates of prairie forbs. In addition, the effects of climate and composition on population growth were driven primarily by responses at the recruitment stage. Taken together, these results highlight the need for field experiments that test the ability of plant species to recruit in novel habitats under warmer temperatures.

Literature Cited

Adler, P. B. 2004. Neutral models fail to reproduce observed species-time and species-area relationships in Kansas grasslands. Ecology 85:1265–1272.

Adler, P. B., J. HilleRisLambers, P. C. Kyriakidis, Q. Guan, and J. M. Levine. 2006. Climate variability has a stabilizing effect on coexistence of prairie grasses. Proceedings of the National Academy of Sciences (USA) 103:12793–12798.

Adler, P. B., and J. M. Levine. 2007. Contrasting relationships between precipitation and species richness in space and time. Oikos 116:221–232.

Adler, P. B., W. R. Tyburczy, and W. K. Lauenroth. 2007. Long-term mapped quadrats from Kansas prairie: a unique source of demographic information for herbaceous plants. Ecology 88:2673.

Albertson, F. W., and G. W. Tomanek. 1965. Vegetation changes during a 30-year period in grassland communities near Hays, Kansas. Ecology 46:714–720.

Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, Illinois, USA.

Baskin, C. C., and J. M. Baskin. 2001. Seeds: ecology, biogeography, and evolution of dormancy and germination. Academic Press, San Diego, California, USA.

Brooks, S., and A. Gelman. 1998. General methods for monitoring convergence of iterative simulations. Journal of Computational and Graphical Statistics 7:434–455.

Callaway, R. M., and L. R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78:1958–1965.

Callaway, R. M., et al. 2002. Positive interactions among alpine plants increase with stress. Nature 417:844–847.

Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. Ecology 81:619–627.

Caswell, H., and T. Takada. 2004. Elasticity analysis of density-dependent matrix population models: the invasion exponent and its substitutes. Theoretical Population Biology 65:401–411.

Christensen, J., et al. 2007. Regional climate projections. *In* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, editors. Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Clark, J. S. 2005. Why environmental scientists are becoming Bayesians. Ecology Letters 8:2–14.

Clark, J. S. 2007. Models for Ecological Data. Princeton University Press, Princeton, New Jersey, USA.

Coulson, T., E. Catchpole, S. Albon, B. Morgan, J. Pemberton, T. Clutton-Brock, M. Crawley, and B. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science 292:1528–1531.

Crawley, M. J. 2004. Timing of disturbance and coexistence in a species-rich ruderal plant community. Ecology 85:3277–3288.

Dormann, C., R. van der Wal, and S. Woodin. 2004. Neighbour identity modifies effects of elevated temperature on plant performance in the High Arctic. Global Change Biology 10:1587–1598.

Dunnett, N. P., and J. P. Grime. 1999. Competition as an amplifier of short-term vegetation responses to climate: an experimental test. Functional Ecology 13:388–395.

Ellison, A. M. 2004. Bayesian inference in ecology. Ecology Letters 6:509–520.

Fair, J., W. Lauenroth, and D. Coffin. 1999. Demography of *Bouteloua gracilis* in a mixed prairie: analysis of genets and individuals. Journal of Ecology 87:233–243.

Fowler, N. 1986. The role of competition in plant communities in arid and semiarid regions. Annual Review of Ecology and Systematics 17:89–110.

Grace, J. B. 2001. The roles of community biomass and species pools in the regulation of plant diversity. Oikos 92:193–207.

Hampe, A., and R. J. Petit. 2005. Conserving biodiversity under climate change: the rear edge matters. Ecology Letters 8:461–467.

Hill, R. R. 1920. Charting quadrats with a pantograph. Ecology 1:270–273.

Hille Ris Lambers, J., W. S. Harpole, D. Tilman, J. Knops, and P. B. Reich. 2004. Mechanisms responsible for the positive diversity–productivity relationship in Minnesota grasslands. Ecology Letters 7:661–668.

Hixon, M. A., S. W. Pacala, and S. A. Sandin. 2002. Population regulation: Historical context and contemporary challenges of open vs. closed systems. Ecology 83:1490–1508.

Ibáñez, I., J. Clark, S. LaDeau, and J. H. R. Lambers. 2007. Exploiting temporal variability to understand tree recruitment response to climate change. Ecological Monographs 77: 163–177.

Jiguet, F., A. Gadot, R. Julliard, S. E. Newson, and D. Couvet. 2007. Climate envelopes, life history traits and the resilience of birds facing global change. Global Change Biology 13: 1672–1684.

Klanderud, K., and R. Totland. 2005. The relative importance of neighbours and abiotic environmental conditions for population dynamic parameters of two alpine plant species. Journal of Ecology 93:493–501.

Lauenroth, W. K., and P. B. Adler. In press. Demography of perennial grassland plants: survival, life expectancy and life span. Journal of Ecology.

Legendre, P., and L. Legendre. 1998. Numerical ecology. Elsevier, Amsterdam, The Netherlands.

Lunn, D. J., A. Thomas, N. Best, and D. Spiegelhalter. 2000. WinBUGS—a Bayesian modelling framework: concepts, structure, and extensibility. Statistics and Computing 10: 325–337.

Menzel, A., N. Estrella, and P. Fabian. 2001. Spatial and temporal variability of the phenological seasons in Germany from 1951 to 1996. Global Change Biology 7:657–666.

Nicholson, A. J. 1954. An outline of the dynamics of animal populations. Australian Journal of Zoology 2:9–65.

Sacchi, C., and P. Price. 1992. The relative roles of abiotic and biotic factors in seedling demography of arroyo willows (*Salix lasiolepis*: Salicaceae). American Journal of Botany 79: 395–405.

Seager, R., M. Ting, I. Held, Y. Kushnir, J. Lu, G. Vecchi, H. Huang, N. Harnik, A. Leetmaa, N. Lau, C. Li, J. Velez, and N. Naik. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Science 316:1181–1184.

Spiegelhalter, D., N. Best, B. Carlin, and A. van der Linde. 2002. Bayesian measures of model complexity and fit. Journal of the Royal Statistical Society: Series B (Statistical Methodology) 64:583–639.

Stenseth, N., K. Chan, H. Tong, R. Boonstra, S. Boutin, C. Krebs, E. Post, M. O'Donoghue, N. Yoccoz, M. Forchhammer, and J. Hurrell. 1999. Common dynamic structure of Canada lynx populations within three climatic regions. Science 285:1071–1073.

Suttle, K., M. Thomsen, and M. Power. 2007. Species interactions reverse grassland responses to changing climate. Science 315:640–642.

Zhang, X., F. Zwiers, G. Hegerl, F. Lambert, N. Gillett, S. Solomon, P. Stott, and T. Nozawa. 2007. Detection of human influence on twentieth-century precipitation trends. Nature 448:461–465.

Zheng, B. 2000. Summarizing the goodness of fit of generalized linear models for longitudinal data. Statistics in Medicine 19: 1265–1275.

APPENDIX A

A table presenting mean survival and recruitment parameter values and upper and lower 95% credibility-interval limits, by study species (*Ecological Archives* E089-177-A1).

APPENDIX B

A figure depicting observed and predicted population density for the 10 study species (*Ecological Archives* E089-177-A2).