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Title: Requirements for the spatial storage effect are weakly evident for common species in natural annual plant assemblages

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Abstract

Coexistence in spatially varying environments is theorised to be promoted by a variety of mechanisms including the spatial storage effect. The spatial storage effect promotes coexistence when: (i) species have unique vital rate responses to their spatial environment and, when abundant, (ii) experience stronger competition in the environmental patches where they perform better. In a naturally occurring southwest Western Australian annual plant system we conducted a neighbour removal experiment involving eleven focal species growing in high-abundance populations. Specifically, we measured species' fecundity across a variety of environmental gradients in both the presence and absence of neighbours. For the environmental variables that we measured, there was only limited evidence for species-specific responses to the environment, with a composite variable describing overstory cover and leaf litter cover being the best predictor of fecundity for a subset of focal species. In addition, although we found strong evidence for intra-specific competition, positive environment-competition covariance was only detected for one species. Thus, positive environment-competition covariance may not be as common as expected in populations of species growing at high abundance, at least when tested in natural assemblages. Our findings highlight the inherent limitations of using natural assemblages to study spatial coexistence mechanisms, and we urge empirical ecologists to take these limitations into account when designing future experiments.

Key words: spatial storage effect, modern coexistence theory, environmental heterogeneity, annual plants, neighbour removal experiment, southwest Western Australia, York gum-Jam woodlands

Introduction

It is well recognised that diversity tends to increase rapidly as the spatial extent of observation expands (MacArthur and Wilson 1967). One of the main hypotheses invoked to explain this phenomenon is that a greater range of niche opportunities become available for species to occupy as a wider variety of environmental conditions are captured at broader scales (Hart et al. 2017). Indeed, with few exceptions, empirical studies reveal a positive relationship between within-community environmental heterogeneity and community-level species richness, suggesting that increasing environmental variation is a reasonable explanation for the scale-dependence of diversity (Stein et al. 2014). However, the mechanisms behind this relationship, although well developed in theory, remain to be widely tested in natural communities.

Chesson's (2000b) modern coexistence theory proposes a series of diversity maintenance mechanisms including some that operate in the presence of environmental heterogeneity. The central tenet of the theory is that long-term species coexistence depends on "stabilising" mechanisms which cause niche differences to outweigh average fitness differences. Stabilising mechanisms effectively drive negative frequency dependent population growth, such that species experience high per capita population growth when they are rare (i.e. at low frequency, or in their 'invader' state), but limit themselves when they become abundant (i.e. at high frequency, or in their 'resident' state).

There are three recognised spatial coexistence mechanisms that operate at scales large enough to capture meaningful environmental heterogeneity - the spatial storage effect, spatial relative nonlinearity and growth-density covariance - and all require that species have differential responses to the spatially varying environment (Chesson 2000a). In this study we focus on the spatial storage effect (Chesson 2000a), which further requires that each species, when in their resident state, experiences strong competition in patches that are environmentally favourable. This environment-competition covariance (covEC) is theorised to be stronger (more positive) when species are abundant because of the increased resource uptake of conspecific individuals in preferred patches. The final requirement of the spatial storage effect is that the invader-state population growth is buffered from the doubly negative effect of being in a poor patch (which is likely favourable for another species) and the intense interspecific competition that results. However, unlike the temporal storage effect, which

requires a long-lived or resilient life history to “buffer” the negative effects of a poor year, buffering occurs in the spatial context automatically when contributions to population growth rate in good patches compensate for bad patches, assuming that individuals have the opportunity to disperse between patches (Chesson 2000a, 2008).

Mathematically, the strength of the spatial storage effect is a product of 1) the difference in covEC between resident and invader states and 2) the magnitude of spatially buffered population growth (Chesson et al. 2013). Coexistence is promoted when resident covEC is greater in magnitude than invader-state covEC. Thus, it is not the sign (positive or negative) of the resident-state covEC that matters but its relative magnitude in relation to invader-state covEC. The ideal experiment to test the requirements of the spatial storage effect, then, would be to sow focal species across a heterogeneous environment and selectively manipulate competitive neighbourhoods such that each focal species experiences competition in different environments at both its resident and invader state (with other focal species at their resident state ; Li 2016). Although such an experiment is feasible for a small number of species, obtaining enough data to sufficiently quantify the mathematical components of the spatial storage effect (and other spatial coexistence mechanisms) quickly becomes intractable as the number of species increases. This logistical complexity may explain the dearth of empirical studies attempting to rigorously quantify spatial storage effects in diverse natural systems to date. But it is perhaps surprising how few empirical studies have used simpler, albeit less rigorous approaches, to detect signals of the spatial storage effect, especially given its potential importance for maintaining diversity in spatially heterogeneous natural systems globally.

Neighbour-removal experiments can test for the operation of spatial storage effects in natural assemblages (Sears and Chesson 2007). However, natural assemblages impose their own limitations in this context. For example, it is often difficult or impossible to locate environmental patches (defined at a scale that can be considered spatially homogenous) in which more than a few focal species consistently co-occur, especially if species occupy segregated spatial niches. In addition, establishing sufficient within-patch replication for many species in these patches is likely to be a challenge. Thus, further methodological adjustments are needed if the goal is to examine signatures of spatial storage effects for a satisfying number of species in realistically diverse natural assemblages, but it is unclear how such compromises affect our ability to detect if the mechanism is operating. In

other words, a trade-off likely exists between the number of species being studied and the ability to detect if the mechanism is operating (Levins 1966).

In this study, we examine environmental and competitive responses of eleven winter annual plant species in woodland understories in southwest Western Australia. We relax the requirement for all species' responses to be measured in the same patches and instead locate patches of each species at many positions along measurable environmental gradients that are strongly associated with species turnover. We also focus only on common species assumed to be near their resident state, as these are most likely to exhibit positive covEC indicative of the spatial storage effect (Chesson et al. 2013). We address the following questions:

- 1) Are species environmental responses related to measured environmental variables, and if so, do relationships differ among species?
- 2) How evident is positive covEC in abundant species assumed to be near their resident state?

Methodology

Study System

The York gum – jam woodlands were once common in southwest Western Australia but now occupy only 3% of their historic range, persisting as discrete remnant patches of varying size and quality within a matrix of pasture, wheat and canola fields (Hobbs and Yates 2000). Occurring on infertile, sandy loam soils, York - gum woodlands have a sparse tree overstory (Appendix S1: Fig. S1b) characterised by two species: York gum (*Eucalyptus loxophleba*) and Jam (*Acacia acuminata*). The woodland understorey is dominated by a high diversity and abundance of annual forbs and winter-growing geophytes interspersed among scattered shrubs, perennial tussock grasses (e.g. *Austrostipa* spp.) and bare ground (Prober and Wiehl 2012). Herbaceous plant alpha diversity can be as high as 29 species per 0.09 m² (Dwyer and Mayfield unpublished data). The sparse distribution of the overstory creates local-scale heterogeneity in shade, tree litter and fallen woody debris (among other environmental variables). These factors are strongly associated with turnover in plant diversity in the York gum – jam woodlands (Wainwright et al. 2017), making it a strong candidate system to investigate the role of spatial environmental variation on species coexistence.

Experimental design

To assess species' responses to the environment with and without neighbours, we conducted a spatially nested neighbour removal experiment in West Perenjori Nature Reserve, WA, Australia (29° 28' 40" S, 116° 12' 00" E) in the warmer, northern extent of the York gum – jam woodlands (Appendix S1: Fig. S1a). Our decision to increase community representation beyond previous field studies of the spatial storage effect (Sears and Chesson 2007) by examining eleven species made it impossible to assess the responses of all species to the very same patches (because all eleven species rarely co-occurred at the patch scale in our natural assemblages). We therefore selected only species that were common and abundant and assessed their fecundity responses individually in 16 patches per species, ensuring that the measured environmental space covered by the patches was similar across species. While this design only examined one focal species per patch, it allowed us to include within-patch replication of thinned and unthinned plants, which strengthened some aspects of our statistical analysis (Sears and Chesson 2007).

At the beginning of the 2018 growing season (late July), 16 patches (1 m²) for each focal species were located across a ~12 ha section of the York-Gum woodlands occurring in the south of the reserve (Appendix S1: Fig. S1a). Patch size was selected to minimise abiotic heterogeneity (Sears and Chesson 2007), while accommodating multiple subplots. To ensure that sufficient variation in the physical environment was captured, patches were systematically established across natural gradients of tree cover, sclerophyllous litter cover and coarse woody debris (branches or logs >5cm diameter). Within each patch, six subplots (7.5 cm radius, at least 15 cm apart) were established, centred on individuals of the focal species. Each subplot was then randomly assigned to be a thinned or unthinned subplot (three of each).

In thinned subplots, the above-ground biomass of all germinants within 7.5 cm of target individuals was carefully removed by hand. This neighbourhood radius was considered to be sufficiently large to minimise local plant-plant interactions based on a prior study in this system (T. Martyn *unpublished data*). Thinning occurred early in the season as soon as focal species could be reliably identified. Unthinned subplots were not manipulated. At peak biomass, the identity and abundance of all neighbours within each unthinned subplot was recorded.

We monitored the survival to reproductive maturity and seed production of each focal individual. To assess seed production, thin mesh bags were fastened over immature fruiting bodies to capture seeds. This occurred shortly prior to seed release to minimise disturbance to the plant. For the majority of species, a target individual's responses to the environment was then recorded as its total seed production, excluding seeds that were unfilled. In the case of *P. airoides*, the number of florets was recorded and then multiplied by two as a measure of fecundity as florets contain two seeds on average. Survival rates were high for all species (Table 1) so instead of modelling survival as a separate vital rate we instead treated all individuals which died before reaching reproductive maturity as having zero seed production.

Patch-level overstory cover was assessed by taking a wide-angle digital photograph of tree canopies from the centre of each patch at 25 cm from the ground and facing north. Because of the sun's daily path across the northern sky during the growing season in our study system, we processed only the northern half of canopy cover photographs in ImageJ (Abràmoff et al. 2004) to estimate overstory cover percentage (%). Percentage cover (%) of sclerophyllous leaf litter was estimated by overlaying a 100-point grid on digital photos of each patch and counting 'hits'. Coarse woody debris (CWD) in or immediately adjacent to the patch was recorded as a binary variable, where branches or logs greater than 5cm diameter that were in contact with the ground were considered a "presence". A soil sample (0 – 70 mm depth, excluding litter) was collected from each patch at the beginning of the growing season to best represent available nutrients before plant uptake and leaching occurred. Soil samples were air-dried and analysed (School of Agriculture and Food Sciences, The University of Queensland) for extractable phosphorous (mg / kg), extractable potassium (mg/kg) and plant-available nitrogen (%).

Statistical Analyses

Are species environmental responses related to measured environmental variables, and if so, do relationships differ among species?

To first assess species-specific responses to the environment in the absence of neighbours, fecundity in thinned subplots for each species was modelled as a function of environmental conditions using generalised linear mixed-effects models (GLMMs) with a negative binomial error distribution and log

link function. Environmental variables included overstory cover, litter cover, CWD, extractable phosphorous (P), extractable potassium (K) and plant-available nitrogen (N). Due to collinearity between certain environmental variables, we first conducted a global principal component analysis (PCA) on all six variables. The global PCA revealed that soil variables were mostly loaded on a different axis to overstory cover and litter cover and so we ran a separate PCA for the soil variables and another for overstory cover and litter cover (Appendix 1: Fig. S2). Preliminary data exploration revealed that CWD was uncorrelated with the other variables and so we excluded CWD from the PCA to maintain its binary distribution. We then extracted the first principal component from each PCA to describe “soil fertility” and “overstory and litter cover”, respectively. Soil fertility, overstory and litter cover and CWD were included in each species’ fecundity model and patch was included as a random effect. Quadratic relationships were also explored for each species and environmental variable. To reduce bias in parameter estimates for linear terms, non-significant quadratic terms were removed in a one-step model simplification process. We also modelled fecundity in unthinned subplots for each species in an intercept-only mixed-effects model (including plot as a random effect) to compare species-average fecundity (Table 2).

Estimating effects of neighbours on fecundity

Overall effects of neighbours on each focal species were assessed using mixed-effects GLMMs (negative binomial error distribution and log link). Treatment (thinned or unthinned) was the sole fixed effect and patch was included as a random effect in each model. Positive responses to thinning when averaged across patches indicate that neighbours had a competitive effect on focal individuals while negative responses indicate that neighbours had a facilitative effect on focal individuals.

We also used neighbourhood composition data to investigate density-dependent effects of local-scale competition. This was done in part to check that our chosen focal species were abundant enough to limit themselves. Specifically, we modelled fecundity in unthinned subplots as a function of the total abundance of all neighbours as well as the absolute abundance of conspecific individuals using GLMMs with a negative binomial error distribution and log link function. We excluded occasional occurrences of the parasitic vine *Cuscuta campestris* when calculating absolute neighbour abundance.

Total neighbour abundance and the abundance of conspecifics was $\ln(\text{fecundity} + 1)$ transformed to improve model fit.

How evident is positive covEC in abundant species assumed to be near their resident state?

We first tested for positive covEC, where E is estimated as the average \ln -transformed fecundity in thinned subplots in a given patch. C in the same patch is the average difference in fecundity due to the presence of neighbours. However, this approach uses the fecundity of thinned plants in the calculation of both E and C . The common sampling error this introduces must be statistically removed before testing for covariance. As per Sears and Chesson (2007), we used maximum-likelihood to estimate values for the E and C using the following models:

$$\overline{\ln(y_{t,x,i})} = E_x + \varepsilon_{t,x,i}$$

$$\overline{\ln(y_{u,x,i})} = E_x - C_x + \varepsilon_{u,x,i}$$

$$C_{x,j} = a + bE_x$$

Where y is the fecundity of individuals, i , in thinned, t , and unthinned, u , subplots nested within patch, x , is the observation-level error, and a , and b , are respectively the intercept and regression coefficient of the relationship between C and E . Parameter estimates for a and b were then calculated using orthogonal regression (Carroll 2006). In contrast to ordinary least squares, orthogonal regression assumes that error variance occurs in both variables, rather than just in the dependent variable. It therefore requires an estimate of the within-patch variance for thinned and unthinned treatments, which are expressed as the ratio θ :

$$\theta_s = \frac{\sum_{x=1}^{n_x} \sum_{i=1}^{n_i} (y_{u,x,i} - \bar{y}_{u,x})^2}{\sum_{x=1}^{n_x} \sum_{i=1}^{n_i} (y_{t,x,i} - \bar{y}_{t,x})^2}$$

Error variance ratios ranged from 0.29 to 3.25 across the eleven focal species. Covariance between C and E was then estimated as b multiplied by the variance in E . An F-test was performed to determine whether b was significantly different to 0 ($\alpha=0.05$) for each species. A positive value for covEC is evidence that neighbours limit fecundity more in favourable patches (Fig. 1), but importantly, covEC

need not be positive for the spatial storage effect to be operating. The removal of common sampling error can substantially alter the slope of the E-C relationship, such that the adjusted relationship may not follow the ‘raw’ data when plotted. To facilitate interpretation of results and how they relate to raw data, we modelled relationships between the average ln-transformed fecundity of thinned and unthinned plants in each patch using Deming regressions. Positive covEC is apparent when the Deming regression slope is significantly less than 1. Analytically derived 95% confidence intervals around the Deming slope estimate were inspected for each species to assess the significance of slope differences. The biological interpretation of Deming regressions was consistent with the results from the maximum likelihood method described above and so we refer herein to the results for maximum likelihood only (but see Appendix S1: Fig. S3 and Table S1).

Statistical analysis was performed in R (R Core Team 2019), Deming regression was performed using the *mcr* package (Manuilova 2014) and mixed-effects modelling was performed using the *lme4* package (Bates et al. 2015)

Results

Are species environmental responses related to measured environmental variables, and if so, do relationships differ among species?

Species’ fecundity in the absence of competition did not exhibit strong differential responses to measured environmental gradients. Out of 33 combinations of species and environmental gradients, we found only five to be significant ($\alpha=0.05$; Table 2). The composite variable describing overstory and litter cover, where high values represent shaded patches with high leaf litter cover and low values represent bare, open patches, was the significant environmental predictor in the majority of these relationships. *A. calendula* had a strong positive relationship, *D. glochidiatus* had a U – shaped relationship and *V. rosea* had a hump-shaped but mostly negative response (Fig. 2).

T. cyanopetala’s fecundity was negatively related to soil fertility while *A. calendula*’s was positively related to CWD (Appendix S1: Fig. S4).

Estimating effects of neighbours on fecundity

Four out of eleven species exhibited significant responses in their fecundity to neighbourhood thinning when averaged across plots and in all cases these responses were positive (i.e. neighbour removal had a positive effect indicating competition; Table 3). Similarly, species' fecundities responded negatively to increasing neighbour density (conspecific and total) in all cases where the relationship was significant (Table 3). Conspecific neighbour density was significantly and negatively related to fecundity for six species, indicating that these species were abundant enough to limit themselves (Appendix 1: Fig. S5 ; Table 3). Interestingly, the total abundance of neighbours explained fecundity for only four species (Appendix 1: Fig. S6), and only *A. calendula* responded significantly to both the number of conspecific neighbours and the total abundance of neighbours.

How evident is positive covEC in abundant species assumed to be near their resident state?

For the majority of species, there was little to no evidence of positive covariance between patch favourability and the effect of competition. CovEC was significant and positive for one common species - *P. airoides* – and then, only when maximum likelihood was used to estimate slope parameters (covEC = 0.21, P = 0.04, Fig. 3). *Hyalosperma glutinosum*, *Plantago debilis*, *Podolepis canescens* and *Trachymene cyanopetala* showed moderately negative covEC, although in no cases was this significant (Table 4).

Discussion

The spatial storage effect is theorised to be an important mechanism stabilising coexistence in spatially varying environments yet empirical tests of the key requirements of this mechanism are extremely rare. Our experimental manipulation of plant neighbourhoods across multiple orthogonal environmental gradients for eleven focal species yielded a number of important findings. Firstly, although we observed moderate differentiation in fecundity responses to the measured environment for some species, fecundities of more than half of the focal species were not significantly related to any examined environmental variables. Secondly, we found evidence for positive covEC for only one species, despite strong evidence of intraspecific competition for most species. These findings suggest that positive covEC, at least when mediated exclusively by species' fecundity responses in this natural system, does not commonly occur for species near their resident state.

Are species environmental responses related to measured environmental variables, and if so, do relationships differ among species?

In order for coexistence to be stabilised by the spatial storage effect species must exhibit partially uncorrelated demographic responses to their environment (Sears and Chesson 2007). For four out of the eleven focal species investigated, we found significant relationships between fecundity and the environment, and the nature of these relationships differed by species. Consequently, we have some evidence that the first requirement of the spatial storage effect is satisfied for a subset of the species studied in this system. The insignificant relationships observed for the remaining species suggest that system wide, spatial niche differentiation is either weak, involves untested environment factors or only operates across larger spatial scales than were tested here (Hart et al. 2017). Alternatively, and most likely, weak responses to the environment may simply reflect the limitations of experiments in natural assemblages.

Sparsely distributed woody plant species often play an important role in structuring understorey community composition in semi-arid ecosystems (Facelli and Brock 2000, Prober and Wiehl 2012, Helman et al. 2017, Tessema and Belay 2017). In the same way, when species in the present study responded significantly to the environment, they tended to respond to the combined effect of overstorey and litter cover. Overstorey cover can facilitate survival and performance in the understorey by limiting direct solar irradiation (Valladares et al. 2016), consequently alleviating water stress, while leaf litter cover can improve soil moisture retention (Walsh and Voigt 1977). Conversely, light interception by the overstorey and a dense leaf litter layer (Scholes and Archer 1997) as well as allelopathic toxins leached from sclerophyllous litter (May and Ash 1990) may limit growth in the understorey. These potential effects of overstorey and litter cover may explain the contrasting responses that we observed between *A. calendula* and *V. rosea* although further work is needed to tease apart the individual mechanisms.

It is important to acknowledge that weak evidence for spatial niche differentiation may simply reflect our choice of environmental variables or the scale over which we studied them. Indeed, the fact that we could not frequently locate all eleven of our species in the same patches suggests that species do exhibit unique responses to the environment, but the environmental variables we measured did not

explain this interspecific variation in responses. Nevertheless, the environmental variables we measured are strongly associated with community turnover in these York gum woodlands (Prober and Wiehl 2012, Wainwright et al. 2017). Thus, we had a reasonable *a priori* expectation that species would exhibit a greater diversity of responses. As highlighted previously, it is also possible that weak species-specific responses were recorded as a result of locating focal individuals in naturally occurring assemblages. As a consequence, we may not have captured positions on environmental gradients where species have been “pre-filtered” from local patches over multiple generations of poor performance (HilleRisLambers et al. 2012). Again, sowing experiments across complete gradients may capture species’ responses more completely in future studies. Finally, it is possible that weak species-specific responses were the result of the benign, above-average rainfall conditions which occurred throughout 2018 when this experiment was conducted. Environmental factors which can ameliorate drought stress, such as the presence of CWD and the amount of overstory and litter cover, may play a much smaller role in mediating species’ performances in wet years (Helman et al. 2017). Given that the spatial storage effect is dependent on partially uncorrelated responses to patch environments, this raises an interesting avenue for future research: does the strength of the spatial storage effect vary systematically with climate through time as a spatiotemporal dynamic?

How evident is positive covEC in abundant species assumed to be near their resident state?

In the only other field study to quantify the second requirement of the spatial storage effect, Sears and Chesson (2007) found that the reserve-scale yield of *Erodium cicutarium* (an abundant species assumed to be in its resident state) was significantly limited by environment-competition covariance, suggesting that spatial storage effect may promote coexistence in this system. Consistent with Sears and Chesson (2007), we found evidence for positive covEC for one common species, the invasive annual grass *P. airoides*. Positive covEC is expected to arise from an increase in per-capita intra-specific competition under preferable environmental conditions. Due to the nature of our experiment, however, we were unable to explore whether this was the mechanistic basis for the positive covEC that we observed for *P. airoides*. Our findings for *P. airoides* are thus consistent with Sears and Chesson (2007) by showing positive covEC for at least one abundant species. By studying more species, however, we were able to show that this phenomenon was not nearly as common as we expected. As highlighted previously, manipulation of conspecific competitor density to predetermined

densities through seed addition and selective thinning, paired with completely thinned neighbourhoods, could allow future studies to isolate variation in per-capita intra-specific competition across environmental gradients (Hart et al. 2017).

For the remaining ten focal species we observed weak covEC despite evidence that intraspecific competition reduced fecundity in most (6) of these species. Thus, most species experienced negative frequency dependence, but its effects were independent of the measured spatial environment. This suggests that stabilising mechanisms operating at the scale of plant neighbourhoods may also be important in promoting coexistence (Adler et al. 2018).

The strength of storage effects are known to vary among systems. When examining the temporal storage effect, Adler et al. (2009) found weak evidence for environment-competition covariance for all four species tested in North American sagebrush steppe despite finding strong evidence for species-specific responses to the environment. In contrast, Adler et al. (2006) found strong evidence for environment-competition covariance in three North American prairie grass species. Our findings add key novel information about the commonality of the requirements of the spatial storage effects in a well-studied annual plant system of the sort in which this mechanism is widely expected to operate. We hope that the results from this study encourage further tests of the key requirements of the spatial storage effect to determine whether similarly low incidences of positive covEC are generalisable to other systems. In particular, we urge future studies to explicitly test resident-invader differences in covEC for multi-species communities where possible, although the spatial design of such an experiment still represents a major empirical challenge.

Despite our aim to select only abundant focal species, the results of our neighbourhood competition analyses (Appendix 1: Fig. S5) suggest that some were not locally abundant enough to create the competitive conditions required for negative frequency dependence. For example, *M. monstrosus* and *D. glochidiatus* had maximum conspecific neighbour counts of three and five respectively, compared to conspecific neighbour counts of over forty for *P. airoides*, *H. glutinosum*, *V. rosea* and *P. debilis* (Appendix 1: Fig. S5) which could potentially explain the weak covariance we observed for these species.

We focussed exclusively on spatial variation in species' fecundity when testing the key requirements of the spatial storage effect. However, annual plant species' long-term population growth rates are a function of multiple demographic rates and covariation in any of these rates with the environment could lead to stabilisation via the spatial storage effect, so long as it causes species to experience greater competition in the patches where they are most successful (Chesson 2000a). For example, species-specific variation in germination rates has been shown to be crucial to the operation of the temporal storage effect in winter annuals in the Sonoran desert (Angert et al. 2009) and we predict that spatial variation in germination rates may be an important driver of spatial coexistence mechanisms in many systems including the York Gum woodlands. Survival in the seed bank is another potentially important, but often overlooked, demographic rate and could vary with patch type for a number of reasons. For example, seed pathogen load is known to vary with microsite conditions such as litter cover in a plant density-independent manner (Beckstead et al. 2012) and this could disproportionately reduce seed survival for species with poor pathogen resistance. Species-specific seed predation post-dispersal may also be spatially dependent (von Euler et al. 2014). For example, many studies have shown that rodents, which are also seed predators in our system, tend to forage in sheltered microsites. Finally, although we observed very high rates of seedling survival in this study, variation in survival to reproductive maturity, especially at very early life stages, may play an important role in promoting coexistence in a manner independent of fecundity. Annual plant models which allow all vital rates to explicitly vary with the environment may provide a more accurate and mechanistic perspective on the effect of spatial variation on coexistence (Bimler et al. 2018).

It is also important to acknowledge that other spatial coexistence mechanisms may be operating in this system. In addition to the spatial storage effect, relative non-linearity of competition and growth-density covariance can promote coexistence as a consequence of spatial variation (Chesson 2000a, Snyder and Chesson 2003, Snyder and Chesson 2004, Holt and Chesson 2016). For example, in the context of temporal variation, recent studies indicate that relative non-linearity of competition plays a much greater role than the storage effect in promoting species coexistence in a variety of systems including different grasslands and nectar yeasts (Letten et al. 2018, Hallett et al. 2019, Zepeda and Martorell 2019). In a similar manner, spatial relative non-linearity of competition and growth-density covariance have not yet been empirically studied but they may play an important role in promoting

coexistence in spatially varying environments (Snyder and Chesson 2003). Thus, we urge future empirical studies to consider these overlooked mechanisms.

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Supporting Information

Additional supporting information may be found online at: [link to be added in production].

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Table 1: Rate of survival to reproductive maturity for the eleven focal species

Species	Survival rate
<i>Arctotheca calendula</i>	0.97
<i>Daucus glochidiatus</i>	0.99
<i>Gilberta tenuifolia</i>	1
<i>Hyalosperma glutinosum</i>	0.98
<i>Medicago minima</i>	1
<i>Monoculus monstrosus</i>	0.87
<i>Pentameris airoides</i>	0.99
<i>Plantago debilis</i>	0.99
<i>Podolepis canescens</i>	0.99
<i>Trachymene cyanopetala</i>	1
<i>Velleia rosea</i>	1

Table 2: Parameter estimates from intercept-only and species-specific environmental GLMMs of fecundity in unthinned subplots. λ is the estimated intercept value in the intercept-only mixed effects model. Values in brackets after intercept values represent one standard deviation around the parameter estimate of the intercept. Values under tree overstory and litter cover, soil fertility and the presence of CWD represent the fixed-effect parameter estimates, while values in brackets after the parameter estimates of linear terms represent the estimated quadratic term where it was significant. Fixed effects parameter estimates are in log(units). The number of asterisks represent the level of significance: * = 0.05, ** = 0.01, *** = 0.001.

Species	λ	Tree overstory and litter cover	Soil fertility	Presence of CWD
<i>Arctotheca calendula</i>	79.44 (54.23- 116.36)	0.63**	-0.29	1.19*
<i>Daucus glochidiatus</i>	19.31 (17.05- 21.86)	-0.08 (0.32**)	-0.04	-0.42
<i>Gilberta tenuifolia</i>	81.66 (69.84- 95.49)	0.06	-0.01	-0.14
<i>Hyalosperma glutinosum</i>	60.30 (50.26- 72.34)	-0.19	-0.08	-0.04
<i>Medicago minima</i>	11.94 (10.62- 13.42)	-0.09	0.18	-0.18
<i>Monoculus monstrosus</i>	8.61 (7.03- 10.55)	0.02	0.23	0.46
<i>Pentameris airoides</i>	234.15 (197.36 – 277.80)	-0.18	-0.05	-0.43

<i>Plantago debilis</i>	46.89 (38.93 - 56.46)	-0.07	-0.27	0.61
<i>Podolepis canescens</i>	489.56 (416.90 - 574.89)	-0.15	0.05	0.12
<i>Trachymene cyanopetala</i>	41.40 (35.69 - 48.01)	-0.16	-0.23*	-0.27
<i>Velleia rosea</i>	18.52 (16.12 - 21.27)	-0.26* (-0.20*)	-0.15	0.16

Table 3: The average effect of neighbours on fecundity and the effect of the total number of neighbouring individuals and number of intra-specific neighbours on fecundity in thinned subplots. The sign of the relationship is indicated when significant where the number of asterisks represent the level of significance: * = 0.05, ** = 0.01, *** = 0.001. n.s. indicates the relationship was not significant.

Species	average	Total	intra
<i>Arctotheca calendula</i>	n.s.	***	*
<i>Daucus glochidiatus</i>	n.s.	n.s.	n.s.
<i>Gilberta tenuifolia</i>	**	***	n.s.
<i>Hyalosperma glutinosum</i>	n.s.	n.s.	***
<i>Medicago minima</i>	n.s.	**	n.s.
<i>Monoculus monstrosus</i>	n.s.	n.s.	n.s.
<i>Pentameris airoides</i>	***	n.s.	*
<i>Plantago debilis</i>	***	n.s.	**
<i>Podolepis canescens</i>	n.s.	n.s.	***
<i>Trachymene cyanopetala</i>	n.s.	n.s.	*
<i>Velleia rosea</i>	*	**	n.s.

Table 4: The slope estimate, b , between the Response to Competition, C, and Response to Environment, E, E-C covariance ($b \times \text{Var}(E)$) and the significance of b from maximum likelihood analysis.

Species	b	E-C covariance	P
<i>Arctotheca calendula</i>	0.13	0.37	0.46
<i>Daucus glochidiatus</i>	0.47	0.06	0.30
<i>Gilberta tenuifolia</i>	0.15	0.03	0.77
<i>Hyalosperma glutinosum</i>	-0.13	-0.04	0.69
<i>Medicago minima</i>	0.50	0.05	0.42
<i>Monoculus monstrosus</i>	0.35	0.17	0.17
<i>Pentameris airoides</i>	1.30	0.21	0.04
<i>Plantago debilis</i>	-0.27	-0.09	0.44
<i>Podolepis canescens</i>	-0.14	-0.02	0.87
<i>Trachymene cyanopetala</i>	-0.09	-0.03	0.67
<i>Velleia rosea</i>	0.14	0.02	0.74

Fig. 1: Conceptual illustration of positive covariance between the favourability of the environment (Response to Environment) and the strength of competition (Response to competition) when using maximum likelihood (see methods). Response to Environment is estimated as the $\ln(\text{fecundity})$ in thinned plots while Response to Competition is estimated as the $\ln(\text{response ratio})$ of fecundity in thinned subplots divided by unthinned subplots. The dashed line is the fitted model when environment-competition covariance is significant and positive while the solid line is the fitted model when neighbours have no effect on fecundity. Dark grey fields represent areas of statistical space where the fecundity in unthinned plots is greater than in thinned plots (i.e. facilitation) while unshaded fields represents areas of statistical space where the fecundity in thinned plots is greater than in unthinned plots (i.e. competition).

Fig. 2: The effect of tree overstory and litter cover on the fecundity of *A. calendula*, *D. glochidiatus* and *V. rosea* in thinned subplots. High values of overstory and litter cover represent shaded patches with high leaf litter cover while low values represent bare, open patches. Each point is the observed fecundity in a subplot. Light grey fields represent the 95% confidence interval Lines represent the fitted slope estimate for each relationship.

Fig. 3: The relationship between Response to Competition and Response to Environment for *P. airoides*. Response to Competition is estimated as the $\ln(\text{response ratio})$ of plot-level average fecundity in thinned subplots divided by unthinned subplots (y-axis) while the Response to environment is estimated as the plot-level average fecundity in thinned subplots (x-axis). The line shows the maximum likelihood fit after correcting for common sampling error between the estimates of C and E. Dark grey fields represent areas of statistical space where the fecundity in unthinned plots is greater than in thinned plots (i.e. facilitation) while unshaded fields represents

areas of statistical space where the fecundity in thinned plots is greater than in unthinned plots
(i.e. competition).





