

Variation in demographic responses to competition and abiotic conditions in an annual plant community

Alexandra Catling¹, Margaret Mayfield², and John Dwyer³

¹The University of Queensland

²The University of Melbourne School of BioSciences

³University of Western Australia

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Abstract

Understanding how plant fitness varies along natural gradients is critical for predicting responses to environmental change. However, individual vital rates are often used as fitness proxies without knowing how other vital rates vary. To address this gap, we investigated how water availability, plant-plant interactions and heterogeneity in shade and soil influenced emergence, survival, seed production, and population growth rates of nine annual plant species in semi-arid Western Australia. We sowed plots of seeds across a reserve, removed all neighbouring plants from half of the interaction neighbourhoods and altered precipitation using rainout shelters. We found high consistency among species' responses to abiotic and biotic factors. Most species exhibited opposing responses of different vital rates along a natural abiotic gradient which translated to neutral trends in population growth rates across the gradient. This research demonstrates the importance of demographic trade-offs and pitfalls of measuring a single vital rate as a fitness proxy.

Introduction

Plant population fitness is determined by multiple vital rate responses to abiotic and biotic factors and their interactions. Vital rates describe discrete components of the lifecycle and include rates such as emergence, survival, and seed production which collectively describe the fitness of a population, often measured as per capita population growth rate (Caswell 2001). Understanding how population growth varies with abiotic conditions and biotic interactions allows us to explain patterns of diversity and predict the response of populations to changes in the environment (Adler *et al.* 2009; Dahlgren & Ehrlén 2009). However, quantifying population growth is an empirical challenge in many natural systems, where measuring multiple vital rates may not be feasible (Laughlin *et al.* 2020). Consequently, many studies measure a single vital rate as a proxy for lifetime fitness, even though it is well appreciated that this approach may be misleading if vital rates trade-off in their effects on population growth (Laughlin *et al.* 2020; Klimeš *et al.* 2022).

Demographic trade-offs have long been described in life-history theory, for example between reproductive effort and survival (Stearns 1989). Demographic compensation has more recently been coined to describe opposing vital rate trends across environments (Doak & Morris 2010), and may be a common phenomenon explaining population growth rates across species' geographical ranges (Villellas *et al.* 2015). Yet at the local scale, few studies have examined the way that different vital rates respond to both abiotic and biotic factors to influence population growth (Dahlgren & Ehrlén 2009).

Understanding how vital rates vary in response to plant-plant interactions is crucial for forecasting how plant communities will respond to future conditions, as species are likely to encounter new interaction neighbourhoods as they track preferred climates at different rates (Alexander *et al.* 2015). Lyu and Alexander (2023) recently revealed evidence of widespread demographic compensation in response to competition among

herbaceous species and highlighted the potential for variation in vital rate responses to influence population dynamics. Hence, a challenge of accurately forecasting the impacts of climate change is predicting the outcomes of existing and novel plant-plant interactions under changed abiotic conditions (Parmesan 2006; HilleRisLambers *et al.* 2013; Alexander *et al.* 2015; Ettinger & HilleRisLambers 2017). Despite a historical focus on abiotic conditions, both abiotic and biotic factors have important effects on vital rates (Ettinger & HilleRisLambers 2013; Morris *et al.* 2020; Paquette & Hargreaves 2021), but isolating their effects is difficult due to interactions among them (Callaway *et al.* 2002; Kraft *et al.* 2015; Germain *et al.* 2018; Funk 2021).

Annual plants provide an ideal system for studying the interactive effects of abiotic and biotic factors on vital rates and population growth (e.g. Angert *et al.* 2009; Alexander & Levine 2019; James *et al.* 2020), as it is possible to measure vital rates across the entire life cycle over relatively short timeframes (Ge *et al.* 2019; Laughlin *et al.* 2020). In addition, their small size is amenable to manipulative experiments which allow us to assess responses to local-scale environmental heterogeneity, such as variation in shade (Towers *et al.* 2020) and neighbourhood composition (Bowler *et al.* 2022). To date, little is known about how vital rates vary with local-scale variation in abiotic conditions and plant-plant interactions simultaneously to determine population growth rates.

To address this knowledge gap, we assessed how abiotic conditions and plant-plant interactions influenced emergence, survival, and seed production within a guild of Australian winter annual species. We manipulated water availability and interaction neighbourhoods across a natural gradient of shade (cast by trees) and soil to answer the following questions:

How do fitness-environment relationships vary among species?

Within species, how do vital rates and population growth rate differ in response to the separate and combined effects of abiotic conditions and plant-plant interactions?

Methodology

Study system

Our study was conducted in the York gum woodlands of West Perenjori Nature Reserve (29°28'01.3"S, 116deg12'21.6"E) in semi-arid south-west Western Australia (Fig. 1). York gum woodlands have a diverse understory of winter annual plant species and a sparse overstory that creates local-scale variation in shade and litter cover, which has been associated with annual plant species turnover (Dwyer *et al.* 2015; Wainwright *et al.* 2017) and population growth of some species (Stouffer *et al.* 2018). In the broader region, substantial inter-annual variation in rainfall significantly influences annual plant community composition (Dwyer *et al.* 2015).

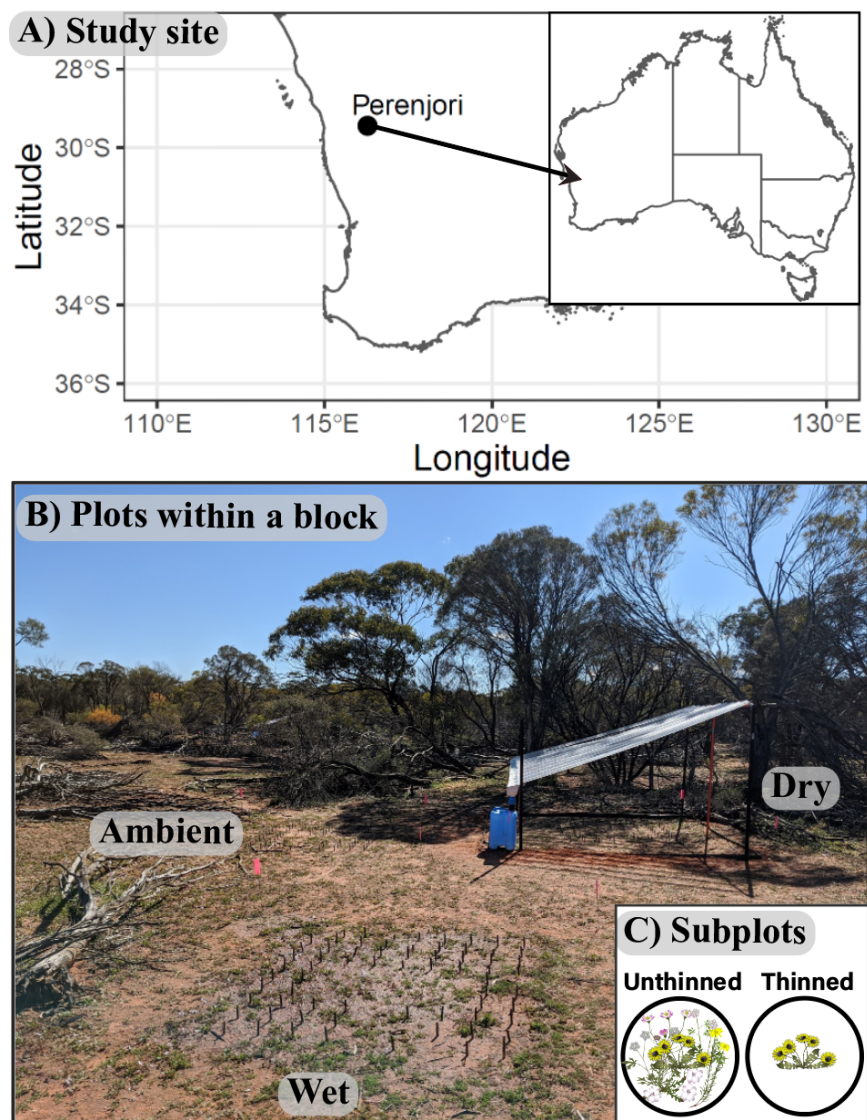


Figure 1. Experimental design for study site at West Perenjori Nature Reserve in Western Australia. A) Study site with inset of Australia. B) A block in an ‘open’ location with a ‘dry’ plot (rainout shelter, 50% reduction in precipitation), a ‘wet’ plot (water addition from intercepted water), and an ‘ambient’ plot (no alteration of precipitation). C) Subplots within each plot had naturally occurring neighbourhoods or were thinned to remove neighbours. Plant cartoon credit: Xingwen Loy.

Experimental design

To assess how shade, water availability and plant-plant interactions influence annual plant fitness, we manipulated water availability and interaction neighbourhoods in four open (0-12% canopy closure) and four shaded (58-100% canopy closure) blocks across the reserve. We measured demographic responses of nine common annual plant species that represent a variety of annual plant strategies (Table 1).

Table 1. The nine focal species by family and their origin (native or exotic).

Family	Species	Origin
Araliaceae	<i>Trachymene cyanopetala</i> (F.Muell.) Benth	Native
	<i>Trachymene ornata</i> (Endl.) Druce	Native
Asteraceae	<i>Arcotheca calendula</i> (L.) K.Lewin	Exotic
	<i>Hyalosperma glutinosum</i> subsp. <i>glutinosum</i> Steetz	Native
	<i>Lawrencella rosea</i> Lindl.	Native
	<i>Podolepis lessonii</i> (Cass.) Benth.	Native
Goodeniaceae	<i>Goodenia rosea</i> (S.Moore) K.A.Sheph.	Native
Plantaginaceae	<i>Plantago debilis</i> R.Br.	Native
Poaceae	<i>Pentameris airoides</i> subsp. <i>airoides</i> Nees	Exotic

Shaded blocks were nestled amongst *Acacia acuminata* and *Melaleuca sp.* trees. Each block contained three plots: one with ambient precipitation, one with a rainout shelter that reduced approximately 50% of incoming precipitation, and one with water manually added after rainfall events (Fig. 1, Figure S1). Each plot was 2.35×2.5 m and divided into 72 15×15 cm subplots to create eight subplots per species.

We collected seeds for the nine focal species across West Perenjori Nature Reserve in September and October 2019. The seeds were after-ripened in the field over summer to maintain conditions similar to those experienced naturally. We secured the seeds in mesh bags and, to minimise potential after-ripening effects (Dwyer & Erickson 2016), distributed the cages across two open and two shaded locations within the reserve. Seeds were pooled and well mixed before sowing in February 2020.

Subplots were randomly assigned to each species and neighbour treatment. We sowed fifteen seeds into shallow holes (approximately 0.5 cm deep) in the centre of each subplot and covered them with a thin layer of topsoil and one teaspoon of water to adhere the seeds to the soil. Toothpicks were used to mark the top of the sown areas to help distinguish emergence of sown seeds from those emerging from the seedbank. In February, one week of unseasonal heavy rainfall cued emergence for predominantly the two exotic species (*A. calendula* with 136 plants from 44 subplots and *P. airoides* with 82 plants from 18 subplots) and some native species (*G. rosea* with 12 plants from 10 subplots and *T. cyanopetala* with one plant). We counted the number of plants that emerged and added 5-10 extra seeds to subplots that had more than five plants emerge. While we did not track the fate of these summer plants, conditions returned to typically hot and dry within 10 days and we are confident that they all died before reproducing.

At the start of winter in July, we counted emergence of the sown seeds for each subplot. We then thinned these emerged plants down to a single focal individual closest to the centre of the subplot. To avoid disturbing the soil, we carefully thinned plants one at a time by snipping the main stem close to the soil.

To assess species' responses to the environment in the presence and absence of neighbours, we randomly assigned three subplots per species per plot to a neighbour removal treatment, and three subplots to remain with naturally occurring assemblages. For the thinned subplots, we removed all neighbouring plants rooting within a 7.5 cm radius of the focal individual as per protocol described in Mayfield and Stouffer (2017), appropriate for capturing most direct plant-plant interactions in this system (Martyn 2020). We recorded the abundance and identity of all neighbouring plants within the interaction neighbourhood during peak flowering in September.

Water manipulation

The long-term mean total rainfall for West Perenjori Nature Reserve in the growing season from June to October (inclusive) is 174.1 mm (± 6.2 mm standard error, Bureau of Meteorology 2021, 105-year means). As there had been an average amount of precipitation preceding the growing season in 2020, we aimed to alter rainfall by 50% such that typical dry and wet years were represented.

To reduce water availability, we built rainout shelters based on the design by Gherardi and Sala (2013, see Figure S1 for design details). We erected the rainout shelters in mid-August after tallying emergence and

thinning interaction neighbourhoods. This allowed an average amount of rainfall to cue emergence across all plots, after which the experimental water manipulation was imposed until seed collection.

To increase water availability, we transferred the water collected from the rainout shelters onto the water addition plots within three days of each rainfall event. We added the water slowly using a watering can to prevent run-off and recorded the amount added. Throughout the growing season, there was 109.8 mm of rainfall across approximately six rainfall events (Bureau of Meteorology 2021). In total, watered plots each received an extra 29.9-38.8 L of water (27-35% increase) compared to ambient plots.

Seed production and abiotic measurements

We collected seeds from surviving focal individuals ($n = 609$) as they senesced in September and October. We prevented seed dispersal by tying thin mesh organza bags over the flowers shortly prior to seed release. Where a substantial number of seeds were lost from an individual despite these efforts, we used flower head count to estimate viable and inviable seed production based on average production from other individuals in the study (two *G. rosea* and eight *L. rosea* individuals, 2% and 9.5% of each species' seed production observations). We considered seeds that were filled and lacking disease and predation to be viable.

To quantify the abiotic environment for each plot, we measured litter cover, soil properties, and canopy closure. We used a spherical densiometer in each corner and the centre of each plot to produce average estimates of shade based on the proportion of overhead area that is covered by foliage versus open sky (Jennings *et al.* 1999). Litter cover was recorded as 0%, <25% (inputted as 12.5% for calculations), 25% or 50% by visual estimate. Soil samples were collected from the centre and two random outer edges of each plot at a 0-15 mm depth (excluding litter) and mixed thoroughly. The soil was air-dried and analysed for a suite of macro- and micro-nutrients by the School of Agriculture and Food Sciences, The University of Queensland.

Data analysis

Population growth rate

We calculated population growth rates by incorporating vital rates into the following classic equation for an annual plant population model (Cohen 1966), with an additional plant survival parameter:

$$\frac{N_{i,t+1}}{N_{i,t}} = s_i (1 - g_i) + f_i z_i g_i \text{ Equation 1}$$

where $\frac{N_{i,t+1}}{N_{i,t}}$ is the per capita growth rate of a given population i , s_i is seed survival probability (proportion of seeds that remain viable in the soil over summer, see Supplementary Methods), g_i is emergence probability, f_i is the number of viable seeds produced per emergent and z_i is survival probability of emerged plants (the proportion of emerged plants that produced at least one viable or inviable seed).

Population growth rate was calculated twice for each plot; with and without neighbours (the latter being intrinsic growth rate, λ). For these calculations, species-specific seed survival and plot-level emergence probabilities were held constant, while plant survival and seed production were calculated with and without neighbours. Plot-level seed production (f_i) was calculated as the exponentiated average of log-transformed viable seed production per focal plant that produced at least one viable seed.

Responses to abiotic and biotic factors

All data analysis was conducted using R version 3.5.3 (R Core Team 2019). To quantify plot-level abiotic conditions we ran a Principal Components Analysis (PCA) including canopy closure, litter cover, soil pH, and phosphorous, ammonium, nitrate, and potassium content (chosen as the most important soil nutrients for plant growth). The first PC axis (PC1) explained 54.2% of the variation in measured abiotic conditions and was mainly loaded with canopy closure, litter cover and soil macronutrients (phosphorous and nitrate). PC2 explained 18.5% of the abiotic variation and was mainly associated with soil pH (see Figure S3).

To assess how demographic rates correlate with abiotic conditions and plant-plant interactions, we modelled emergence, survival, seed production, and population growth rate separately per species using mixed-effects models. Emergence was modelled as the number of seeds that emerged, accounting for the number of seeds that were sown into each replicate, and survival was modelled as a binary outcome of whether a focal plant survived to produce at least one seed (viable or inviable). Due to low emergence fractions and hence insufficient focal plants to model survival and seed production, *Podolepis lessonii* was only assessed for emergence responses, whereas the remaining eight species were modelled for all demographic rates.

Prior to modelling, we log-transformed total neighbour abundance to improve linearity with vital rates and standardised all continuous explanatory variables to a mean of 0 and standard deviation of 1. Block and plot (nested in block) were included as random effects in all models. An observation-level random effect (OLRE) of sub-plot ID was nested within plot for emergence models to assist with potential overdispersion for all species, except for the *G. rosea* model which was not over-dispersed and including the OLRE led to convergence issues.

Emergence and survival were modelled using binomial errors and logit-link functions with the “glmer” function from the ‘lme4’ package (Bates *et al.* 2015). Seed production was modelled with negative binomial error distributions and log link functions using the “glmmTMB” function from the ‘glmmTMB’ package (Brooks *et al.* 2017). Population growth rate was log-transformed and modelled with a normal error distribution using the “lmer” function from the ‘lme4’ package.

To allow for quadratic responses to the environment, we initially modelled each vital rate with main and quadratic terms for PC1 (soil fertility, canopy closure and litter cover), PC2 (soil pH) and neighbour abundance. Where quadratic terms were significant (see Table S1), they were retained in all subsequent models. Emergence was modelled in response to PC1 and PC2 only (because it was measured before the watering and neighbour treatments were implemented). Survival, seed production, and population growth were modelled in response to PC1, PC2, watering treatment (dry, ambient, or wet) and neighbour abundance (for survival and seed production) or presence (for population growth). The presence of *Cuscuta campestris*, a parasitic invasive annual plant, was included as a covariate as it appeared to impact host plant performance. To allow for interactions between factors, we included all pairwise interactions between watering treatment, PC1 and neighbour abundance in a full model, and then removed non-significant interaction terms to create the final models from which results are reported.

Results figures were plotted in base R or using the “ggplot” function in the package ‘ggplot2’ (Wickham 2016) and tables were built using the “kable” function in kableExtra (Zhu 2021). We calculated marginal and conditional pseudo- R^2 values using the “r.squaredGLMM” function in the ‘MuMIn’ package (Bartón 2022) to estimate the proportion of variance explained by fixed effects and combined fixed and random effects (Nakagawa & Schielzeth 2013). All data and R code to reproduce our results are available at https://github.com/acatling/Perenjori_watering_exp.

Life table response experiment

For species with significant differences in population growth rates with and without neighbours (*A. calendula* and *P. debilis*), we used life table response experiment (LTRE) analysis to decompose differences in population growth rates into contributions from each transition between life stages. We modelled a simple two-stage life cycle of seeds and adults with a one-year time step estimated in Spring, before seed rain (Figure S2). We also included seed dormancy probabilities to incorporate the potentially important role of the seed bank (Nguyen *et al.* 2019, see Supplementary Methods). Using the “exactLTRE” package (Hernández *et al.* 2023), we carried out directional fixed design LTRE using intrinsic lambda (in the absence of neighbours) as the reference matrix compared to lambda in the presence of neighbours as the treatment.

Results

Among-species responses to abiotic and biotic factors

Responses to abiotic heterogeneity in shade and soil varied by vital rate but were similar among species.

Emergence fractions increased along PC1 (higher emergence in more open, low-fertility plots) for 5/9 species, and 2/9 species demonstrated convex responses (Fig. 2, Table S2, $p < 0.05$). One species had low emergence and therefore insufficient replicates to model survival, seed production, or population growth, and hence these responses are reported throughout for the other eight species only. In contrast to emergence responses, survival was only influenced by PC1 for 2/8 species, both of which varied interactively with neighbour abundance (Fig. 2, $p < 0.05$). Seed production decreased with PC1 for two species (more seeds produced in shaded, high-nutrient plots) and the relationship depended on neighbour abundance for a third species (Fig. 2, $p < 0.05$). There was no apparent main effect of PC1 on population growth, however, there was a significant interaction with neighbour presence for half of the species (4/8 species, $p < 0.05$) such that population growth declined along PC1 (as conditions became less shaded and less fertile) in the presence, but not absence, of neighbours (Fig. 2).

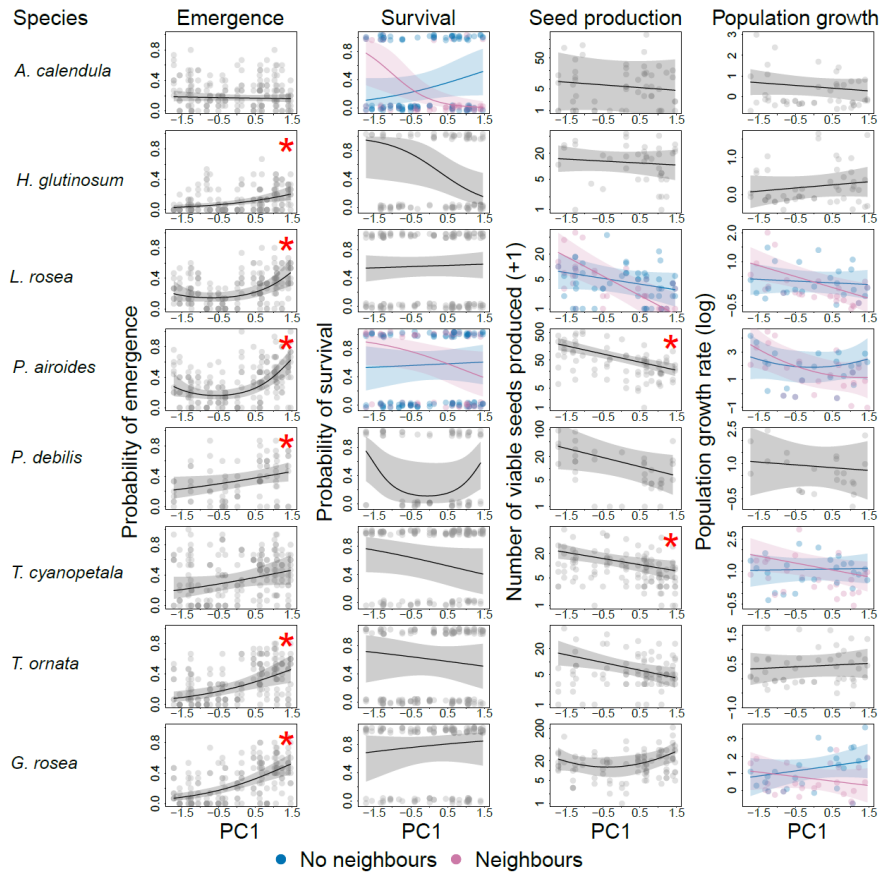


Figure 2. Vital and population growth rate relationships with PC1 for each focal species. Low values of PC1 represent closed canopy, high litter, high soil fertility plots. PC1 is standardised to a mean of 0 and standard deviation of 1. Black lines and light grey fields represent linear regressions from models with 95% confidence intervals holding continuous explanatory variables at their means, under the ambient watering treatment. Points for emergence and survival represent emergence fractions and survival of individuals. To facilitate plotting, we have added one to seed production values and show them on a log scale. Significant interactions between PC1 and neighbour abundance or presence (for population growth) are plotted with points and regressions representing the presence (red) or absence (blue) of neighbours, holding abundance at their respective means for survival and seed production. Asterisks indicate significance of the main effect of PC1 where models did not include interactions of other factors with PC1: * $p < 0.05$.

Soil pH and the watering treatment had few main effects on species' vital and population growth rates. Soil pH (PC2) had a negative or convex relationship with emergence for 3/9 species, was positively related to survival for 1/8 species, negatively related to seed production for 1/8 species, and positively related to population growth rate for 1/8 species (Table S2, $p < 0.05$). Interestingly, survival responses to PC1 depended on the watering treatment for half of the species but without a clear pattern in directions of responses among species (Table S2 and Figure S4). This interaction was more prevalent for survival than seed production (1/8 species) or population growth rate (2/8 species, Table S2 and Figure S4). There was consistently no evidence that the watering treatment influenced species' responses to neighbour abundance or presence, except for *T. cyanopetala* which had lower population growth rate in the dry compared to ambient watering treatment but only where neighbours were present, not absent (Table S2).

Survival, seed production, and population growth rate responses to biotic factors were similar among species. We found no clear main effects of neighbour abundance on survival or seed production for any species, except for *P. debilis* where seed production decreased as the number of neighbours increased (Fig. 3, Table S2). Mean population growth rates were lower in the presence than absence of neighbours for all species, although the main effect of neighbours on population growth rate (where there were no interactions with other factors) was only significant for 2/8 species, including *P. debilis* (Fig. 3, Table S2, $p < 0.05$). The presence of the invasive parasitic *C. campestris*, did not affect survival, and only influenced seed production, negatively, for 1/8 species (Table S2).

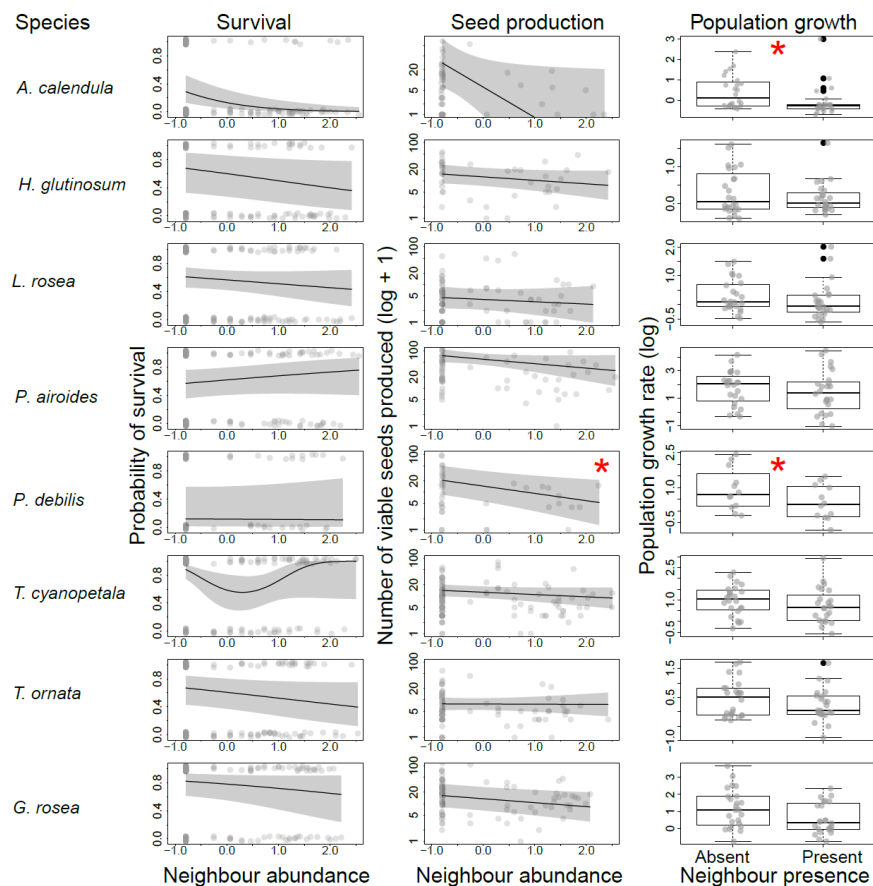


Figure 3. Vital and population growth rate relationships with neighbour abundance (survival and seed production) or presence (population growth rate). Neighbour abundance is standardised to a mean of 0 and standard deviation of 1. Black lines and light grey field represent linear regressions with 95% confidence

intervals from models holding continuous explanatory variables at their mean, under the ambient watering treatment. Points for emergence and survival represent emergence fractions and survival of individuals. Outliers are duplicated as black points in population growth boxplots. Asterisks indicate significance of the main effect of neighbours where models did not include interactions of other factors with neighbours: $*p < 0.05$.

Within-species responses to abiotic and biotic factors

Within species, vital and population growth rate responses to abiotic heterogeneity in shade and soil separated into three distinct response profiles. One species, *P. airoides*, exhibited clear evidence of demographic compensation, whereby a convex emergence response to PC1 coupled with a negative seed production response resulted in a non-significant population growth rate response (Fig. 2). For a further five species (all but *A. calendula* and *H. glutinosum*), we found similar compensatory trends along PC1 between emergence and seed production, but relationships were only significant for one of the vital rates (mainly emergence). Hence, most of the species (6/8) had one significant vital rate response (positive or convex) to PC1 yet a non-significant population growth response (Fig. 2). *Hyalosperma glutinosum* had a positive emergence response to PC1 but no other significant vital or population growth responses (Fig. 2). The final species, *A. calendula*, had no significant responses of any vital rate or population growth rate to PC1 (Fig. 2).

There were three response profiles for the influence of neighbour abundance (or presence for population growth) on vital and population growth rates within species. Most of the species (6/8) had non-significant vital and population growth rate responses (Fig. 3, Table S2). One species, *P. debilis*, produced fewer seeds as neighbour abundance increased and had lower population growth rates in the presence of neighbours (Fig. 3). *Arctotheca calendula* did not have significant survival or seed production responses to neighbour abundance yet had lower growth rates in the presence of neighbours (Fig. 3). For most species, within-species population growth responses to neighbours were in the same direction as seed production responses (for 6/8 species) and survival responses (for 5/8 species, Table S2). Two species had significantly lower population growth rates in the presence compared to absence of neighbours (Fig. 3, Table S2, $p < 0.05$).

The LTRE analysis showed that the life stage transitions contributing most to the difference in population growth rate in the absence versus presence of neighbours differed for the two species assessed. Survival probability and seed production were the only rates allowed to vary between population growth rates as they were the only vital rates measured in response to neighbour removal. For *A. calendula*, the transition representing a dormant seed remaining viable, emerging, and surviving to reproduction made the largest contribution (52%, Figure S5). This contrasted to *P. debilis*, for which the transition representing an adult plant producing seeds that stays dormant and viable in the seed bank accounted for 73% of the difference in population growth between neighbour treatments.

Discussion

Our study revealed high similarity in fitness-environment relationships among species, and greater within-species variation in vital rate responses to abiotic conditions than plant-plant interactions. We found weak but frequent evidence of demographic trade-offs between emergence and seed production across a local-scale gradient from shaded, fertile plots to sun-exposed, lower-fertility plots. Competitive effects on survival and seed production were surprisingly rare, and effects on population growth depended on abiotic conditions for half of the species. Altogether our results highlight the importance of interactive abiotic and biotic factors for plant demography in a diverse annual plant system. Our results also demonstrate the risk of assuming fitness responses based on a single vital rate.

Consistent vital rate-environment relationships among species

We found vital rate-environment relationships among species were largely consistent in the direction of response. As values of PC1 increased (becoming more open and less fertile), species tended to have higher emergence, neutral survival, neutral or negative seed production and neutral population growth rates. Although emergence rates tend to increase with light availability, this pattern can be highly variable among

systems (Carta *et al.* 2017) and species (Grime *et al.* 1981; Baskin & Baskin 1988). Indeed, one of the core tenants of niche theories is that species differ in their responses to environmental variation (Grubb 1977; Chesson 2000). Previous annual plant studies have reported spatial variation in species' emergence (James *et al.* 2020) and temporal variation in species' responses to precipitation (Angert *et al.* 2009) as mechanisms promoting local diversity. Hence, the high consistency observed among species' responses to environmental variation in our study was surprising, although in line with another study in this system that found limited evidence of species-specific fecundity responses to the environment (Towers *et al.* 2020).

By sowing seeds across habitats and removing neighbours from half of the focal plants, we were able to test species' demographic responses along gradients of abiotic conditions alone and in combination with plant-plant interactions (Chesson 2000; Adler *et al.* 2013; Bimler *et al.* 2018). We found a surprising, near ubiquitous lack of responses to main effects of neighbour abundance among species for survival and seed production. However, weak negative effects of neighbours on both survival and seed production resulted in clear competitive effects on population growth for two of the eight species in this study. We expected survival and seed production to be negatively related to PC1, with lower survival and seed production in more open and less fertile environments. Although infrequent among species, for three species these relationships were only observed where neighbour abundance was high, which could reflect responses to competition for water and nutrients in the higher light and lower nutrient environment (Maestreet *et al.* 2005).

Variation in demographic responses to abiotic and biotic factors within species

For one species (*P. airoides*), we found clear evidence of demographic compensation along PC1 arising from a significant convex emergence relationship coupled with a significant negative seed production relationship. For a further five species we found similar compensatory trends along PC1 between emergence and seed production, but relationships were only significant for one of the vital rates (mainly emergence). This result highlights the risk of using single vital rates as proxies for fitness without considering how different vital rates may trade-off in their effects on population growth (Laughlin *et al.* 2020; Klimeš *et al.* 2022). Since emergence trends were frequently different to population growth rate trends along PC1 in our study, we would caution against using emergence rate as a proxy for fitness in studies involving light availability gradients.

In contrast to the variation observed within species' demographic responses to abiotic conditions, survival and seed production responses to neighbour abundance were almost always consistent with population growth responses to neighbour removal. Surprisingly, only two species experienced main effects of competition on population growth, *A. calendula* and *P. debilis*. Neither species had strong survival or seed production responses to neighbour abundance, illustrating the potential for weak vital rate relationships with the environment to result in strong relationships for population growth rate (Dahlgren & Ehrlén 2009). For these species, variation in survival and seed production respectively contributed most to the difference in population growth rates between the presence and absence of neighbours. Unlike Lyu and Alexander (2023) who revealed nearly ubiquitous demographic compensation in response to competition, we did not observe demographic compensation among vital rates in response to competition. Although main effects of competition were not widespread, for four species, competitive effects on population growth were only observed in low nutrient, high light conditions. This result reinforces that responses to competition may be stronger in high light, low nutrient environments in this system, and highlights the importance of interactions between abiotic and biotic factors for fitness.

Few direct responses to water availability

Our results did not support the expectation that water availability plays a direct role in survival, seed production, and population growth rates of herbaceous plants (Mu *et al.* 2021). We found the impact of water availability depended on other abiotic conditions and was more frequently important in models of survival than seed production or population growth rate. For three species, the wet treatment appeared to buffer the negative effects of increasing light and decreasing nutrients on survival, whilst the fourth species only experienced reduced survival along PC1 in the dry treatment. This result supports existing knowledge that interactions among shade, soil nutrients, and moisture influence plant survival, particularly in arid

environments (Valladares 2003). In contrast, water availability rarely modified the effect of neighbours on vital or population growth rates. In perennial grasses, Adler *et al.* (2009) similarly reported little evidence of interactive effects between precipitation and the presence of neighbours, however unlike our results they found strong support for direct effects of precipitation.

One reason why the watering treatment had few direct impacts on vital and population growth rates, and indirect impacts via interactions with competition, may simply be that the watering treatment did not significantly alter soil moisture compared to ambient conditions. In the year we conducted the study, conditions were drier than average at 110 mm of rainfall over the growing season and as such our watering treatments represented 30-90% of average rainfall. Based on our study and results from other watering trials in this system (Wainwright *et al.* 2018; Towers *et al.* 2020), it seems likely that in many years water is not limiting performance during the growing season.

The timing of rainfall events is an important driver of variation in vital rates, plant-plant interactions, and population dynamics (Levine *et al.* 2008; Compagnoni *et al.* 2016; Conquet *et al.* 2023). Even in the single year studied here, unseasonably heavy summer rainfall cued emergence outside the growing season for the two exotic species almost exclusively. In the future, it would be interesting to implement the watering treatment before the onset of winter rainfall to assess emergence responses, which can have large contributions to population growth rates (James *et al.* 2020). It would also be valuable to track soil moisture in each plot after rainfall events to measure the magnitude and duration of the effect of the watering treatment on soil conditions. Since annual plants can employ different ecological strategies to buffer performance over time in water-limited environments, the effect of interannual variation in water availability on vital rates is another important avenue of research (Angert *et al.* 2007).

Conclusion

Our study provides empirical evidence of variation in species' vital and population growth rate responses to local-scale heterogeneity in abiotic conditions and plant-plant interactions in a natural system. We illustrate the potential for demographic trade-offs between emergence and subsequent vital rates to counteract the effect of natural variation in shade and soil nutrients on population growth rate. We found a surprising lack of significant effects of neighbours on survival and seed production among species but show the potential of weak vital rate responses to competition to generate strong patterns for population growth rate. We also demonstrate the importance of interactions between different abiotic factors (shade and nutrient availability with water availability) and between abiotic and biotic factors for vital and population growth rates. Linking functional traits to variation in demographic responses is the next aim of this research and will help to generalise our understanding of the mechanisms driving fitness-environment relationships.

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