

NEW METHODS FOR QUANTIFYING THE SPATIAL STORAGE EFFECT: AN ILLUSTRATION WITH DESERT ANNUALS

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Abstract. Recent theory supports the long-held proposition that coexistence is promoted by species-specific responses to a spatially varying environment. The underlying coexistence mechanism, the spatial storage effect, can be quantified by the covariance between response to the environment and competition. Here, “competition” is generalized to encompass similar processes such as facilitation and apparent competition. In the present study, we use a model field system of desert annual plants to demonstrate this method and to provide insight into the dynamics of the field system. Specifically, we use neighborhood competition experiments to quantify the spatial storage effect and compare it to the separate (but not mutually exclusive) process of neighborhood-scale resource partitioning. As our basic experimental design has been used frequently in community ecology, these methods can be applied to many existing data sets, as well as future field studies.

Key words: *coexistence mechanisms; competition along gradients; environmental variation; facilitation; neighborhood competition; spatial heterogeneity; spatial storage effect.*

INTRODUCTION

According to theory, species can coexist stably in a community if each has a positive population growth rate at low population density (Ellner 1989, and see review in Chesson 2000b). This also applies when species' densities fluctuate, provided the population growth rate is measured as an average over time. However, each species in the community must be in some way self-limiting, and the overall negative effects of a species' density on its own growth (intraspecific competition) must be greater than the negative effects it imposes on other species (interspecific competition). In such cases, the population dynamics of each species depend on the relative abundance (frequency) of individuals of different species.

Feedback loops of this sort can arise from a variety of mechanisms, but all involve some form of niche differentiation between species, defined by the ways they interact with the physical or biological environment (Chesson 2000a). The spatial scale at which frequency dependence emerges is the spatial scale of the coexistence mechanism. Frequency dependence arises at the neighborhood scale for local resource partitioning. For environmental niche partitioning and the spatial storage

effect, frequency dependence arises at scales that encompass environmental heterogeneity, for example, patches with different soil conditions.

Local resource partitioning—in which different species' populations are limited by different resources, such as water, sun, or nitrogen—promotes coexistence if it causes intraspecific competition to exceed interspecific competition on neighborhood scales. Many studies have looked for this mechanism by evaluating competition intensity in plant neighborhoods (e.g., Pantastico-Caldas and Venable 1993, Aguiar et al. 2001, Howard and Goldberg 2001). Although demonstrated in algal systems (Tilman 1982), there has not been consistent evidence for coexistence via resource partitioning in terrestrial plants (e.g., Goldberg and Barton 1992). But the failure of experiments to find intraspecific competition more intense than interspecific competition on small scales, consistent with resource partitioning, does not mean that frequency dependence is absent at all scales. Frequency dependence can arise from interactions with spatial or temporal environmental heterogeneity, or from spatial distribution patterns (see review in Chesson 1997, Bolker and Pacala 1999, Snyder and Chesson 2004).

It is not a new idea that environmental variation can contribute to coexistence if species have different competitive abilities under different microhabitat conditions (spatial niches), but storage effect theory lets us quantify this mechanism (Chesson 2000b). Storage effect theory provides a general approach to identifying spatial niches, and applies specifically to the situation where physical environmental conditions favor different species in different patch types, and competition for common resources occurs. To be nontrivial, patches of

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different relative quality must be connected by dispersal. When the scale of environmental variation includes different patch types, high population growth rates in favorable patches buffer or compensate for low population growth-rates in unfavorable patches. In the analogous temporal case, from which the term “storage effect” was derived, seed banks or long-lived adults “store” the effects of favorable years, which buffer the effects of bad years when population sizes may decline (Chesson 1994). To promote coexistence through the spatial storage effect, the buffering of the effects of bad patches by good patches must be accompanied by species-specific spatial niches and covariance between plant responses to the environment and competition (Chesson 2000b).

Positive covariance between response to the environment and competition (environment–competition covariance) means that the intensity of competition experienced by a population increases as the environment improves for that species. Increases in competition intensity along environmental gradients were predicted by Bertness and Callaway (1994), and have since been explored and demonstrated in other systems (e.g., Tielborger and Kadmon 2000, Choler et al. 2001, Peltzer and Wilson 2001, Pugnaire and Luque 2001). Unlike the studies above, storage effect theory defines habitat quality separately for each species based on its response to spatially varying conditions, rather than by discrete characteristics of the physical environment (such as nitrogen levels). In practice, this means that instead of attempting to quantify an absolute measure of environmental quality, which is limited by our perceptions and ability to discriminate relevant parameters, gradients are defined by individual plant responses to the sum of environmental conditions at each growing location. With this approach, competition along natural gradients can be directly related to a population-level coexistence mechanism, and can be used to quantify and test this mechanism.

According to spatial storage effect theory, when a species is abundant, competition is expected to be highest in favorable patches, where conspecifics have the highest germination, survival and rate of individual growth. Vigorously growing individuals require more resources, and high germination and survival rates increase local density. The benefits of good conditions are thus offset by greater intraspecific competition. When a species is sparse or low in frequency, it experiences mostly interspecific competition, and when it has different environmental preferences than abundant species, the relationship between competition intensity and patch quality will be weak. In favorable patches, sparse species can respond with high population growth rates, promoting recovery to higher population numbers. Therefore, if the spatial storage effect is promoting coexistence, abundant species will have a positive environment–competition covariance, and the effect of covariance will be lessened for sparse species.

Because more than one coexistence mechanism is likely to be in effect in any given system, and some may depend on environmental fluctuations in time and space, it will always be difficult to predict whether co-occurring species will coexist over time. However, by quantifying the separate effects of different mechanisms, we can evaluate whether any particular mechanism has a substantial effect on community trajectories. This approach provides much more information than qualitative analyses that show, for example, whether competition is statistically significant, but do not show how it affects population dynamics.

In this study, we demonstrate a method for comparing the separate effects of neighborhood competition and spatial storage on the coexistence of two annual plant species in the Chihuahuan Desert of Arizona: *Erodium cicutarium*, which is locally abundant and *Phacelia popeii*, which is locally sparse, hereafter referred to as *Erodium* and *Phacelia*. The following effects are possible: (1) Coexistence will be promoted by resource partitioning within neighborhoods if *Erodium*’s intra-specific competition is greater than the interspecific competition it imposes on *Phacelia*. (2) Coexistence will be promoted by the spatial storage effect, as indicated by the relative strength of *Erodium* and *Phacelia*’s environment–competition covariance: *Erodium* (abundant) must have greater positive environment–competition covariance than *Phacelia* (sparse). A positive environment–competition covariance for *Erodium* would indicate that competition limits *Erodium*’s gains in population growth from favorable patches.

Species differences in covariance indicate spatial niche differentiation, assuming homogeneity at the local (within block) spatial scale, because they illustrate differences in relative response to neighbors and the environment (see Chesson [2000a, b] for full theoretical details). In this field system, using naturally occurring seedlings, it was not possible to test the reciprocal effects of *Phacelia* on *Erodium*, because *Phacelia* is currently at low density.

THEORY

In discrete time, a population’s finite rate of increase is given by

$$\lambda_j = N_j(t+1)/N_j(t) \quad (1)$$

which quantifies changes in population size for species j over a unit of time (t): in the case of annuals, a single growing season. Although Eq. 1 defines this concept at the population level, it can be defined at the individual level as the individual’s contribution to population growth in one unit of time. It is then identified with individual fitness, and the population-level λ_j of Eq. 1 is the average over the population of the individual λ_j (Chesson 2000b, Chesson et al. 2005). Spatial variation in the environment can cause spatial variation in the individual level λ_j by causing variation in reproduction or other life-history parameters (e.g., germination,

survival; see Chesson 1994, 2000b). Here we focus on the effect of spatial variation on yield. For simplicity, we assume random dispersal, which allows average individual yield (\bar{Y}_j) to be linearly related to the average over individuals of λ_j .

Inflorescence numbers are log-transformed before analysis, to put the data on an additive, instead of multiplicative, scale. In our studies of annual plants, we assume that initial differences between seedlings can be treated as random variables. The yield at each growing location x is given by

$$\ln(Y_{jx}) = E_{jx} - C_{jx} \quad (2)$$

where E_{jx} is the natural log (ln) yield of an individual with no neighbors (the environmental response), and C_{jx} is the reduction in yield when neighbors are present (the competitive response). Although C is usually defined as competition, there is no sign restriction, and C may also reflect facilitation.

Additivity on a log scale, Eq. 2, reflects the usual expectation that environmental and competitive responses will combine multiplicatively to determine Y_{jx} (Chesson 2007). To scale up to the population level, Eq. 2 must be converted back to the natural scale of Y_{jx} whose average over individuals gives the seed yield contribution to population-level λ_j . Thus,

$$Y_{jx} = e^{E_{jx} - C_{jx}} = e^{E_{jx}} \times e^{-C_{jx}}. \quad (3)$$

Scaling up to the population level entails averaging these yield estimates across spatial variation. As both E and C can vary in space, the average per capita yield is

$$\bar{Y}_j = \overline{e^{E_{jx}} \times e^{-C_{jx}}} + \text{cov}(e^{E_j}, e^{-C_j}) \quad (4)$$

where the overbars represent spatial averages. The average yield is thus a product of the separate mean effects of environment and competition, plus the covariance between them. This covariance then shows how spatial variation affects the average yield. Each of the components in Eq. 4 has approximations that facilitate both their computation and interpretation, as described in the *Methods* section and justified in Appendix A:

$$\begin{aligned} \bar{Y}_j = & \underbrace{\overline{e^{E_{jx} + (1/2)\text{var}(E_j)}}}_{\overline{e^{E_{jx}}}} \times \underbrace{\overline{e^{-C_{jx} + (1/2)\text{var}(C_j)}}}_{\overline{e^{-C_{jx}}}} \\ & - \underbrace{e^{(\bar{E}_{jx} - \bar{C}_{jx})} \times \text{cov}(E_j, C_j)}_{+ \text{cov}(e^{E_j}, e^{-C_j})}. \end{aligned} \quad (5)$$

Here, variance in E reflects variance in reproductive response, in the absence of competition. However, variance in C , the competitive response, can arise both from variance in competitive effect, which may be related to variance in E (e.g., as demand for resources varies with individual-growth responses to environmental factors), and from variance in local competitor density. Their covariance quantifies the spatial storage

effect: it shows how much increasing environmental quality is offset by increasing competition, which the spatial storage effect theory predicts will be greater for abundant species than sparse species. This change in covariance with density is the mechanism promoting population growth in species that have fallen to low density, and allows them to be maintained in the community.

In the form given here, variance in density influences coexistence when density is higher in more favorable patches, contributing to environment–competition covariance. Density variance related to dispersal, germination, or survival can also generate environment–competition covariance; but in these cases, E and C reflect different kinds of responses (e.g., to germination conditions rather than resources) and their direct effects and covariances have separate additive contributions to per capita growth rates (Chesson 2000b). When clustering results from chance establishment and short-distance dispersal, coexistence still requires niche differentiation (Bolker and Pacala 1999, Chesson and Neuhauser 2002), and can be accounted for by a quantity called fitness–density covariance (Chesson et al. 2005), which also has the potential also to enhance the spatial storage effect (Chesson 2000b, Snyder and Chesson 2003, 2004).

METHODS

Site

Our field study was conducted near Portal, Arizona (31°55'48" N, 109°4'48" W; see Plate 1). Both *Erodium* and *Phacelia* are rosette-forming annuals that germinate in October or November with the winter rains and senesce in spring. The populations of both species have fluctuated over time, depending on annual rainfall (P. Chesson and N. Huntly, *unpublished data*). However, since the mid-1990s the population of *Erodium*, a nonnative, has become dominant in the study area, likely in response to changing precipitation patterns. *Phacelia* is native to the region and though comparatively sparse, was the second most common annual during the year of our study (Sears 2004).

The study area is a gently sloping desert plain structured with widely spaced shrubs, including *Acacia*, *Ephedra*, and *Flourensia* species. Annuals germinate in patchy clusters across a clay and gravel-rich soil. The soil surface, although relatively homogeneous, is contoured with minor depressions, scattered accumulations of dead plant material, and patchy variation in soil particle size. The seeds of both *Erodium* and *Phacelia* are dispersed by wind and sheet-flow from summer rains; and to a certain extent by animals. The scale of seed dispersal for both species is likely to be substantially greater than the scale of heterogeneity experienced by plants in this environment.

Estimating competition

We used a standard neighbor removal experiment to evaluate competition between naturally occurring *Ero-*

dium and *Phacelia* plants. In each of 10 blocks, 1 m² in size, we chose two individual *Phacelia* and two individual *Erodium* seedlings as target plants, each growing in the center of a separate *Erodium* cluster. These blocks were laid out in open areas, avoiding shrub canopies. Neighborhoods were defined to include all plants growing within 8 cm of the target individual: approximately twice the radius of adult plants. In each block, species pairs were randomly assigned to neighbor removal or non-removal treatments. At senescence, we counted each target's inflorescences; and log-transformed these numbers before analysis. As several *Phacelia* plants did not flower, we added one to *Phacelia* numbers before transformation, but report corrected values.

We used mixed-model two-way analysis of variance (ANOVA) to test whether competition with neighbors had a significant effect on inflorescence production. The factors were block and treatment (removal or non-removal). Because the experiment had no within-block replication, the error term was given by the interaction mean square. A companion experiment (Sears 2004), found that the disturbance related to neighbor removals did not affect inflorescence production. The responses of paired individuals from this experiment were used to develop a conservative estimate of within-block error variance for evaluating the robustness of environment-competition covariance tests, below.

Estimating cov(*E*, *C*)

We estimated the covariance between plant response to the environment and competition for both *Erodium* and *Phacelia* using data from the neighbor-removal experiment. Each block is considered to be a point on an environmental gradient, where the gradient is defined by the responses of individual plants, and is a random rather than predefined factor. This permits us to account for environmental variation occurring on fine spatial scales. Plant response to the environment (*E*) is approximated as the log yield of plants in removal (*T*) treatments, $\ln(Y_{jT})$. Our experimental estimate of response to competition (*C*) roughly corresponds to the log response ratio of plants in removal and non-removal (*U*) treatments, $\ln(Y_{jT}/Y_{jU})$. However, the estimates for *E* and *C* contain common sampling error which must be removed statistically before calculating covariances, to avoid spurious correlation. Assuming that competition is a linear function of environmental response, we used maximum-likelihood methods to estimate actual values of *E* and *C*, defining $y_{mx} = \ln(\text{plant response})$, in treatment type *m* at the *x*th growing location using the model

$$y_{Tx} = E_x + \varepsilon_{Tx} \quad (6)$$

$$y_{Ux} = E_x - C_x + \varepsilon_{Ux} \quad (7)$$

where

$$C_x = a + bE_x. \quad (8)$$

Here, E_x is the response in the absence of neighbors, C_x is the response to the presence of neighbors, ε_{mx} is the error, *a* is a constant, and *b* is the regression coefficient of plant response.

We used orthogonal regression (Carroll et al. 1995) to calculate parameter values, and estimated $\text{cov}(E, C)$ as $b \times \text{var}(E)$. The statistical significance of this covariance was evaluated using an *F* test for the hypothesis $b = 0$, and bootstrapping was used to correct test bias (see Appendix B for details). This method assumes that removal and non-removal treatments have equivalent error variance, $\sigma_{\varepsilon U}^2/\sigma_{\varepsilon T}^2 = 1$, an assumption that cannot be assessed with data from un-replicated block designs. Thus, we tested the robustness of our results to a range of error variance ratios. Our companion experiment estimated *Erodium* and *Phacelia*'s error-variance ratios as 0.60 and 1.18, respectively. Ratios were also estimated from 10 neighborhood competition studies that had within-block replication and were conducted on other species in other field systems (range = 3.36–0.37, mean \pm SE = 0.98 ± 0.27 , median = 0.71 [Sears 2004]).

As the neighbor-removal experiment tested the effects of *Erodium* on itself and *Phacelia*, without reciprocally testing *Phacelia*'s competitive effects, the *C* term in *Erodium*'s covariance arises from intraspecific competition, whereas *Phacelia*'s reflects interspecific competition.

Model fitting

To quantify the separate effects of local competition and environment-competition covariance, we used the estimates of *E* and *C* from Eqs. 6–8 in the yield model, Eq. 4. The spatial average of yield in the absence of competition is estimated by averaging the response to removal treatments across blocks:

$$\bar{Y}_j = \overline{e^{E_{jx}}} \approx \overline{e^{E_{jx} + (1/2)\text{var}(E_j)}}. \quad (9)$$

The effects of local-scale competition are given by comparing the predicted maximum yield, Eq. 9, with the yield in the presence of neighbors, Eq. 10, assuming there is variance in both response to the environment and response to competition, but no covariance between them:

$$\bar{Y}_j = \overline{e^{E_{jx}}} \times \overline{e^{-C_{jx}}} \approx \overline{e^{E_{jx} + (1/2)\text{var}(E_j)}} \times \overline{e^{-C_{jx} + (1/2)\text{var}(C_j)}}. \quad (10)$$

The difference between these yields (Eqs. 9 and 10) is tested by the AOV from the neighbor-removal experiment, evaluating the average effect of neighbors in the average environment.

It is important to note, however, that the mean yield estimates from this AOV cannot be used to quantify the actual effects of competition on inflorescence numbers. Analysis of variance tests the difference between $\ln(\bar{Y}_T)$ and $\ln(\bar{Y}_U)$, whose theoretical means are equal to \bar{E}_j and $\bar{E}_j - \bar{C}_j$, respectively. But back-transformations of these means do not account for the yield-increasing effects of variance in E_j or C_j demonstrated by the models above,

TABLE 1. *F* statistics from ANOVA for the effects of neighbors on inflorescence production.

Source	df	Inflorescence number		Biomass	
		<i>Erodium</i>	<i>Phacelia</i>	<i>Erodium</i>	<i>Phacelia</i>
Removal treatment	1	0.01	16.22**	0.16	1.48*
Block (random)	92	3.69*	1.73	8.41**	5.02
Error	9				

* $P \leq 0.05$; ** $P < 0.01$.

or the effects of covariance. As illustrated by Eq. 5, yield from back-transformed ANOVA means will be overestimated if covariance is positive, and further underestimated if covariance is negative. To quantify the effect of environment-competition covariance we evaluated the extent that yield is influenced by $\text{cov}(E, C)$, comparing the results from the full yield model Eq. 4 with yields from Eqs. 9 and 10.

RESULTS

Estimating competition

Our ANOVA found that local-scale competition by *Erodium* had a significant negative effect on *Phacelia* inflorescence production. However, *Erodium* had no net effect on its own inflorescence production (Table 1). *Erodium* intraspecific competition had no effect on average, because in four of the 10 plots, focal plants with neighbors had more inflorescences than focal plants without neighbors, giving negative C values (Fig. 1A). *Erodium* neighbors had no corresponding facilitative effect on *Phacelia* (Fig. 1B).

Covariance, $\text{cov}(E, C)$, and yield model fit

Erodium inflorescence numbers had a significant positive covariance [$\text{cov}(E, C) = 0.274$, $F_{1,9} = 6.093$, $P = 0.05$] between response to the environment and intraspecific competition, when the error variance of non-removal treatments was assumed to be greater than or equal to that of removals, $\sigma_{\epsilon U}^2 / \sigma_{\epsilon T}^2 \geq 1$. This corresponds to the mean of ratio estimates from 10 replicated experiments in other field systems (Sears 2004). Ratios less than one increase uncertainty in the reported $\text{cov}(E, C)$ value. When $\text{cov}(E, C)$ was calculated using an error variance ratio equal to the median of other field systems (0.71), or the estimate from our companion disturbance experiment (0.60), significance was only marginal ($P = 0.07$, $P = 0.10$, respectively). However, ratio estimates are likely to be conservatively small (see Appendix B). *Erodium*'s MLE parameter estimates were $a = -1.312$, $b = 0.542$, $\text{var}(E) = 0.505$ ($\text{df} = 8$); and *Phacelia*'s were $a = 0.333$, $b = 0.379$, $\text{var}(E) = 0.186$ ($\text{df} = 8$).

According to these analyses, $\text{cov}(E, C)$ reduced *Erodium*'s average inflorescence production from 15 to 12 inflorescences per plant (Fig. 2A). *Phacelia* did not show a significant $\text{cov}(E, C)$, and was only affected by local interspecific competition (Fig. 2B).

DISCUSSION

The natural environment is heterogeneous on a variety of scales; but it is rarely clear how this variation affects plant communities. Here, we demonstrate a method by which plant responses are used to define the quality of the environment, and neighbor-removal

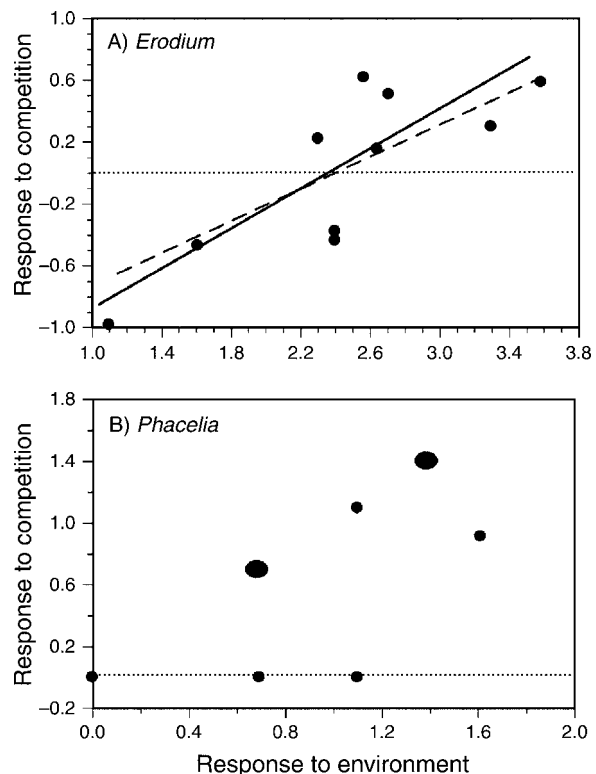


FIG. 1. Relationship between plant responses to competition (C) and to the environment (E) for (A) *Erodium* and (B) *Phacelia*. Each point gives the raw data from individual blocks, in units of $\ln(\text{inflorescence number})$ for *Erodium* and $\ln(\text{inflorescence number} + 1)$ for *Phacelia*. Response to the environment is estimated as the response of target plants in the removal treatments, and response to competition is estimated as the log response ratio of plants in removal and non-removal treatments. Model fitting is given for significant $\text{cov}(E, C)$. The solid line shows least-squares fit to raw data. The dashed line shows maximum-likelihood fit, which corrects for the common correlation induced by sampling error between these estimates of the response to competition and response to the environment. The horizontal dotted line indicates the zero-competition threshold: neighbors have a positive effect in blocks with values positioned below this line. Enlarged symbols are given when more than one block takes these values.

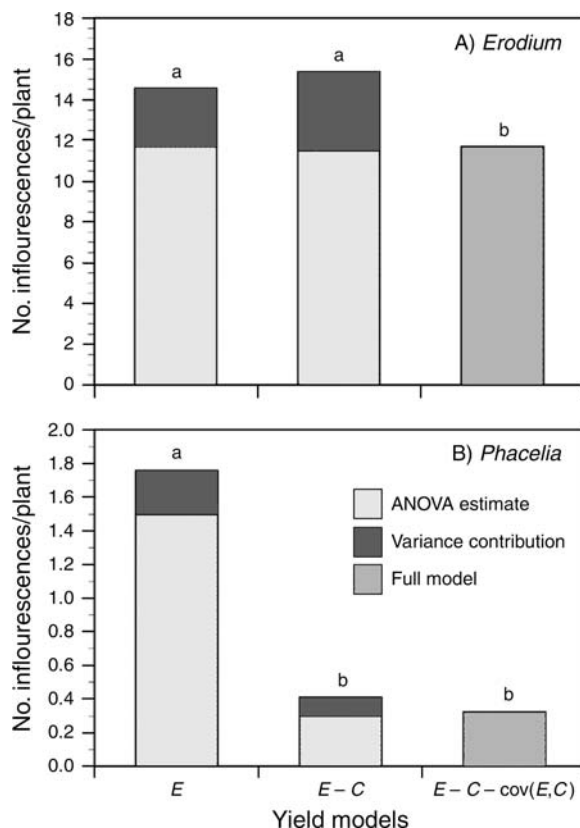


FIG. 2. Population model fits for per capita inflorescence production of (A) *Erodium* and (B) *Phacelia*, showing the predictions of different models. Model E gives the response of plants to the environment alone; see Eq. 9. Model $E - C$ gives the response of plants to both the environment and competition, assuming no covariance, Eq. 10. Model $E - C - \text{cov}(E, C)$ gives the yield response to the full model, Eq. 5. Shading differences illustrate the discrepancy between back-transformed means from ANOVA and estimates from the fitted yield models (see *Methods*). In each panel, bars with the same lowercase letters represent statistically homogeneous groups.

experiments show how the environmental variation affects interactions between individuals. Using *Erodium* and *Phacelia* as a model system, we show that spatial heterogeneity can affect coexistence in ways that are not apparent at the neighborhood scale; and that this information can be extracted from standard experiments.

The presence of *Erodium* neighbors strongly reduced *Phacelia*'s yield, but had only negligible net effects on *Erodium*'s own inflorescence production at the neighborhood scale. Nonetheless, *Erodium*'s competitive ability was partly balanced by the spatial storage effect, as environment–competition covariance reduced *Erodium*'s yield at the scale of the entire study area. The blocks most favorable to *Erodium* (with the greatest potential for reproduction) were those where it had the greatest competition intensity. In some of the least favorable blocks, the presence of neighbors increased inflorescence production.

This transition between positive and negative effects in response to environmental conditions is probably common in nature (Sears 2004), and is in line with the predictions of Bertness and Callaway (1994) and the results of other competition studies (e.g., Choler et al. 2001). Previously, we have not had the methodological tools to separate out these transitions at small spatial scales (i.e., the scale of a single study area). However, with traditional methods that average across block-level responses, such transitions could erroneously lead to a conclusion that neither competition nor facilitation plays a role in a species' population dynamics.

In contrast, we did not find a relationship between *Phacelia*'s response to patch quality and its response to competition from *Erodium*. If both species shared environmental preferences, *Phacelia*'s environment–competition covariance would mirror *Erodium*'s, with greatest inflorescence production in the blocks where *Erodium* was also most productive, but experiencing high levels of competition where *Erodium* density was high. Instead, *Phacelia* having a negligible covariance indicates that some patches were both environmentally favorable for *Phacelia*'s inflorescence production and not subject to high competition from *Erodium*, providing spatial opportunities to thrive. In general, environment–competition covariance will favor coexistence to the degree that it limits the population growth rates of dominant species, while providing opportunities for sparser species.

In this study, one of our primary goals was to test whether the spatial storage effect could be demonstrated in a natural field system; as a consequence we were not able to test the reciprocal effects of *Phacelia* on *Erodium* because *Phacelia* was at very low density. Researchers working in similar systems who wish to test a broader range of dynamics could experimentally increase the abundance of sparse species with seed additions. Likewise, in this study we did not test the dominant mechanisms of competition and facilitation. In the desert, these most likely relate to the availability of water and the effects of shade and wind. Understanding the processes underlying competition and facilitation can be extremely useful; for example, in predicting how environmental changes (such as increased precipitation) may influence populations. Nonetheless, for testing the presence of the spatial and temporal storage effect, knowing the mechanisms of competition and facilitation is less critical than testing their net effects and how these interact with species-specific responses to the environment.

Although at the scale of the individual, the spatial storage effect and neighborhood resource competition are driven by the same ecological interactions, there are a number of reasons it is essential to view environment–competition covariance as an independent, emergent process. First, environment–competition covariance requires environmental heterogeneity, and thus can not be considered at small spatial scales, as can resource



PLATE 1. The San Simon Valley, Arizona, USA, where the study was conducted, showing extensive annual plant habitat, with scattered shrubs and the Chiricahua Mountains in the distance. Photo credit: P. Chesson.

partitioning. The effects of environment–competition covariance are also somewhat independent of neighborhood-scale interactions: although resource partitioning can promote coexistence in the absence of environmental variation, environment–competition covariance, through the spatial storage effect, can promote coexistence when the relative intensity of intraspecific and interspecific neighborhood competition predicts competitive exclusion, as shown here.

This is the first study to explicitly demonstrate the spatial storage effect in a field system, and to show how these processes may run counter to neighborhood-scale interactions. Previous analyses could not evaluate the effect of spatial heterogeneity on yield, or transitions between positive and negative interactions at small spatial scales. With greater replication within and between blocks and additional sampling, it will likely be possible to expand this analysis to include the additive effects of environment–competition covariance associated with survival, germination and aggregated distributions (Chesson 2000*b*, Snyder and Chesson 2003). We expect that the spatial storage effect is common, and studies that do not account for it may miss an important element of community dynamics above the neighborhood scale. With the methods given here, information on the spatial storage effect can be

extracted from many existing and future studies that use standard designs for testing competition along gradients (see review in Sears 2004). To facilitate this, we provide R code for the calculations in the text as a supplement. Appendix C illustrates the analysis using this code with simulated data.

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LITERATURE CITED

- Aguiar, M. R., W. K. Lauenroth, and D. P. Peters. 2001. Intensity of intra- and interspecific competition in coexisting shortgrass species. *Journal of Ecology* 89:40–47.
- Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities. *Trends in Ecology and Evolution* 9:191–193.
- Bolker, B. M., and S. W. Pacala. 1999. Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. *American Naturalist* 153:575–602.
- Carroll, R. J., D. Ruppert, and L. A. Stefanski. 1995. *Measurement error in nonlinear models*. First edition. Chapman and Hall, London, UK.

- Chesson, P. 1994. Multispecies competition in variable environments. *Theoretical Population Biology* 45:227–276.
- Chesson, P. 1997. Making sense of spatial models in ecology. Pages 151–166 in J. Bascompte and R. V. Solé, editors. *Modeling spatiotemporal dynamics in ecology*. Landes Bioscience, Berlin, Germany.
- Chesson, P. 2000a. Mechanisms of maintenance of species diversity. *Annual Reviews of Ecology and Systematics* 31: 343–366.
- Chesson, P. 2000b. General theory of competitive coexistence in spatially-varying environments. *Theoretical Population Biology* 58.
- Chesson, P. 2007. Quantifying and testing species coexistence mechanisms. In F. Valladares, A. Camacho, A. Elosegui, M. Estrada, C. Gracia, J. C. Senar, and J. M. Gili, editors. *Unity in diversity: ecological reflections as a tribute to Ramon Margalef*. Fundación BBVA, Barcelona, Spain, *in press*.
- Chesson, P., M. J. Donahue, B. A. Melbourne, and A. L. W. Sears. 2005. Scale transition theory for understanding mechanisms in metacommunities. Pages 279–306 in M. Holyoak, M. A. Leibold, and R. D. Holt, editors. *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press, Chicago, Illinois, USA.
- Chesson, P., and C. Neuhauser. 2002. Intraspecific aggregation and species coexistence. *Trends in Ecology and Evolution* 17: 210.
- Choler, P., R. Michalet, and R. M. Callaway. 2001. Facilitation and competition on gradients in alpine plant communities. *Ecology* 82:3295–3308.
- Ellner, S. 1989. Convergence to stationary distributions in two-species stochastic competition models. *Journal of Mathematical Biology* 27:451–462.
- Goldberg, D. E., and A. M. Barton. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *American Naturalist* 139:771–801.
- Howard, T. G., and D. E. Goldberg. 2001. Competitive response hierarchies for germination, growth, and survival and their influence on abundance. *Ecology* 82:979–990.
- Pantastico-Caldas, M., and D. L. Venable. 1993. Competition in two species of desert annuals along a topographic gradient. *Ecology* 74:2192–2203.
- Peltzer, D. A., and S. D. Wilson. 2001. Variation in plant response to neighbors at local and regional scales. *American Naturalist* 157:610–625.
- Pugnaire, F. I., and M. T. Luque. 2001. Changes in plant interactions along a gradient of environmental stress. *Oikos* 93:42–49.
- Sears, A. L. W. 2004. Quantifying the effects of spatial environmental variation on dynamics of natural plant populations: field tests for covariance between response to the environment and competition. Dissertation. University of California, Davis, California, USA.
- Snyder, R. E., and P. Chesson. 2003. Local dispersal can facilitate coexistence in the presence of permanent spatial heterogeneity. *Ecology Letters* 6:301–309.
- Snyder, R. E., and P. Chesson. 2004. How the spatial scales of dispersal, competition and environmental heterogeneity interact to affect coexistence. *American Naturalist* 164:633–650.
- Tielbörger, K., and R. Kadmon. 2000. Indirect effects in a desert plant community: Is competition among annuals more intense under scrub canopies? *Plant Ecology* 150:53–63.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, New Jersey, USA.

APPENDIX A

The theory behind the formulas (*Ecological Archives* E088-134-A1).

APPENDIX B

Statistical methods for estimating $\text{cov}(E, C)$ (*Ecological Archives* E088-134-A2).

APPENDIX C

An example with simulated data (*Ecological Archives* E088-134-A3).

SUPPLEMENT

R code for assessing covariance between environment and competition (*Ecological Archives* E088-134-S1).