



Accurate predictions of coexistence in natural systems require the inclusion of facilitative interactions and environmental dependency

Malyon D. Bimler¹ | Daniel B. Stouffer² | Hao Ran Lai^{3,4} |
Margaret M. Mayfield¹

¹School of Biological Sciences, The University of Queensland, St Lucia, QLD, Australia

²Centre for Integrative Ecology, School of Biological Sciences, University of Canterbury, Christchurch, New Zealand

³Yale-NUS College, Singapore, Singapore

⁴Department of Biological Sciences, National University of Singapore, Singapore, Singapore

Correspondence

Margaret M. Mayfield, School of Biological Sciences, The University of Queensland, St Lucia, 4072, Queensland, Australia
Email: m.mayfield@uq.edu.au

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Abstract

1. Coexistence between plant species is well known to depend on the outcomes of species interactions within an environmental context. The incorporation of environmental variation into empirical studies of coexistence are rare, however, due to the complex experiments needed to do so and the lack of feasible modelling approaches for determining how environmental factors alter specific coexistence mechanisms.
2. In this article, we present a simple modelling framework for assessing how variation in species interactions across environmental gradients impact on niche overlap and fitness differences, two core determinants of coexistence. We use a novel formulation of an annual plant population dynamics model that allows for competitive and facilitative species interactions and for variation in the strength and direction of these interactions across environmental gradients. Using this framework, we examine outcomes of plant–plant interactions between four commonly co-occurring annual plant species from Western Australian woodlands. We then determine how niche overlap and fitness differences between these species vary across three environmental gradients previously identified as important for structuring diversity patterns in this system: soil phosphorus, shade and water.
3. We found facilitation to be a widespread phenomenon and that interactions between most species pairs shift between competitive and facilitative across multiple environmental gradients. Environmental conditions also altered the strength, direction and relative variation of both niche overlap and fitness differences in nonlinear and unpredictable ways.
4. *Synthesis.* We provide a simple framework for incorporating environmental heterogeneity into explorations of coexistence mechanisms. Our findings highlight the importance of the environment in determining the outcome of species interactions and the potential for pairwise coexistence between species. The prevalence of facilitation in our system indicates a need to improve current theoretical frameworks of coexistence to include noncompetitive interactions and ways of translating these effects into explicit predictions of coexistence. Our study also suggests a need for further research into determining which factors result in

consistent responses of niche overlap and fitness differences to environmental variation. Such information will improve our ability to predict outcomes of coexistence, invasion events and responses of whole communities to future environmental change.

KEYWORDS

annual plants, coexistence, competition, competitive outcomes, environmental heterogeneity, facilitation, fitness differences, niche

1 | INTRODUCTION

Understanding what allows species to coexist, and thus how diversity is maintained in local communities, is a long-standing goal of community ecology (Hutchinson, 1961). For close to a century, a core element of most coexistence mechanisms has been the strength of interactions among neighbouring individuals of co-occurring species (Connell, 1980; Lotka, 1925; Tilman, 1982; Volterra, 1926). Chesson (1994, 2000a, 2000b) brought together many of these historical seminal predictions about the role of species interactions in coexistence in a cohesive framework that has become known as modern coexistence theory (Barabás, D'Andrea, & Stump, 2018), henceforth referred to as MCT. Among other insights, this framework explains how coexistence between two competing species can arise from the interplay between two categories of competition, which are now most widely known as niche overlap and fitness differences (Chesson, 2000b, 2008). Niche overlap is defined by how much a species limits itself over its competitors. Fitness differences, on the other hand, reflect the competitive advantage one species has over another (Adler, HilleRisLambers, & Levine, 2007). It is well known that many specific mechanisms can affect both niche overlap and fitness differences in natural systems, such as differences in resource use (McKane et al., 2002), phenology (Godoy & Levine, 2014) and tolerances to consumers (Sedio & Ostling, 2013). It is also well known that both categories of competition rely ecologically (and mathematically) on the ratios of fitness outcomes of intra- and interspecific interactions between species (HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012).

Functionally, quantifying the relative magnitude of niche overlap and fitness differences allows us to unravel the mechanisms promoting coexistence, within the framework provided by MCT. For example, a fitness difference value which differs from one means that one species has a larger fitness advantage and can hence outcompete the other. In order to coexist over the long-term, large fitness differences must be overcome by small values of niche overlap, such that a species suffers little intraspecific competition when rare and can hereby recover from low abundances (Adler et al., 2007). Understanding the strength and relative variation of these components is not only important for theory but also has important ecological implications for conservation and management, such as predicting the successful establishment of an invasive species (Gross, Liancourt, Butters,

Duncan, & Hulme, 2015; MacDougall, Gilbert, & Levine, 2009) or the response of a species to climate change via indirect competitive interactions (Adler, Dalgleish, & Ellner, 2012; Kleinhesselink & Adler, 2015).

Niche overlap and fitness differences are both impacted by the many mechanisms which induce variation in interaction strength and interaction outcomes, from phenotypic plasticity (Turcotte & Levine, 2016) to environmental variation in time and space (Adler & Drake, 2008; Adler, Ellner, & Levine, 2010; Adler, HilleRisLambers, Kyriakidis, Guan, & Levine, 2006; Angert, Huxman, Chesson, & Venable, 2009; Chu & Adler, 2015; Godoy & Levine, 2014). Fluctuations in interaction strength have been deemed crucial in many theoretical models of coexistence (Abrams, 1980, 1984; Chesson & Huntly, 1997) and are often the result of frequency-dependent mechanisms (Fox, 1977; Hanski, 1981; Holt, 1984; Molofsky, Durrett, Dushoff, Griffeth, & Levin, 1999; Pacala & Crawley, 1992). Though this natural variation in interaction strengths is implicit in coexistence theory (Chesson, 1994), it has rarely been accounted for in empirical tests of the theory (see Levine & HilleRisLambers, 2009; Godoy, Kraft, & Levine, 2014, for tests of this framework in annual plant systems).

Consequently, much of the complexity inherent to natural systems has been omitted from empirical studies of coexistence and its component mechanisms. Some of the major assumptions made by the MCT framework are that species interactions are all competitive and that the environment is homogeneous. Empirical evidence clearly demonstrates, however, that interactions between plants are more complex and the outcomes more variable than predicted under these assumptions (Bengtsson, Fagerstram, & Rydin, 1994; Thompson, 1988). First, the importance of non-competitive interactions in structuring communities is being increasingly acknowledged (Goldberg & Barton, 1992; Mayfield & Stouffer, 2017; Michalet et al., 2015; Thompson, 1988). Numerous studies, for instance, have shown that facilitation, whereby a species has a positive effect on another's growth rate, is common and strong in many plant communities, particularly in harsh environments (Bertness & Callaway, 1994; Brooker et al., 2008; Callaway & Lawrence, 1997; He, Bertness, & Altieri, 2013; Kawai & Tokeshi, 2007; Maestre, Callaway, Valladares, & Lortie, 2009; Maestre, Valladares, & Reynolds, 2005). In these cases, facilitation is likely to promote coexistence between species. In

other cases, however, facilitation may limit species diversity—for example, when facilitation-driven priority effects prevent late-arriving colonisers from expanding into new habitats (Fukami, Mordecai, & Ostling, 2016). How facilitation might affect coexistence dynamics is, therefore, context dependent. Despite the need to resolve this incomplete understanding of facilitation and its role in coexistence across natural communities, it has not been formally incorporated into MCT or the frameworks available to study it in real systems (Bruno, Stachowicz, & Bertness, 2003; Chu & Adler, 2015).

The outcomes of species interactions are also highly dependent on environmental heterogeneity (Callaway, Pennings, & Richards, 2003; Chamberlain, Bronstein, & Rudgers, 2014; Soliveres, Smit, & Maestre, 2015; Thompson, 1988). Species-specific responses to the environment can affect the relative strength of interactions, and hence niche overlap and fitness differences. Furthermore, variation in the relative fitness of species over space, or variation in dispersal into different environments, can also allow different species to have the upper hand in different environmental contexts (Chesson, 2000a, 2000b). Despite a rich history investigating coexistence within spatially variable environments and theoretical predictions that variation in competitive effects is important for mediating the effects of environmental heterogeneity on coexistence (Amarasekare, 2003), fluctuations in interaction strengths are typically kept implicit within these models and few studies investigate how this variation may affect niche overlap, fitness differences or variation in coexistence predictions (but see Lanuza, Bartomeus, & Godoy, 2018).

Current developments in the coexistence literature are gradually moving beyond proof-of-concept experimental tests of the MCT framework (such as Levine & HilleRisLambers, 2009) towards applying it to broader questions about community-level diversity. Our study illustrates some of the major hurdles in achieving this goal. Notably, the environment experienced by most plant communities is variable in important ways which undoubtedly affect coexistence (Chesson, 2000a; Sears & Chesson, 2007). Though MCT was not developed to predict coexistence dynamics in complex, diverse and heterogeneous communities, the theoretical concepts underlying this framework can still be applied. In this study, we present a novel formulation of an annual plant population dynamics model which allows species interactions to vary from competitive to facilitative and along environmental gradients. This allows us to explore how environmental variation affects niche overlap and fitness differences, two key components determining coexistence. We then test this framework on data from four annual plant species living along three environmental gradients in annual wildflower communities from SW Western Australia. Using these data, we answer the following questions:

- How does environmental variation affect the strength and sign of pairwise species interactions?
- How do niche overlap and fitness differences vary relative to each other along environmental gradients?

In answering these questions, we hope this study will stimulate discussion and theory development that will build upon the helpful framework provided by MCT and towards approaches that are more useful for scaling up predictions of coexistence outcomes to populations and communities occupying heterogeneous natural environments.

2 | MATERIALS AND METHODS

2.1 | Data

2.1.1 | Study system

Data were collected in 2014 from annual plant communities in the understories of York gum-jam woodlands in SW Western Australia. All data were collected from two study sites with distinct climate profiles but highly overlapping understory communities: the semi-arid West Perenjori Nature Reserve (29°28'01.3"S 116°12'21.6"E) and relatively mesic Bending Nature Reserve (32°23'06.1"S 118°22'42.4"E). York Gum woodlands range over a 1000-km gradient spanning the Mediterranean and semi-arid climates of SW Western Australia. They are defined by a variable but generally open canopy composed almost entirely of two tree species: *Eucalyptus loxophleba* and *Acacia acuminata*. York gum-jam understoreys are dominated by dense winter annual plant communities, which typically support a diverse mixture of native and exotic forbs and exotic annual grasses. Soils in these woodlands are relatively rich in nitrogen, in part because one of the dominant canopy species (*A. acuminata*) is a nitrogen fixing species, but have very low levels of plant-available phosphorus (Lambers, Raven, Shaver, & Smith, 2008). Agricultural runoff into reserves contributes to patchy phosphorus (P) enrichment, resulting in heterogeneous soil mosaics ranging from high to low P levels within local communities (Dwyer, Hobbs, Wainwright, & Mayfield, 2015). Observational studies of York Gum understory communities across the range of this woodland type have provided strong evidence that phosphorus concentration, tree canopy cover and water availability are structuring factors for the plant diversity found in the understories of this system (Dwyer et al., 2015; Wainwright, Dwyer, & Mayfield, 2017).

2.1.2 | Experimental treatments

Data were collected as part of a watering experiment designed to examine the effects of native and exotic neighbourhoods on focal individuals under elevated and ambient watering conditions in mesic and arid regions. Across the two study sites, we selected fifty ~15-m² blocks (24 blocks in Perenjori and 26 in Bending) in areas containing ≥2 of four focal species: natives *Trachymene cyanopetala* (F. Muell.) Benth. (Araliaceae) and *Waitzia acuminata* Steetz (Asteraceae), and the exotics *Arctotheca calendula* (L.) Levyns (Asteraceae) and *Hypochaeris glabra* L. (Asteraceae). Within each block, ten 50 × 50 cm² plots were established to include one or two

focal individuals of two focal species (one per $25 \times 25 \text{ cm}^2$ quadrat). Each plot was then assigned to one of two possible watering treatments (added water or ambient water) and one of five possible composition treatments (totalling 10 treatment levels). Soils in the York Gum woodlands have poor water retention capacity and thus a high potential for uncontrolled runoff during experimental waters into ambient plots. This risk prevented us from randomly selecting watered and ambient plots, and instead, plots receiving the same watering treatment were clustered within blocks to prevent runoff into ambient plots. Across watered and ambient plots, however, composition treatments were randomised. Composition treatments were solo (one focal individual, no competitors), native-dominated (one focal individual with predominantly native competitors), exotic-dominated (one focal individual with predominantly exotic competitors), monocultures (one focal individual with conspecific competitors only) and control (no weeding, i.e., natural species composition). All treatment plots except the controls were thinned by hand to achieve the desired composition. Treatment thinning also limited the potential confounding effects of location on plant densities. Focal individuals experienced interaction neighbourhoods ranging from 1 to 255 individuals (overall $M = 23$ individuals per plot, $SE = 0.91$, median = 14), with a mean density of 33 individuals for the native-dominated treatments, 25 for exotic-dominated, 7 for monocultures and 50 individuals for the control treatments. The final total density of individuals in each plot was not associated with any consistent changes in soil phosphorus or canopy cover (results not shown).

Both watering and composition treatments were systematically maintained throughout the growing season (four watering events spaced approximately 1–3 weeks apart). Watering was done manually such that watered plots received 180% of ambient rainfall at Perenjori and 185% at Bending. For each watering event, we added the same volume of water per plot as the volume of rainfall which ambient plots had received since the last watering event (or since the beginning of the experiment, in the case of the first event). Water additions for some plots were capped at 1 L per plot after September 11, 2014, as some soils had reached field water capacity and additional water ran off plots. Species composition was maintained by regular thinning throughout the experiment, except in the control composition plots. There is no evidence that after accounting for neighbour density and identity, neighbourhood origin further impacted individual fitness outcomes (results presented in Supporting Information 1, Supporting Information Table S1), and thus, neighbourhood composition treatment was not included as an effect in this study.

2.1.3 | Focal species fecundity and neighbourhood data

The four selected focal species were among the most commonly found species in both study reserves. They were selected for their commonness in both sites, their representation in communities found across the three examined environmental gradients and for the commonness with which they were found growing at a range

of local population densities. Once experimental treatments had been applied to our study plots and community-wide germination had slowed (24 July 2014 at West Perenjori, 10 August 2014 at Bending), we recorded the neighbourhood composition in each of our plots. In total, we followed 989 focal individuals and the composition of their local plot communities. Focal individuals were divided among the four focal species as evenly as possible (215, 271, 248 and 255 individuals of *T. cyanopetala*, *W. acuminata*, *A. calendula* and *H. glabra*, respectively) and between the two sites (628 individuals from Perenjori and 361 from Bending).

As described later, our plant population model requires the quantification of plant fecundity, germination rate and seed survival rate. Fecundity was measured as the number of seeds produced by each focal individual and was directly measured as total seed production from each of our 989 focal individuals. To obtain this count, seeds were collected from each individual starting soon after seed maturity. For both exotic species and some *W. acuminata* individuals, which all have wind dispersed seed, many seeds were dispersed before we were able to collect them. In these cases, seed production was extrapolated from the number of inflorescences produced by each plant by multiplying the average seed count per flower which had not dispersed on that plant by the number of dispersed flower heads. Seed and flower counts are highly correlated for those species (*A. calendula*: $cor = 0.455$, $p < 0.0001$; *H. glabra*: $cor = 0.630$, $p < 0.0001$; *W. acuminata*: $cor = 0.707$, $p < 0.0001$). Neighbourhood data included the identity and number of individuals of each species within the interaction neighbourhood ($25 \text{ cm} \times 25 \text{ cm}$ quadrat) of each focal individual. Neighbourhood plots contained between 1 and 15 neighbour species and between 1 and 255 neighbouring individuals.

Germination and seed survival rates for focal species were obtained from field and lab studies. Both germination and seed viability rates for *A. calendula* were collected in a laboratory-based germination trial (Manietta et al. unpublished data). This germination trial assessed *A. calendula* seeds from the Bending area over a 2-month period across a range of temperature and light exposure treatments. The highest germination rate across all treatments (cold, light) was used as the germination rate for this study. Seed viability for *A. calendula* was done using gibberellic acid and TZ staining as described for the other species below but from seed collected but not reburied in the field. Germination and seed viability rates for the other three focal species were estimated separately at Perenjori and Kunjin Reserve ($32^{\circ}21'19.31''\text{S}$, $117^{\circ}45'42.32''\text{E}$; 65 km west of Bending Reserve), using seed from those locations, respectively. For these three species, five replicate sets of 30 seeds of each species (150 seeds total per species) were buried in fine-aperture mesh bags approximately 5 cm beneath the soil surface in December 2013. In early winter 2014, we dug up the bags and returned seeds to the laboratory at the University of Queensland. We estimated germination rates (g) by counting the number of seeds that appeared to have germinated while in the field (broken seed coat, protruding radicles, etc.). Missing seeds were assumed to have been lost to granivory or decomposition and thus were scored as dead. Seeds that remained

but had not germinated in the field were used to assess seed survival (s) in the lab. To do this, we imbibed ungerminated seeds on germination paper with a 400 ppm GA3 solution, placed them in a temperature-controlled growth chamber and scored germination over a 3-day period. Those seeds that did not germinate in this time-frame were further tested for viability using standard AOSA/SCST Tetrazolium (TZ) staining (Miller, 2010). Seed survival was considered the sum of lab-germinated and TZ-identified living seeds. We were unable to estimate germination or seed survival rates for *H. glabra* at Perenjori reserve because all seeds were either missing or failed to germinate in field and lab conditions, and thus, we used the estimates from Kunjin reserve instead.

2.1.4 | Environmental variables

We focused on three environmental factors which past studies have shown to explain extensive orthogonal variation in plant diversity patterns in this system (Dwyer et al., 2015). Notably, Dwyer et al. (2015) examined multiple environmental factors (including nutrients other than phosphorus) and found little evidence that any other environmental factor explained diversity patterns in this system more than the three selected for this study. The selected factors were overhead canopy cover (a proxy for shade), soil P concentrations and water availability. Canopy cover in this system varies very locally (<1 m), turn over in soil P is evident over 5–15 m, whereas moisture availability, as measured for the region (not including the watering treatments applied at the plot scale) varies along a regional gradient, with turnover occurring at the 100-km scale (Dwyer et al., 2015). Percent overhead tree canopy cover (%) was measured at each plot from hemispherical photographs taken above each plot. Phosphorus concentrations were measured as average (P) using three 5-cm deep topsoil samples collected from three locations across the ambient plot cluster and three from the watered plot cluster of each block. Soil samples were mixed within each plot cluster to measure soil phosphorus (mg/kg) via a standard Colwell extraction. Averages for watered and ambient plot clusters for each block were kept separate and those values were used, respectively, for the focal individuals from each appropriate plot cluster. We selected phosphorus rather than other nutrients as Dwyer et al. (2015) found it to have a significant effect on species richness and plant biomass, as well as an interaction with water availability in determining exotic species dominance in this system. Water availability was a categorical factor based on plot watering treatment and site climate, which was based on calculated moisture availability—the ratio of mean annual precipitation to mean annual evapotranspiration. Focal individuals were assigned one of four ranks for water availability based on which reserve and watering treatment their plot was in. Water availability categories were ordered from most xeric to most mesic. This order corresponded to Perenjori ambient, Perenjori watered, Bending ambient and Bending watered. Perenjori reserve had a relatively lower annual moisture availability index of 0.14 in 2014 (BOM 2016, station ID 008025), and Bending reserve had a relatively greater annual moisture availability index of 0.23 in 2014 (BOM 2016, station ID 010536).

2.1.5 | Model framework

We used a well-supported annual plant population model (Levine & HilleRisLambers, 2009), which describes the rate of change in the abundance of seeds of focal species' i in the seed bank from 1 year ($N_{i,t}$) to the next ($N_{i,t+1}$):

$$\frac{N_{i,t+1}}{N_{i,t}} = (1 - g_i) s_i + g_i F_{i,t} \quad (1)$$

where $F_{i,t}$ is the number of viable seeds produced per germinated individual, while g_i and s_i are the seed germination and seed survival rate, respectively. We defined $F_{i,t}$ as the focal species' intrinsic fecundity (measured as seed number) λ_i in the absence of competition. In the simplified case of focal species i interacting with only one neighbouring species j , $F_{i,t}$ is given by:

$$F_{i,t} = \lambda_i e^{-\alpha_{ii} g_i N_{i,t} - \alpha_{ij} g_j N_{j,t}} \quad (2)$$

where α_{ii} and α_{ij} are the per capita interaction strengths between species i and germinants of its conspecific and heterospecific neighbours, respectively.

2.1.6 | Including environmental variation

In order to explore how coexistence between species may be affected by different environmental conditions, we developed a novel modelling approach which explicitly accounts for the effect of environmental variation on intrinsic fitness and species interactions. In the population dynamics model described above, we allow intrinsic fitness (λ_i) and all interaction coefficients ($\alpha_{..}$'s defined as either α_{ii} or α_{ij}) to vary along an environmental gradient ξ : available phosphorus, tree canopy cover or available water. For each environmental gradient, intrinsic fitness and interaction coefficients each vary according to two species-specific terms: an intercept which determines an average for either intrinsic fitness or interaction strength, and the species response to the environmental gradient. In the case of intrinsic fitness λ_i , the average intrinsic fitness is defined as \bar{a}_i and the environmental response as \bar{b}_i :

$$\lambda_i = e^{\bar{a}_i + \bar{b}_i (\xi - \xi_i)^2} \quad (3)$$

Here, \bar{b}_i is applied to the squared difference between the local environmental value ξ and the environmental maximum or minimum ξ_i for species i . By squaring the term in the exponential, we allow intrinsic fitness to vary across the environmental gradient in a way that need not be monotonically increasing or monotonically decreasing. In other words, Equation 3 describes intrinsic fitness as a parabolic function which varies along values of an environmental gradient (ξ). ξ_i denotes the environmental value for which the parabola is at its highest or lowest point, depending on whether it opens upwards or downwards. Both ξ_i and the orientation of the parabola are determined by which best captures observed changes in a species' performance, according to our empirical data (see Supporting Information 2 for more details on how ξ_i was estimated).

Variation in the interaction coefficients is determined by $\bar{\alpha}$, the average interaction strength and δ , the response of that interaction to the environmental gradient. As with intrinsic fitness, these terms are specific to the species involved and the environmental gradient considered.

$$\alpha_{ii} = \bar{\alpha}_{ii} + \delta_{ii} (\xi - \xi_{ii})^2 \quad (4)$$

$$\alpha_{ij} = \bar{\alpha}_{ij} + \delta_{ij} (\xi - \xi_{ij})^2 \quad (5)$$

The difference between the local environmental value ξ and the environmental maximum or minimum ξ_{ij} for that interaction is also squared such that interaction coefficients can vary nonmonotonically with the environment and reflect facilitative (negative) or competitive (positive) effects, as is explained in depth in Mayfield and Stouffer (2017).

2.2 | Analysis

We conducted all analyses and model fitting using R (R Development Core Team, 2016). The best-fit parameter values for Equations 2–5 above were estimated separately for each focal species (for $i = 1, 2, 3$ and 4) by fitting a negative binomial generalised linear model using the `manyglm` function from the `mvabund` package (Wang, Naumann, Wright, & Warton, 2012). This allowed us to infer parameter estimates including intrinsic fitness (\bar{a}_i, \bar{b}_i), interaction coefficients ($\bar{\alpha}_{..}, \bar{\delta}_{..}$) and maximum or minimum abiotic values ($\xi_i, \xi_{ip}, \xi_{ij}$) for each focal species and interaction. A more thorough description of how we calculated these parameters from the coefficients obtained by the generalised linear model is available in Supporting Information 2.

Model fits were first performed without an environmental factor (henceforth referred to as our “baseline model”), where the environmental parameters for both intrinsic fitness and interaction coefficients, \bar{b}_i and δ , are set to 0 (Equations 3–5). Then, for each focal species, three separate environmental models were run, one for each of the three environmental factors: phosphorus, tree canopy cover and water availability. Because water availability is a categorical factor, we used the categories as ranked values, ranking by each reserve \times watering treatment in order of increasing water availability: Perenjori ambient = 0.1, Perenjori watered = 0.4, Bending ambient = 0.7 and Bending watered = 1.0. All environmental variables were then scaled to lie between 0 and 1 to improve convergence. Note that the optima for each focal species and each interaction (ξ , the highest or lowest point of the parabola describing intrinsic fitness or the interaction coefficients) may lie outside the range of measured environmental variation (e.g., if a focal species prefers higher phosphorus concentration than what is naturally available in these soils, see Supporting Information 3 and Supporting Information Figure 3.1.a and Figure 3.1.b), and hence beyond the 0–1 scale.

Separate pairwise interaction coefficients were estimated between all focal species i and each of the other three focal species,

with a fourth term encapsulating the remaining interactions with the rest of the community. The number of species in this fourth term varied. There were 0–15 nonfocal species found in each individual plot, with up to 52 nonfocal species in individual models. (We note that this means that each focal species interacted with up to 52 nonfocal species over all plots, not in any single plot). This fourth term was always very close to 0 and showed little variation over the three tested environmental gradients. We, therefore, felt it was appropriate not to include it in our analysis of changes in the processes contributing to coexistence. Interaction coefficients inferred by the regressions were not constrained to be competitive, and were instead allowed to vary between positive (competitive) and negative (facilitative) values as determined by the observed fecundities.

2.3 | Estimating niche overlap and fitness differences

We used the regression coefficients estimated by individual baseline and environmental models (Equations 2–5) to calculate the parameters of the annual plant population models (Equation 1). We examined changes in the processes driving coexistence by calculating ratios of inter- to intraspecific interaction coefficients analogous to recent expressions of niche overlap (Equation 11) and fitness differences (Equation 12), as described below. A detailed explanation of how we scaled the interaction coefficients, how these expressions were derived from our annual plant model and how they uphold the invasibility criterion are available in the Supplementary Methods (Supporting Information 4 and 5). We first rescale the interaction coefficients estimated by the regression to include intrinsic fecundity and germination rates. This step is not strictly necessary, but has the benefit of making comparisons between the interaction coefficients of species with different demographical parameters simpler (Hart, Freckleton, & Levine, 2018) and clarifies the link between our annual plant population model and the classic Lotka-Volterra model used by Chesson (2000b) to describe MCT. We define β_i as the loss rate of seeds in the seed bank, and η_i as the productivity, that is, the annual seed production per seed lost from the seed bank.

$$\beta_i = 1 - (1 - g_i) (s_i) \quad (6)$$

$$\eta_i = \frac{\lambda_i g_i}{\beta_i} \quad (7)$$

Note that η_i depends on intrinsic fitness (λ_i) and hence varies with the environment. We can then rescale the $\alpha_{..}$ by defining α' :

$$\alpha'_{ii} = \frac{g_i \alpha_{ii}}{\ln(\eta_i)} = \frac{g_i (\bar{\alpha}_{ii} + \delta_{ii} (\xi - \xi_{ii})^2)}{\ln(\eta_i)} \quad (8)$$

and

$$\alpha'_{ij} = \frac{g_j \alpha_{ij}}{\ln(\eta_i)} = \frac{g_j (\bar{\alpha}_{ij} + \delta_{ij} (\xi - \xi_{ij})^2)}{\ln(\eta_i)} \quad (9)$$

We replace the α 's in our annual plant population model (Equation 1) with the rescaled α' and simplify:

$$\frac{N_{i,t+1}}{N_{i,t}} = (1 - \beta_i) + \beta_i \eta_i e^{-\ln(\eta_i)(\alpha'_{ij} \delta_i N_{i,t} + \alpha'_{ji} \delta_j N_{j,t})} \quad (10)$$

The α' now has an analogous effect on plant fitness as the interaction coefficients in Chesson's original Lotka-Volterra model (see Supporting Information 4 for more detail). This step is similar to the approach used in Appendix A of Godoy & Levine (2014).

To account for the presence of facilitative interactions in our system, we modified Chesson's (2000b) and Chesson and Kuang's (2008) expressions for niche overlap, ρ and fitness differences, $\frac{k_j}{k_i}$, in a way in which was both meaningful to our annual plant model and allowed for both competitive and facilitative interactions (i.e., values of $\alpha' > 0$ and < 0):

$$\rho \approx \frac{e^{\alpha'_{ij}} e^{\alpha'_{ji}}}{e^{\alpha'_{ii}} e^{\alpha'_{jj}}} \quad (11)$$

$$\frac{k_j}{k_i} \approx \frac{e^{\alpha'_{ij}} e^{\alpha'_{ji}}}{e^{\alpha'_{ii}} e^{\alpha'_{jj}}} \quad (12)$$

Here, the α' corresponds to α 's estimated by the regression which have then been rescaled. Note that for Equations 11 and 12 above, the ratios of relative interaction strengths remain similar to the expressions used in Chesson (2000b) and Chesson and Kuang (2008). Our definition of niche overlap, therefore, reflects the ratio of intra- to interspecific competition, such that ρ tends towards 0 when species i and j limit themselves more than they limit each other. Our definition of fitness differences is a ratio of how sensitive species i is to interactions over how sensitive species j is. Both measures of niche overlap and fitness differences do, however, behave somewhat differently to the measures defined by Chesson. Notably, the exponential treatment of alpha terms in Equations 11 and 12 means that both of our niche overlap and fitness difference measures are bound between 0 and $+\infty$, and that stable coexistence between a pair of species can no longer be predicted simply by comparing these values. Identifying exactly how to convert these niche overlap and fitness difference values to coexistence space will require the development of a novel

framework that is beyond the goals of this study. In this study, we focus on determining whether the environment has impacts on niche overlap and fitness differences in ways that may drive variation in coexistence outcomes. This goal is compatible with our approach as explained above.

3 | RESULTS

3.1 | Environmental gradients

In order to determine which environmental factors were important for the outcomes of species interactions, we compared the model fits for fecundity (Equations 2–5) of each focal species using a log-likelihood test between each environmental model formulation (phosphorus, canopy cover and water availability) and the baseline model (Table 1). The addition of tree canopy cover to the fecundity model provided a significant improvement to model fit for *W. acuminata*, *T. cyanopetala* and *H. glabra*, and the addition of water availability provided a significant improvement in model fit for *W. acuminata*, *T. cyanopetala* and *A. calendula*. Adding soil phosphorus only significantly improved model fit for *H. glabra*.

We observed variation in both intrinsic fitness and species interactions across all three environmental gradients. The extent of this variation was highly specific to both the identity of the species involved and the environmental gradient in question. Figure 1 shows a range of ways in which interactions within (Figure 1a) and between (Figure 1b and c) species were observed to switch between facilitative (negative) and competitive (positive) values. Outcomes were so conditional on details that a summary of results was not insightful, but comprehensive outcomes are provided in the Supporting Information 3.

Over two-thirds of interactions had their minima or maxima within the observed range of the relevant gradient, as illustrated by the interaction between *H. glabra* and *A. calendula* (Figure 1b). Here, *A. calendula* has the strongest competitive effect at intermediate values of tree canopy cover, corresponding to an environment with heterogeneous shade (specifically, plots which were half-shaded and half-open). Only six relationships (out of 48) were found to be entirely competitive along any environmental axis, such as the effect of *W. acuminata* on *H. glabra* under different watering levels (Figure 1c).

TABLE 1 Log-likelihood-derived model fits (LL) for each focal species, with *df* indicating the number of degrees of freedom, *LL* as the log likelihood and *p* the reported *p*-value from a likelihood ratio test between each environmental model form and the baseline model

Model type	Environ. variable	<i>Trachymene cyanopetala</i>			<i>Waitzia acuminata</i>			<i>Arctotheca calendula</i>			<i>Hypochaeris glabra</i>		
		<i>df</i>	LL	<i>p</i>	<i>df</i>	LL	<i>p</i>	<i>df</i>	LL	<i>p</i>	<i>df</i>	LL	<i>p</i>
Baseline	NA	6	-1064		6	-1715		6	-1158		6	-1179	
Environ.	Canopy	18	-1051	0.048 ^a	18	-1697	0.001 ^a	18	-1149	0.102	18	-1163	0.007 ^a
	P	18	-1054	0.157	18	-1711	0.683	18	-1151	0.365	18	-1167	0.027 ^a
	Water	18	-1045	0.002 ^a	18	-1705	0.047 ^a	18	-1146	0.026 ^a	18	-1174	0.645

^aDenotes models which are a significant improvement over the baseline.

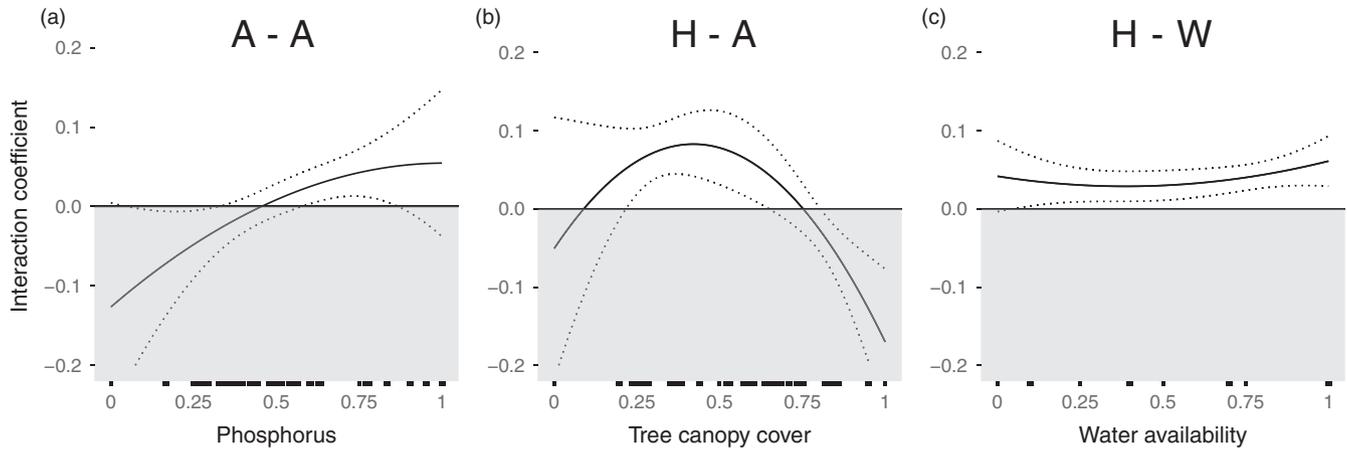


FIGURE 1 Estimates of interaction strengths (α_{ij}) between different focal species along gradients of phosphorus, tree canopy cover and water availability. (a) Intraspecific interactions between individuals of *A. calendula*, (b) the effect of *A. calendula* on *H. glabra* and (c) the effect of *W. acuminata* on *H. glabra*. Any value over 0 (in white) indicates competition, and any value below 0 (in grey) indicates facilitation. Lines represent model fits and dotted lines give the simulated 95% confidence intervals. The darker ticks along the x-axis indicate actual observations of fecundity collected along each environmental gradient. Model tails are outside of observed data space, which is why confidence intervals at the edges are wider

Species interactions differed in the strength, direction and shape of their relationship independently along multiple environmental gradients. As such, no general pattern was evident in the variability in interaction outcomes along each environmental gradient for any focal species (see Supporting Information 3, Supporting Information Figures 3.1–3.4 for a breakdown of all intrinsic fitness and interaction coefficient values by focal species and environmental gradients).

3.2 | Facilitation

Most outcomes of intra- and interspecific species interactions were competitive for all species pairs and across all environmental gradients (Figure 2). That said, facilitation was also reasonably common and found across all focal species and environmental gradients (Figure 2). There were no discernible trends in when interaction outcomes were facilitative or competitive. Many competitive and facilitative interactions were similarly strong (Figure 2), but very strong interactions were more likely to be competitive than facilitative (as seen in the long positive tails of the boxplots in Figure 2). Both intra- and interspecific interactions took on facilitative values in equal measures. Though less common than competitive interaction outcomes, facilitation was common enough and ubiquitous enough across all species pairs and environmental conditions that it limited our ability to predict coexistence between species pairs using the modern coexistence framework and associated annual plant models, which mathematically requires all interactions to be competitive to work. In the rare cases where coexistence could be predicted, we found very little evidence of coexistence and that, as expected, coexistence outcomes between species pairs varied along all tested environmental gradients (see Supporting Information 6, and Supporting Information Figure 6.1 & 6.2).

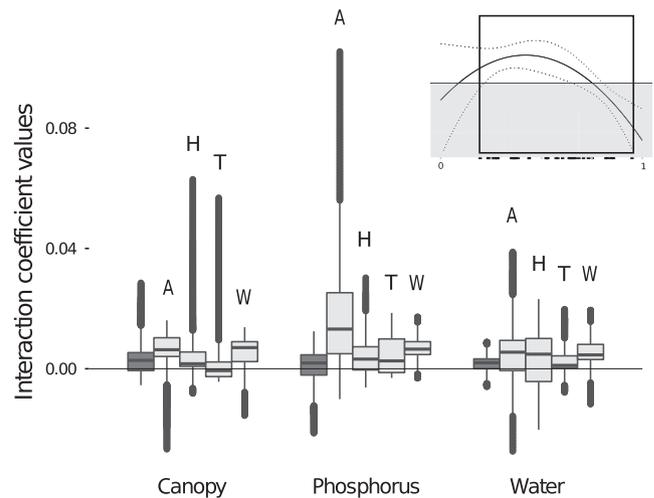


FIGURE 2 Distributions of the strength of interaction coefficients according to interaction type, focal species and environmental gradient. The three dark grey boxplots show the distribution of intraspecific interactions α_{ii} . The light grey boxplots show the distribution of interspecific interactions α_{ij} , where j is *A. calendula* (A), *H. glabra* (H), *T. cyanopetala* (T) and *W. acuminata* (W), respectively. Only estimates taken within the range of observed fecundities (actual data) along each environmental gradient were included (i.e., the range of estimates within the black outline in the upper right corner, corresponding to the range of dark ticks along the x-axis in Figure 1). We restricted this range to avoid including estimates of interaction strengths where the confidence intervals were very large due to a lack of data

3.3 | Niche overlap and fitness differences

Using the modified expressions defined in Equations 11 and 12, we were able to explore how niche overlap and fitness differences varied between species pairs and along our three environmental

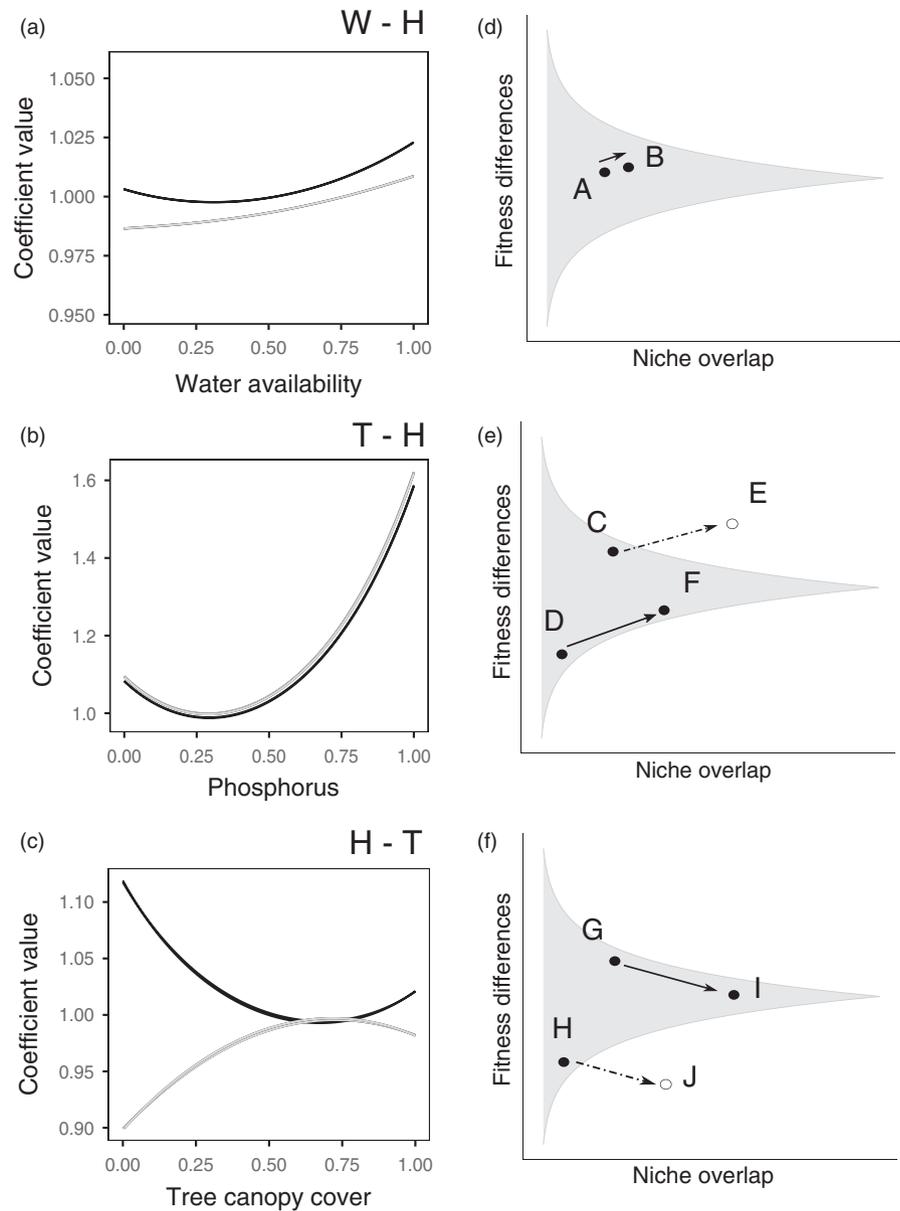


FIGURE 3 Variation in niche overlap and fitness differences along different environmental gradients (panels a, b and c, in the first column), and a conceptual illustration of the resulting effect on coexistence (panels e, d and f, in the second column). The first column shows niche overlap (ρ , Equation 11) in black, and fitness differences ($\frac{K_i}{K_j}$, Equation 12) in grey for: a and d) *W. acuminata* and *H. glabra* along a gradient of water availability, b and e) *T. cyanopetala* and *H. glabra* along a phosphorus gradient, and c and f) *H. glabra* and *T. cyanopetala* along a gradient of tree canopy cover. The second column conceptualises how variation in niche overlap (on the x-axis) and fitness differences (on the y-axis) may affect coexistence between a species pair. The grey-shaded area represents the region of conceptual coexistence space where a species pair is predicted to coexist. Each dot represents a species pair under a given set of environmental conditions, shaded dots show species which can coexist and empty dots show species which cannot. Arrows show how a species pair may move in conceptual coexistence space as environmental conditions change

gradients despite widespread facilitation. As with species interactions, how both measures varied across environmental gradients was highly dependent on the species and environmental factor considered, with no generalisable patterns evident (see the Supporting Information Figures 7.1–7.4 for a full breakdown of how niche overlap and fitness differences varied between different species pairs and across environmental gradients). These relationships, however, typically fell within one of three categories, as illustrated by the example results shown in Figure 3: no change in either relationship (3a), coordinated change in both (3b) or divergent changes across the environment (3c). Note that panels a, b and c are results inferred from our data, whereas panels d, e and f are speculative and only serve to illustrate how coexistence might be affected by observed types of variation in niche and fitness differences.

4 | DISCUSSION

Using our modelling approach in an annual plant system in SW Western Australia, we show that the outcomes of species interactions are incredibly variable across three distinct environmental variables that have previously been identified as structuring diversity in this system: soil phosphorus, shade and water availability (Dwyer et al., 2015). Observed variation in interaction outcomes translated to substantial changes in niche overlap and fitness differences across the studied communities and for all four focal species assessed. Variation in niche overlap and fitness differences, however, were not clearly generalisable across any of the environmental gradients measured. This suggests that variation in the environment is not the sole mechanism involved in structuring coexistence, and that other unmeasured factors may be more important (such as resource limitation).

In examining the effects of environmental heterogeneity on interaction outcomes, we also found that facilitation was very common and that species interactions frequently switched between competitive and facilitative across our study system. This finding highlights the limitations of current competition-based annual plant fitness models for estimating total population coexistence outcomes across variable natural communities.

4.1 | The prevalence of facilitation

Facilitation was more widespread than expected in this study, though we could not draw any general patterns regarding when facilitation occurred for our four annual plant species. Though competitive interactions were more common and stronger (on average), than facilitative interactions, both intraspecific and interspecific facilitative interactions were found for all species pairs across all environmental gradients. This suggests that positive- and negative-frequency dependence affects coexistence in this system. The prominence of plot level intra- and interspecific facilitation was consistent with a growing literature on the prevalence of facilitative interactions in natural communities (Callaway, 2007) and highlights the need for novel approaches to modelling coexistence in systems where local facilitation is common (Bruno et al., 2003).

Evidence of facilitation between plants has been recognised for many decades (Rathcke, 1983), but was largely neglected in favour of competition until Bertness and Callaway's (1994) review established it as an important force in structuring plant communities. Since then, a majority of theoretical work suggests that facilitative interactions should increase with abiotic stress, though empirical evidence is mixed (Brooker et al., 2008; Callaway & Lawrence, 1997; He et al., 2013; Kawai & Tokeshi, 2007; Maestre, Valladares, & Reynolds, 2006; Maestre et al., 2005, 2009). Additionally, several recent studies have discussed the ramifications of common facilitation to coexistence dynamics and models. Bruno et al. (2003) suggested including facilitative interactions into multiple ecological concepts, including expansion of the realised niche concept, positive density dependence at high population densities and the diversity-invasibility relationship. Fukami et al. (2016) and Ke and Letten (2018) link priority effects, which can be driven by facilitation, to niche overlap and MCT. Schreiber, Yamamichi, and Strauss (2017) modelled the effects of positive frequency dependence on plant fitness and highlighted the need to account for such interactions in coexistence theory. Despite these discussions, no formal attempts have been made to include facilitation in theoretical coexistence frameworks or models (but see Gross et al., 2015).

Given the lack of coexistence models that incorporate facilitation, we explore our results in reference to more general expectations for how facilitation impacts on coexistence. For instance, it is well known that facilitation can negate or minimise the effects of intra- and interspecific competition, which are integral to the niche and fitness differences that underlay coexistence. Though plants may still compete, the benefits of having neighbours can outweigh the costs. For example, neighbouring plants might buffer a focal

individual from abiotic stresses by providing a micro-climatic refuge (Choler, Michalet, & Callaway, 2001; Michalet et al., 2006), say through moisture retention (Holmgren, Scheffer, & Huston, 1997; Schöb, Armas, Guler, Prieto, & Pugnaire, 2013). Such buffering can act to reduce niche overlap and promote coexistence. Though we did not test this directly, such a buffering effect seems a likely possibility in this system given its harsh semi-arid climate and strong evidence for the structuring importance of shade and moisture availability in these plant communities (Dwyer et al., 2015; Wainwright, Dwyer, Hobbs, & Mayfield, 2016).

Intraspecific facilitation, which we also found evidence for, occurs when a species promotes its own success. This concept is central to our understanding of coexistence dynamics but is rarely acknowledged as a form of facilitation. Classic replacement-series competition experiments (Goldberg & Barton, 1992; Goldberg & Werner, 1983), for example, assume that below a certain density threshold, a species will perform better when surrounded by conspecifics as opposed to heterospecific individuals. Above this threshold, population densities become too high and negative density-dependent processes act to suppress intraspecific success and allow heterospecific competitors to gain an advantage. There are instances from the literature, however, where there is little evidence of this threshold (e.g., Wainwright et al., 2016). Though certain processes must limit the intraspecific growth of such species (e.g., predation or environmental filtering) such that they do not entirely dominate the system they inhabit, strong intraspecific facilitation may operationally exist without detectable control at the plot scales we use to test the MCT. Given that in our system there is little evidence of runaway domination of any of our focal species across site scales in these woodlands (personal observation; Dwyer et al., 2015), this scaling effect is also a likely factor explaining the amount of facilitation observed. We, thus, expect such facilitation at the plot scale to promote local coexistence.

4.2 | Niche overlap and fitness differences vary in heterogeneous environments

Our novel modelling framework provides a simple way of evaluating the effect of environmental conditions on the individual fecundity outcomes of species interactions within our existing competitive framework for annual plant coexistence. In highly competitive systems, our approach offers a simple way of incorporating environmental heterogeneity into models of coexistence. In systems such as ours, which have extensive facilitation, this framework allows for species interactions to vary between competitive and facilitative values and for niche overlap and fitness differences to be calculated. In such cases, however, it is not possible to directly translate niche overlap and fitness differences to specific predictions of coexistence using MCT, as explained above.

Using our novel framework, we found strong evidence that the strength and outcome of species interactions fluctuated extensively along environmental gradients, which in turn led to extensive variation in niche overlap and fitness differences. The effect of

environmental heterogeneity was not, however, clearly generalisable across species, with details varying by species pair. Variation in interaction strength along environmental gradients have been empirically demonstrated in this (Mayfield & Stouffer, 2017; Wainwright et al., 2016) and other plant systems (Choler et al., 2001; Lanuza et al., 2018; Maestre et al., 2005; Mod, Le Roux, & Luoto, 2014; Soliveres et al., 2014). Given that fluctuations in interaction strength, niche and fitness differences and coexistence outcomes were observed along multiple environmental gradients, it is likely that all three environmental factors (shade, phosphorus and water) are involved in structuring these wildflower communities, a finding consistent with observational studies of diversity in this system (Dwyer et al., 2015).

In the rare instances where all interactions for one of our species pairs were competitive under several values observed for one of our tested environmental factors, we were able to apply MCT. In these cases, there was little evidence of coexistence between species, but a lot of evidence that species pairs moved extensively through coexistence space (see Supporting Information 6 on “Predicting coexistence”). When taking facilitation into account, we were also able to show that niche and fitness differences fluctuated significantly across gradients of all three tested environmental factors. What was not evident was any systematic structure to this variance. These results suggest that it will take many more species pairs to identify if such generalisations exist. In the future, it would be interesting to test if a species’ functional traits drive particular interaction outcomes associated with these environmental factors.

4.3 | Why is variation in coexistence important?

In the current literature, many annual plant-based coexistence studies focus on predicting the probability of coexistence outcomes. Our findings suggest that the outcome of such studies will be highly specific to the set of conditions under which interactions were measured. We argue that a broader view of coexistence which explores how much coexistence outcomes vary across environmental conditions paves the way towards a more holistic understanding of species diversity (Hart, Usinowicz, & Levine, 2017).

Given that MCT does not account for facilitative interactions, we defined new measures analogous to niche overlap and fitness differences which allowed for their inclusion in our framework. In keeping with their Chessonian equivalents, our measure of niche overlap reflects how much a species limits another over how much it limits itself, while our measure of fitness differences reflects how sensitive it is to these interactions. Though our new measures do not allow us to predict stable coexistence between two species, they do allow us to explore how niche overlap and fitness differences vary under different environmental conditions, even when facilitation occurs. Functionally, this enables us to measure how sensitive coexistence is to different environmental factors. Furthermore, variation in environmental factors operate at different spatial scales (see methods), allowing us to explore variation in coexistence across the small scales over which plant–plant interactions take place as well as across the regional scales over which

these species are found to co-occur. For example, niche overlap and fitness differences between *W. acuminata* and *H. glabra* varied little according to water availability (Figure 3a), such that the outcomes of coexistence between this species pair are expected to vary little. In this scenario, coexistence (or the absence of it) can be said to be “generally stable”—in other words this pair of species should consistently coexist (or not) over a range of water availabilities. This situation can arise when a certain resource varies but is never limited, such that it does not meaningfully affect the outcome of interactions between two species. Given that water availability varies across a wide regional gradient, any variation in coexistence between *W. acuminata* and *H. glabra* is instead likely to be driven by local-scale processes such as soil phosphorus or shade availability. In other cases, coexistence varies but only within the boundaries of the abiotic space that corresponds to resource limitation. In the case of *H. glabra* and *T. cyanopetala*, for example, niche overlap and fitness differences stay relatively constant when tree canopy cover lies between the scaled values of 0.5 and 0.75 (Figure 3c). Outside of this range, both measures vary extensively with tree canopy cover. These regions likely reflect instances where shade becomes limiting in some way. Coexistence is, therefore, likely promoted in some ranges of the abiotic space (for instance when shade is not limiting) and hindered in others (when shade is limiting).

Building on this research, a next step would involve moving beyond the relationship between coexistence and variability of resources, and towards testing how coexistence explicitly relates to limited resources. Specifically, we could ask whether clear associations can be detected between the degree of resource limitation and variability in coexistence outcomes. Furthermore, gaining an understanding of which factors cause coexistence to vary in heterogeneous environments is key to scaling theoretical expectations of coexistence dynamics to population and community scales.

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AUTHORS' CONTRIBUTIONS

M.M.M. and D.B.S. conceived the ideas and designed the methodology and are joint senior authors on this manuscript; M.M.M. and H.R.L. collected the data; M.D.B. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.q41m844> (Bimler et al., 2018).

ORCID

Malyon D. Bimler  <http://orcid.org/0000-0003-0059-2360>

Daniel B. Stouffer  <http://orcid.org/0000-0001-9436-9674>

Hao Ran Lai  <http://orcid.org/0000-0001-6871-0146>

Margaret M. Mayfield  <http://orcid.org/0000-0002-5101-6542>

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