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Weak effect of climate variability on coexistence in a sagebrush steppe community

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Abstract. Climate variability, which is expected to increase in the future, can promote coexistence through a mechanism called the storage effect. Currently, we have little understanding of how the importance of the storage effect varies among ecosystems. We tested for the three conditions of the storage effect in a sagebrush steppe plant community in Idaho (USA) by combining long-term observational data with statistical models. The four sagebrush steppe species that we studied satisfied the first two conditions of the storage effect: a long-lived life stage and species-specific responses to the environment. But the critical third condition, environment-competition covariance, was very weak in this community. While the direction of the covariance was consistent with a stabilizing effect of variability (stronger competition in more favorable years), its magnitude was small, reflecting low temporal variability in both competition and species responses to the environment. Consistent with this result, simulations of species population growth rates when rare showed that climate variability had no consistent stabilizing effect on coexistence. This case study provides an important reminder that species-specific responses to the environment are not sufficient for coexistence via the storage effect. Instead, the magnitude of temporal variability in species performance also plays an important role. Comparison of our results with those from a similar study in Kansas mixed prairie suggests that temporal variability in species performance may reflect both the strength of environmental variability as well as life history strategies.

Key words: climate variability; coexistence; competition; population growth; sagebrush steppe; survival.

Introduction

Recent work has focused attention on the potential importance of species interactions in mediating the ecological effects of climate change (Davis et al. 1998, Suttle et al. 2007, Adler and HilleRisLambers 2008, Levine et al. 2008, Tylianakis et al. 2008). These studies show that the direct effect of a change in mean temperature or precipitation on a given species could be amplified or dampened by the response of other species in the community. But climate change will also alter the variability of climate factors. Both observational data and models indicate a higher frequency of heat waves, severe storms, and severe droughts in the future (Karl and Trenberth 2003, Jain et al. 2005, Salinger 2005, Allan and Soden 2008). Little research has examined how a change in climate variability will impact ecological communities (e.g., Knapp et al. 2002).

In theory, climate variability can promote species diversity through two mechanisms, the storage effect and relative nonlinearity (Chesson 2000). However, the storage effect has attracted more attention from empiricists and theory suggests it may play a more important role than relative nonlinearity in multispecies communities (Chesson 2000). The temporal storage effect operates when different competitors experience fitness advantages at different times and can store the gains made during favorable periods. For this to occur, three conditions must be satisfied (Chesson and Warner 1981, Warner and Chesson 1985, Chesson and Huntly 1989, Chesson 1990, 2000). First, organisms must have some mechanism for persisting during unfavorable periods, such as a seed bank, quiescence, or diapause. This condition, which gives the storage effect its name, buffers negative population growth; without it, populations would go extinct after a brief unfavorable period and environmental variation could never promote coexistence. Second, species must respond differently to environmental variation, making it possible for one species to experience a relatively good year while its competitor is experiencing a relatively bad year. Third, the effects of competition on a species must covary with the effects of the environment so that competition limits growth more in favorable than unfavorable years. Given condition two, which tends to partition intraspecific and interspecific competition into different years, this environment–competition covariance ensures that intraspecific competition will be stronger than interspecific

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competition, one basic requirement for stabilized coexistence (Chesson 2000).

Testing for the three conditions of the storage effect determines whether or not it is operating, but does not quantify its strength. The overall effect of climate variability on coexistence can be estimated using an invasibility approach. Stable coexistence occurs when each species can recover from low abundance (its invader state) in the presence of competitors (the resident species) at their stochastic equilibrium abundances (Chesson 2000). If climate variability helps stabilize coexistence, then, on average, species should recover from a fall to low density more quickly in a variable climate than in a constant environment. The difference in the low-density growth rate between the variable and constant scenarios measures the overall effect of climate variability on coexistence (the overall effect includes contributions from both the storage effect and relative nonlinearity).

A growing body of empirical evidence suggests that a temporal storage effect may operate in many natural ecosystems (Pake and Venable 1995, 1996, Caceres 1997, Kelly and Bowler 2002, Descamps-Julien and Gonzalez 2005, Facelli et al. 2005). Given that climate variability is a primary cause of environmental fluctuations, future increases in climate variability could impact species diversity in systems where the storage effect is important (Adler and Drake 2008). Understanding the historical influence of climate variability on coexistence across a variety of ecosystems is therefore a prerequisite for anticipating the future effects of changes in variability on species diversity.

At present, however, we remain unable to generalize about the role of the temporal storage effect in maintaining diversity. The handful of empirical studies cited above rarely test for all three conditions of the storage effect or quantify its strength. We recently developed tools that combine long-term observational data and models to test for the three conditions of the storage effect and to quantify the overall effect of climate variability on coexistence (Adler et al. 2006). When we used these tools to analyze the dynamics of a Kansas mixed prairie community, we found evidence for all three conditions of the storage effect and showed that historical climate variability had a very strong stabilizing effect on coexistence (Adler et al. 2006). The next step is to explain variation in the importance of this effect across ecosystems.

Here we analyze the effect of historical climate variability on coexistence in a North American sagebrush steppe. We focus on this community for a number of reasons. Because it is a semiarid ecosystem, water is a primary limiting factor (Noy-Meir 1973) and plant performance should be sensitive to precipitation variation. The dominant species, perennial grasses and shrubs, are long-lived species clearly able to survive unfavorable periods. The functional diversity among these dominants might allow them to respond differently to variation in precipitation timing or amount, or it could promote coexistence through fluctuation-independent mechanisms (Chesson 2000). Finally, we had access to long-term, mapped data (Blaisdell 1958, West et al. 1979) that made it possible to estimate the demographic rates of co-occurring species, conditional on neighborhood interactions and climate variability. Our four objectives were (1) to test for the three conditions of the storage effect, (2) to estimate the overall effect of climate variability on coexistence, (3) to evaluate the sensitivity of our results to assumptions, and (4) to compare and contrast the sagebrush steppe results with our previous analysis of the Kansas mixed prairie community.

METHODS

Study site and data set description

Our sagebrush steppe data set comes from the U.S. Sheep Experiment Station (USSES) near Dubois, Idaho, USA (44°12′ N, 112°1″ W). The site is approximately 1500 m above sea level, has a mean annual temperature of 6.2°C, and receives on average 307 mm per year of precipitation, distributed throughout the year but peaking in May and June. The dominant perennial grasses are *Pseudoroegneria spicata*, *Poa secunda*, and *Hesperostipa comata*, and the dominant shrub is *Artemisia tripartita*. These four species, which account for over 70% of total basal cover and 60% of canopy cover, were the focus of our analysis.

In the late 1920s, scientists at the USSES began establishing permanent 1-m^2 quadrats. In most years until 1957, they used pantographs to map all the individual plants in each quadrat (Hill 1920). We digitized the original maps into a geographic information system. Our storage effect analysis focuses on 18 ungrazed quadrats, distributed among four exclosures, censused between 1929 and 1957. Monthly temperature and precipitation data collected on site are available for the entire period of record.

Modeling approach

We used statistical and simulation models to link the historical data with storage effect theory. More specifically, we fit a statistical model to the observational data, and then simulated this model to test the conditions of the storage effect and to estimate the overall effect of climate variability on coexistence. Here we describe the main features of the model (Adler et al. [2006] contains additional detail on the same modeling approach applied to a different plant community).

We took a lattice approach, turning the quadrat maps into grids of 2-cm cells, with each cell occupied by one of the three grass species or bare ground. The shrub species is included in a second, canopy layer. It is possible for grass and shrub to overlap: A basal cell can be occupied by a grass species while the canopy cell at the same coordinate is occupied by the shrub. Large plants appear as clusters of cells all in the same state. Although the fates of these cells are not formally linked, we account for local interactions with neighboring cells belonging to the same individual plant, to other conspecific plants, and to heterospecifics, meaning that a cell in the center of a large plant can behave quite differently from an isolated cell.

The goal of the model is to predict the states of each cell in the basal and canopy grids at time $t+1$, based on their states at time t. We assume that cell states depend on both a survival process (for occupied cells) and a colonization process (for all cells). The survival probability, S, of species i in cell j and quadrat q from time t to $t+1$ is

$$\text{logit}(S_{ijqt+1}) = \alpha_{it} + \phi_{iq} + \beta_{it}^{S1}\text{Self}_{jt} + \beta_{it}^{S2}\text{PS}_{jt} + \beta_{it}^{S3}\text{PO}_{jt} + \beta_{it}^{S4}\text{HC}_{jt} + \beta_{it}^{S5}\text{AT}_{jt} \quad (1)$$

where α is an intercept, ϕ is a quadrat random effect, and the remaining terms describe the effects of local neighborhood crowding: Self refers to cells occupied by the same individual plant as the focal cell, PS refers to *Pseudoroegneria spicata*, PO to *Poa secunda*, HC to *Hesperostipa comata*, and AT to *Artemisia tripartita*. The β_{it}^{S}'s describe the effect of each class of neighbor on the survival of species i at time t. Survival for any species not currently occupying the cell is set to zero.

We quantify neighborhood crowding as the distance-weighted cover of all species or bare ground within a 10-cm radius of the focal cell, normalized to sum to 1. We used a negative exponential function to weight cells closer to the focal cell more heavily than cells far away. We determined the values of the exponent through model fitting (see last paragraph in this section), choosing the value (1.5) that minimized the summed deviance from the basal and canopy components of the model (Appendix A).

The colonization probability, C, for species i in cell j and quadrat q at time $t+1$ is

$$\text{logit}(C_{ijqt+1}) = \delta_{it} + \theta_{iq} + \beta_{it}^{C1}\text{PS}_{jt} + \beta_{it}^{C2}\text{PO}_{jt} + \beta_{it}^{C3}\text{HC}_{jt} + \beta_{it}^{C4}\text{AT}_{jt} \quad (2)$$

where δ is an intercept, θ is a quadrat random effect, and the remaining terms describe the effects of local neighborhood crowding as for survival. In this case, however, Self is added to the corresponding species. The intercept determines the probability of colonization in an empty neighborhood, presumably by establishment from seed, while the neighborhood parameters represent both vegetative reproduction (probably the dominant form of spread for our study species) and competitive and/or facilitative effects.

Once the survival and colonization probabilities are known, we combine them to calculate the overall probability of presence, p, in cell j at time $t+1$. For occupied cells, this probability equals the probability of survival plus the probability that the occupying species dies but then recolonizes the cell. For unoccupied cells, survival is defined as 0, so the probability of presence depends only on the colonization probability. For *A. tripartita*, the canopy species, the probability of presence at time $t+1$ in cell j is

$$p_{\text{AT}jt+1} = S_{\text{AT}jt+1} + (1 - S_{\text{AT}jt+1})C_{\text{AT}jt+1}. \quad (3)$$

For the basal species, the approach is identical, but the colonization term is longer to recognize that the probability of colonization by, for example, *P. spicata*, is the sum of the probability that *P. spicata* is the only colonizer in the cell, plus the probability that *P. spicata* and another species arrive in the cell and *P. spicata* wins the resulting lottery. More formally, dropping the cell and time subscripts for clarity, the probability of presence, p, for *P. spicata* is

$$p_{\text{PS}} = S_{\text{PS}} + (1 - S_{\text{PS}})[C_{\text{PS}}(1 - C_{\text{PO}})(1 - C_{\text{HC}}) + (C_{\text{PS}})(C_{\text{PO}})(1 - C_{\text{HC}})/2 + (C_{\text{PS}})(1 - C_{\text{PO}})(C_{\text{HC}})/2 + (C_{\text{PS}})(C_{\text{PO}})(C_{\text{HC}})/3] \quad (4)$$

where PS, PO, and HC refer to *P. spicata*, *Poa secunda*, and *H. comata*, respectively.

We parameterized the survival and colonization functions using a hierarchical Bayesian approach and Markov Chain Monte Carlo (MCMC) methods (see Adler et al. [2006] for information on prior distributions). We assumed that the canopy data, y, were binomially distributed

$$y_{\text{AT}jt+1} \sim \text{binomial}\,(p_{\text{AT}jt+1}) \quad (5)$$

and that the data for the basal species, X, followed a multinomial distribution of dimension four (three species and bare ground) and one trial (per cell)

$$\mathbf{X}_{jt+1} \sim \text{multinomial}(\mathbf{p}_{jt+1}, 1). \quad (6)$$

We fit the canopy and basal models separately, after excluding all cells within 10 cm of edges or whose neighborhoods were influenced by species not included in the model (60% of all grid cells were excluded). The hierarchical structure allowed us to estimate year-specific parameters as random draws from underlying mean parameters. We interpret these mean parameters to represent species performance in a hypothetical constant environment.

Testing the three conditions of the storage effect

We tested for the first condition of the storage effect, involving mechanisms of persistence, by performing a survival analysis for each species, using spatial locations to track individual genets through time. We followed the methods of Lauenroth and Adler (2008) with one modification: we allowed genets to survive across two years of missing data, which reduced the number of records to be censored. Even if juvenile survival is low, high adult survival can buffer species against unfavorable periods, provided that adult survival is relatively insensitive to competition. In fact, storage of reproductive potential in the rhizomes and dormant meristems of long-lived perennials provides a direct analogy to the seed storage that forms the basis of much of the theory (Chesson and Huntly 1989, Chesson et al. 2004). Only when these rhizomes or meristems are activated, and vegetative growth initiated, will they become vulnerable to negative effects of competition.

To test for condition two, species specific responses to the environment, we used the lattice model to simulate each species' yearly intrinsic growth rate. In the storage effect theory, a species' response to the environment is measured when it is unconstrained by intra- or interspecific competition (Chesson 2000). For each species in each year, we initialized an empty lattice with one individual (3-cm radius) of the focal species, drew survival and regression parameters for the appropriate year (averaging across quadrat effects), and calculated population growth as

$$r = \log[E(P_1)] - \log(P_0)$$

where P_0 is the proportion of the lattice in which the focal species is present at time 0 and P_1 is the proportion expected at time 1. For each set of year-specific parameters we repeated this one time step projection 250 times to account for parameter uncertainty. After estimating the yearly intrinsic growth rates, we calculated species' pairwise correlations. The weaker, or more negative, the pairwise correlations, the greater the potential for species to exploit unique temporal niches. To identify the climate variables driving these species-specific responses, we performed multiple regressions of each species' yearly intrinsic growth rates on the following seasonal precipitation and temperature variables recorded on site: total precipitation and mean temperature in each of the four seasons of the current year, and total annual precipitation and mean annual temperature in the previous year (Craddock and Forsling 1938 and the National Climatic Data Center [data *available online*]).[5] We then used a stepwise AIC procedure to select the final models for each species.

We tested for condition three, environment–competition covariance, by combining the estimated yearly intrinsic growth rates with results from a second simulation to determine the effect of competition, or crowding, on growth. We initialized a series of grids in which we randomly varied the total abundance and the relative abundances of the three basal grasses and the canopy shrub. To create initial conditions with realistic spatial structure, we used sequential indicator kriging (as in Adler et al. [2006]), assuming random spatial associations among the four species. (Although we had expected negative associations between the shrub and the grasses, we found that the probability of grass–shrub overlap in the observed data was not significantly different from that expected by chance.) For each year, we drew the appropriate survival and colonization parameters and projected species growth rates forward one time step. Again, we repeated each projection many times to account for parameter uncertainty. We then regressed the projected growth rates for each species against square root transformed total cover, which serves as a proxy for intra- plus interspecific crowding. The slope of this relationship represents the effect of that crowding on population growth rates for a particular year. Finally, for each species, we plotted the slope of this competition relationship for each year against the corresponding yearly intrinsic growth rate. Negative covariance, meaning stronger negative effects of crowding in more favorable years (higher intrinsic growth rates), is required for fluctuations to stabilize coexistence.

Quantifying the strength of fluctuation-mediated coexistence

If all three conditions of the storage effect are satisfied, we can conclude that temporal environmental fluctuations should have a stabilizing effect on coexistence. The next step is to determine the strength of this effect. To quantify the overall effect of interannual variability on coexistence (the combined effects of the storage effect and relative nonlinearity), we need to compare species' long-term average low-density growth rates in constant and variable environments.

We simulated each species' long-term low-density growth by initializing 500 grids with the resident species at their stochastic equilibrium abundances (using sequential indicator kriging to create realistic spatial structure). We then introduced one individual (3 cm radius) of the focal or invader species at a random coordinate. To simulate a variable environment, we randomly selected one set of year-specific parameters and projected the focal species growth, r, over one time step. We repeated these steps for each of the 500 grids. To simulate a constant environment, we used the mean parameters to project growth from the same initial grids. For both the constant and variable environments, the long-term low-density growth rate is the mean of the respective r's over all replicate grids (the geometric mean of the multiplicative growth rates).

A challenge of these simulations is defining the stochastic equilibrium of the resident species. This equilibrium cannot be observed directly in our data, because we never observe our focal species invading a community in which they are not present. In addition, we want to define the stochastic equilibrium of the resident species for both variable and constant environments.

One way to estimate the stochastic equilibria of the resident species is with simulations of the lattice model: initialize a grid with the three residents at some low abundance, and project the system forward until some stochastic equilibrium is reached. The advantage of this simulation approach, used in Adler et al. (2006), is that

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[5] ⟨http://www4.ncdc.noaa.gov/cgi-win/wwcgi.dll?wwDI~StnSrch~StnID~20005317⟩

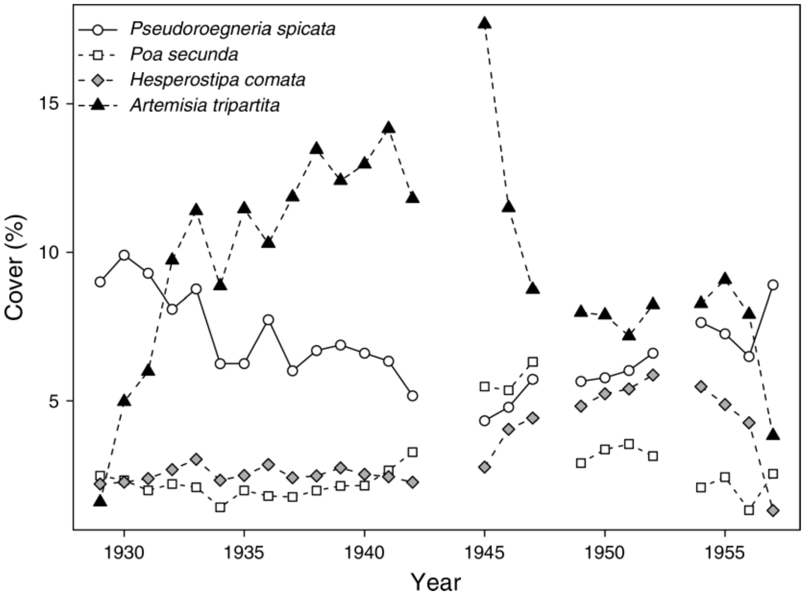

FIG. 1. Observed abundances of the four modeled species. Abundance is measured as absolute basal cover for the three grass species and as absolute canopy cover for the shrub *Artemisia tripartita,* calculated after transforming the original maps to grids of 2-cm cells. Mean annual abundances were estimated using a linear mixed model with quadrats as random effects and year as a fixed effect.

it is based on vital rates estimated from data and allows projection of resident communities in both constant and variable environments. The disadvantage is that the effects of inaccurate model assumptions (e.g., survival is linearly related to neighborhood densities on the logit scale) may be compounded as the simulation is carried forward in time. Presumably because of such errors, we found that the simulated resident Idaho communities reached unrealistically high levels of total cover. Note that all other simulations used for testing the conditions of the storage effect involved projections of only one time step.

To evaluate the sensitivity of our results to assumptions about the resident community, we repeated the invasibility analysis using a second, null method based only on the historical data. For each focal species, we altered the 21 years of observed abundances, setting the focal species to zero and transferring its cover to the remaining residents proportionally, so that the relative abundance of the residents remained unchanged. We assume that the resulting 21 years of resident abundances represent the residents' stochastic equilibria, and draw from them to initialize the replicate grids. Although this approach avoids compounding model assumptions and generates realistic levels of total cover, it assumes that the relative abundances of the residents should remain constant after the focal species is removed, implying that interactions between the focal species and the residents do not differ. In addition, this approach assumes that the resident community is the same in both variable and constant environments.

RESULTS

Observed patterns and model fit

The two most abundant species, *P. spicata* and *A. tripartita*, had opposite trends in abundance over time. *P. spicata* started at relatively high cover and then decreased through the middle of the time series before recovering at the end, while *A. tripartita* peaked in the middle (Fig. 1). *Poa secunda* and *H. comata* stayed at relatively low abundances throughout the time series, with subtle peaks towards the end (Fig. 1). The lattice models for the basal and canopy layers successfully converged. The models did a reasonable job of predicting quadrat-level cover one time step ahead (Appendix B).

The three conditions of the storage effect

The survival analysis showed strong evidence for the first condition of the storage effect, a long-lived life stage. For all four species, survival during the first years of life was low, but once individuals reached three to four years of age, annual survival rates exceeded 90% (Fig. 2). The maximum observed life spans, which are constrained by the length of the dataset, were greater than 30 years for all four species.

We also found evidence for species-specific responses to the environment, the second condition of the storage effect. Correlations of simulated yearly intrinsic growth rates between pairs of species ranged from −0.22 to 0.44 (Table 1). The only negative correlations occurred for comparisons between *A. tripartita* and the grasses. These weak and/or negative correlations mean that species are responding in different ways to interannual variability.

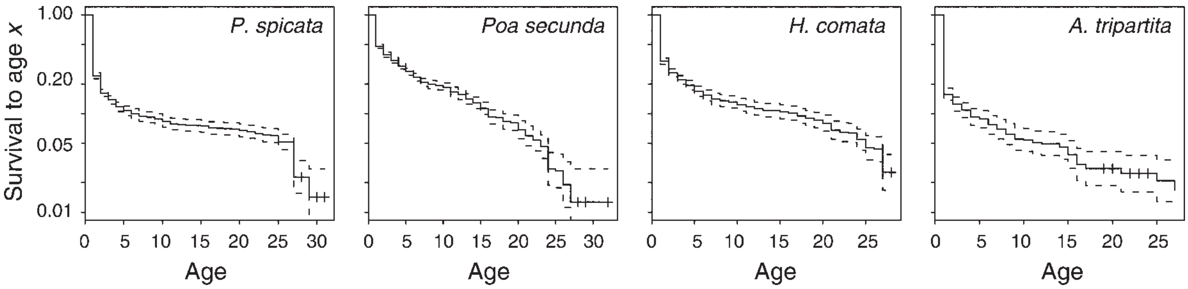

FIG. 2. Kaplan-Meier survival curves for the four modeled species.

The species-specific responses are shown by multiple regressions of the yearly intrinsic growth rates on seasonal climate variables (Table 2). The models for the different species often contained different climate variables, and in some cases where two species responded to the same climate variable, the direction of their response differed. For example, spring precipitation had a positive effect on the grass *Poa secunda*, but a negative effect on the shrub *A. tripartita* (Table 2).

Evidence for the third condition of the storage effect, environment–competition covariance, was very weak. Although the sign on the covariance was negative for all four species (Fig. 3), meaning that competition was more limiting in more favorable years, as required by the theory, the covariances were close to zero, ranging from −0.02 to −0.13.

The overall strength of fluctuation-mediated coexistence

Quantifying the overall effect of interannual fluctuations on coexistence using an invasibility approach requires first estimating the abundances of the resident species. Different methods of defining the stochastic equilibrium abundances of the resident species produced very different resident communities. The simulation approach produced much higher levels of total cover than the null approach. Relative abundances among the residents differed as well. These patterns are illustrated in Fig. 4, which shows the resident communities when *Poa secunda* is set to low abundance. Results for the other three focal species were similar.

For the three grasses, the simulated long-term, low-density growth rates were either higher in the constant environment (*P. spicata*), or virtually equal in the constant and variable environment (*Poa secunda* and *H. comata*) (Fig. 5). *A. tripartita*'s long-term, low-density growth rate was slightly higher in the variable environment. The small growth rate differences between the constant and variable environment were similar for resident communities defined by the simulation and null approaches. However, the average values of the growth rates differed depending on the choice of resident communities, with *P. spicata* and *Poa secunda* showing higher growth rates in the simulated resident communities, and the other two species showing the opposite trend (Fig. 5).

DISCUSSION

Our main finding is that temporal environmental fluctuations had little effect on coexistence in this sagebrush steppe community during the study period. For three of our four species, long-term, low-density, growth rates were not higher in a variable environment and, for the fourth species, the variable environment provided only a small advantage. This analysis predicts that future increases in climate variability should have little effect on coexistence in our study system.

The sagebrush steppe results provide an important reminder that species-specific responses to the environment do not guarantee that the storage effect is operating. We found clear evidence for the first two conditions of the storage effect, the presence of a storage mechanism and species-specific responses to the environment. But without the third condition, environment–competition covariance, the storage effect cannot stabilize coexistence. Unfortunately, environment–competition covariance is the hardest condition of the storage effect to quantify, and previous studies of desert annuals (Pake and Venable 1996, Adondakis and Venable 2004, Facelli et al. 2005) have inferred an important role for the storage effect in coexistence based only on evidence for the first two conditions. Our analysis highlights the danger of drawing such conclusions without information on the strength of environment–competition covariance.

The weak stabilizing effect of climate variability in the sagebrush steppe community suggests that other coexistence mechanisms are operating. In fact, fluctuation-independent coexistence mechanisms provide the only plausible explanation for the positive low-density growth rates that we found for three of four species in a simulated constant environment (Fig. 5). The function-

TABLE 1. Correlation matrix for the simulated yearly intrinsic growth rates of the four modeled species.

Species	*Poa secunda*	*Hesperostipa comata*	*Artemisia tripartita*
Pseudoroegneria spicata	0.28	0.44	−0.22
Poa secunda		0.13	−0.05
Hesperostipa comata			−0.03

TABLE 2. Multiple regressions of yearly intrinsic growth rates on climate variables show differences in species responses to the environment.

Variable	Estimate	SE	t	P
Pseudoroegneria spicata ($R^2 = 0.46$, $F = 2.53$, df = 5, 15, $P = 0.075$)				
Intercept	−1.85	2.11	−0.877	0.39
Fall precipitation ($t = 0$)	−0.014	0.004	−3.427	<0.01
Annual precipitation ($t = -1$)	0.002	0.001	1.608	0.13
Mean winter temperature ($t = 0$)	0.057	0.038	1.518	0.15
Mean fall temperature ($t = 0$)	−0.125	0.062	−2.004	0.063
Mean summer temperature ($t = 0$)	0.176	0.111	1.573	0.14
Poa secunda ($R^2 = 0.82$, $F = 6.94$; df = 8, 12, $P = 0.002$)				
Intercept	−4.081	1.340	−3.045	0.010
Winter precipitation ($t = 0$)	0.004	0.002	2.052	0.063
Spring precipitation ($t = 0$)	0.002	0.002	1.557	0.15
Fall precipitation ($t = 0$)	−0.008	0.003	−2.855	0.014
Annual precipitation ($t = -1$)	0.004	0.001	4.967	<0.001
Mean winter temperature ($t = 0$)	0.096	0.030	3.168	<0.01
Mean spring temperature ($t = 0$)	−0.202	0.051	−3.966	<0.01
Mean fall temperature ($t = 0$)	−0.152	0.040	−3.805	<0.01
Mean summer temperature ($t = 0$)	0.335	0.075	4.466	<0.001
Hesperostipa comata ($R^2 = 0.29$, $F = 7.81$, df = 1, 19, $P = 0.011$)				
Intercept	−0.04754	0.15735	−0.302	0.7659
Mean winter temperature ($t = 0$)	−0.075	0.027	−2.795	0.012
Artemisia tripartita ($R^2 = 0.48$, $F = 2.17$, df = 6, 14, $P = 0.11$)				
Intercept	−5.70	3.865	−1.474	0.16
Winter precipitation ($t = 0$)	0.005	0.004	1.275	0.22
Spring precipitation ($t = 0$)	−0.006	0.004	−1.494	0.16
Summer precipitation ($t = 0$)	0.007	0.003	2.063	0.058
Annual precipitation ($t = -1$)	0.002	0.002	1.225	0.24
Mean summer temperature ($t = 0$)	0.257	0.176	1.464	0.17
Mean annual temperature ($t = -1$)	0.172	0.098	1.745	0.103

Notes: Climate variables can exert effects in the present year ($t = 0$) or as lag effects from the preceding year ($t = -1$). Model selection was based on a stepwise AIC procedure, which may result in inclusion of variables with $P > 0.05$.

ally diverse mix of dominant perennial grasses and shrubs may create more opportunity for other forms of niche differentiation, such as vertical partitioning of soil water (Walter 1971, Walker et al. 1981). Temporal variability within a year, which the historical data cannot reveal, may also play a role. For example, *Poa secunda* has much earlier phenology than the other two grasses, while *A. tripartita* has a much longer growing season.

Our conclusion that the effect of climate variability on coexistence is weak for these sagebrush steppe species is robust to our model assumptions. The portion of the analysis most sensitive to these assumptions is the invasibility analysis, which requires information about the stochastic equilibrium of the resident community. If we had found strong stabilizing effects, then knowing the absolute sign of the growth rate when rare would be important. For example, a negative growth rate in a constant environment but a positive growth rate in the variable environment would imply that climate variability is essential for coexistence. But because we found very weak environment-competition covariance, and little difference between low-density growth rates in constant and variable environments, uncertainty surrounding the resident communities has little bearing on

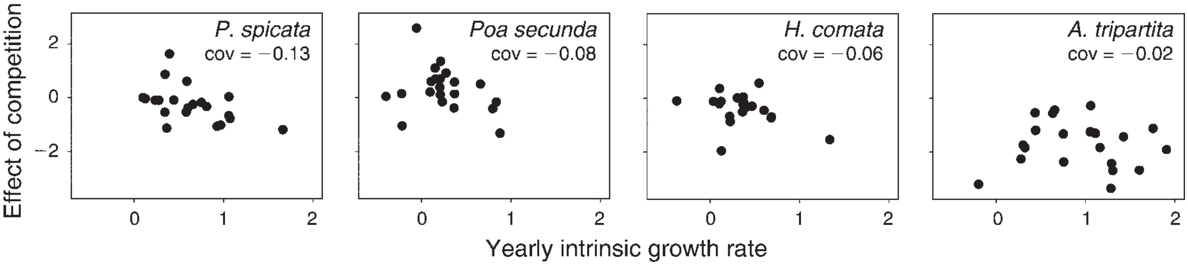

FIG. 3. Covariance between the environment and the effect of competition on growth for each of the four modeled species. The favorability of the environment is measured by each species' simulated yearly intrinsic growth rate. The effect of competition in each year is measured by the slope relating total cover to the growth rate. Negative values indicate that an increase in total cover decreases the simulated growth rate.

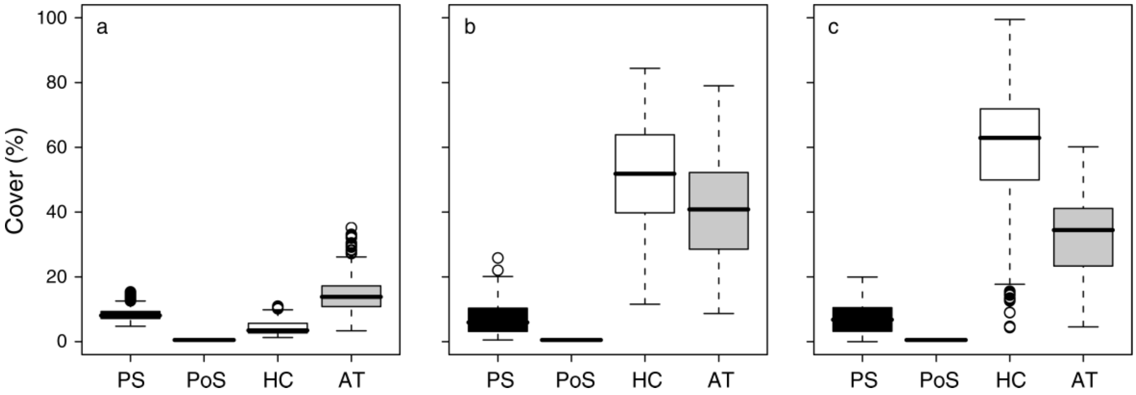

FIG. 4. Boxplots for the cover of the resident species (PS, *Pseudoroegneria spicata*; HC, *Hesperostipa comata*; AT, *Artemisia tripartita*) when *P. secunda* (PoS) is set to low abundance for the invasibility analysis. (a) Resident abundances based on a null approach using historical abundances, (b) resident abundances based on model simulations for a variable environment, and (c) resident abundances based on model simulations for a constant environment. The box indicates the lower and upper quartiles of the data, while the horizontal line inside the box shows the median. The bars extend to the most extreme data points not exceeding 1.5 times the interquartile range from the box. Data points falling outside this range are shown by circles.

our conclusion that climate variability plays a small role in coexistence.

Comparison of sagebrush steppe and mixed prairie

The sagebrush steppe results contrast sharply with a similar analysis of a Kansas southern mixed prairie community, in which all three conditions of the storage effect were present and climate variability had a strong stabilizing effect on coexistence (Adler et al. 2006). Our analysis allows us to determine the key difference between the sagebrush and prairie case studies. In both communities, the modeled perennial species had high adult survival and responded differently to climate variability. In fact, the sagebrush steppe species showed stronger species-specific responses to the environment than we found among the prairie species. Correlations of yearly intrinsic growth rates involving the shrub, *A. tripartita*, were negative, whereas we found no negative correlations among the Kansas prairie species (Adler et al. 2006). However, the environment-competition covariances for the sagebrush steppe species (ranging from −0.02 to −0.13) were an order of magnitude weaker than those for the prairie species (ranging from −0.50 to −1.12).

The weaker environment–competition covariances in sagebrush steppe reflect relatively low interannual variability in both intrinsic growth rates (which represents species response to the environment) and in competition. Yearly intrinsic growth rates had variances ranging from 0.11 to 0.30 for the sagebrush steppe species, compared to a range of 0.58 to 1.07 for the prairie species. For the sagebrush steppe species, variances of the effect of competition on growth ranged from 0.33 to 0.78, compared to a range of 1.6 to 2.6 for the prairie species. Apparently, the prairie community is simply more demographically dynamic than the sagebrush steppe community.

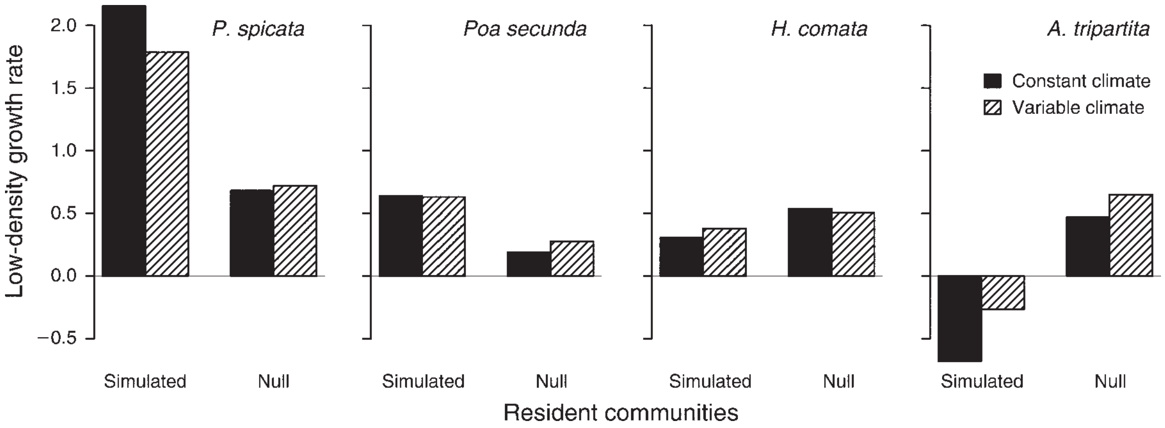

FIG. 5. The overall effect of climate variability on coexistence is measured as the difference in low-density growth rates projected for constant (solid bars) and variable (hatched bars) environments. Focal species growth rates were projected for resident communities defined using either a simulation approach or a null approach based on historical abundances.

Differences in the climatic regimes of the two sites could explain differences in the interannual variability in species performance. Compared to the sagebrush steppe site, the prairie site is warmer (mean annual temperature of 12°C vs. 6°C), wetter (mean annual precipitation of 580 mm vs. 307 mm), receives precipitation primarily in spring and summer rather than fall through spring, and supports C_3 and C_4 species (C_4 is very rare in sagebrush steppe). One possibility is that the prairie climate simply offers more interannual variability for species to exploit. However, the coefficients of variation for annual precipitation over the study periods were similar: 27% for the prairie site and 23.5% for the sagebrush steppe site. Differences in seasonality of precipitation might offer a better argument for greater consistency of the sagebrush steppe climate. Because of low evaporation and transpiration during the wet sagebrush steppe winters, soil water availability peaks reliably in early spring. Furthermore, interannual variability in water availability may be lower at the sagebrush steppe site if even relatively dry winters can recharge the soil profile.

A second possible explanation is that the sagebrush sites drier climate may select for life history traits that minimize between-year variability in species performance. If harsh or arid conditions rarely permit recruitment, dominance would require high investment in survival. Plants allocating more resources to survival will suffer fewer losses in unfavorable years, but may sacrifice rapid growth during favorable conditions (Seger and Brockman 1987, Phillippi and Seger 1989, Gleeson and Tilman 1990). The somewhat ironic implication is that very high allocation to storage may reduce the potential for a strong storage effect. Perhaps the sagebrush steppe species most likely to benefit from the storage effect are not the long-lived dominants we analyzed, but the shorter-lived forb species capable of rapid population growth in favorable years.

Conclusion

The comparison of the sagebrush steppe and mixed prairie emphasizes that species-specific responses to temporal fluctuations are not sufficient to stabilize coexistence. Rather, the magnitude of environment–competition covariance is critical. While the lower temporal variability of species performances in the sagebrush steppe site compared to the prairie site may simply reflect differences in the magnitude of environmental variability that we could not detect, we speculate that differences in life history strategies may play an important role. Selection for life history strategies that minimize temporal variability in vital rates at the individual level will limit the potential for the storage effect to stabilize coexistence at the community level. Empirical investigations of the storage effect have tended to focus on systems in which long-lived dormant stages are conspicuous, such as communities of desert annuals. But given that most species have some storage capacity (such as high adult survival), perhaps we should expect to find the strongest effects of climate variability on coexistence, at least on the time scales that we investigated, in communities with less dormancy but a greater potential for rapid growth during favorable periods. Completion of similar analyses for additional communities will make it possible to test these ideas and to build a general understanding of when and where climate variability plays an important role in maintaining species diversity.

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APPENDIX A

Summed deviance of the canopy and basal layer models as a function of the neighborhood distance weighting exponent (*Ecological Archives* E090-235-A1).

APPENDIX B

Observed and predicted quadrat cover by species (*Ecological Archives* E090-235-A2).