Title: Distinct responses of niche and fitness differences to water availability underlie variable coexistence outcomes in semi-arid annual plant communities

Running title: Water availability and coexistence outcomes

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Abstract

1. Climate change is predicted to have profound consequences for multispecies coexistence, and thus, patterns of biological diversity. These consequences will be mediated by direct and indirect impacts of environmental change on species' vital rates and interactions. While the impacts of environmental change on individual species has received much attention to date, the consequences for coexistence mediated by changes in the strength and direction of species interactions are not as well understood.

2. To investigate how coexistence dynamics may be sensitive to environmental change, we conducted a field experiment in a diverse semi-arid annual plant system. We imposed a water manipulation treatment in two sites that vary in aridity and associated rainfall. Focusing on four common annual plant species in these sites, we quantified the fecundity (seed production) of individuals in response to a gradient of intra- and inter-specific competitor densities and aridity. We then used these fecundities to parameterize an annual plant population model and examine the influence of aridity and species identity on resultant coexistence dynamics (as a function of stabilizing niche differences and fitness inequalities).

3. While the responses of some vital rates and competitive impacts to watering varied somewhat predictably across sites, coexistence metrics encapsulating changes in these vital rates and interaction strengths did not. Fitness inequalities among our focal species were driven largely by differences in sensitivity to competition, which were almost always much greater than the magnitude of stabilizing niche differences. These findings were surprising given observational evidence suggesting that these species do coexist at local scales in these natural communities.

4. *Synthesis* Our study is one of the first to explicitly consider the influence of environmental variation on the individual components of coexistence outcomes. We show that environmental change has the ability to influence coexistence not only through direct pathways (i.e. vital rates), but indirect pathways as well (i.e. species interactions). Despite the consistency of many of the responses of these individual components to environmental variation, their combined influence on predictions of both current and future coexistence remains unclear.

Second Version of Abstract (Mandarin Chinese)

摘要

1、气候变化对物种的共存（coexistence）和多元化的影响，取决于环境变化如何操控物种的生产力和互动。虽然目前已有较多报告针对气候变化对单一物种的影响，我们仍对气候变化对物种之间的互动了解不深。

2、我们在西澳半干旱一年生植物系统内操纵土壤的水份，以及各植物周遭的同、异物种密度，以进一步了解环境变化如何影响物种之间的互动。此实验涵括两处不同干旱度和年雨量的林地，并涉及四个普遍的植物物种。各物种在不同的干旱度下与同、异物种邻居竞争后，其生产力（种子产量）被用于参数化种群模型，最终预测同、异物种之间两个重要的共存机制：生态位差异（stabilising niche differences）和适应度差异（fitness inequalities）。

3、实验结果显示，各物种的生产力通常随着水份增长，但它们之间的竞争度上下浮动并难以预测。在多数实验环境下，模型预测生态位差异小于适应度差异，代表物种难以互相共存，即使本篇作者经常观察到这些物种在小范围内的重叠分布。

4、*总结*：环境变化不只直接影响各物种的生产力，也能间接改变物种之间的竞争度。物种的生产力和竞争度能在环境变化下作出多元化的反应，导致其共存与否难以预测。

Keywords: Annual plants, climate change, coexistence, competition, fitness differences, niche differences, stabilization

Introduction

Climate change is anticipated to have profound consequences for biological diversity (Bellard et al. 2012). Indeed, recent climate change has already affected the distribution of many species, causing both range expansions and range contractions (Parmesan & Yohe 2003; Root et al. 2003) that are often attributed to the direct effects of climate change on physiological tolerances. Climate, however, may also influence the strength of interactions among persisting species. Since community composition is driven by the environment as well as by species interactions, effects of climate change on species interactions are also likely to influence compositional changes. Unfortunately, the simultaneous impacts of climate change on multi-species interaction strengths and vital rates are far less understood than impacts on individual species (Tylianakis et al. 2008). Indeed, our inability to anticipate climate change impacts on species interactions is a commonly identified limitation in studies of individual species (Sexton et al. 2009; Gilman et al. 2010).

Our understanding of how climate change may affect coexistence dynamics, and potentially biodiversity, is limited for a number of reasons. Few studies quantify how climate change simultaneously alters the strength of two key components of coexistence: species interactions as well as intrinsic differences in species performance in natural communities (Alexander et al. 2016). Although many studies focus on the potential impacts of climate change on community and ecosystem-level properties (Knapp et al. 2002; Shaw et al. 2002; Ainsworth & Long 2005), they often report responses that result in part from changes in species interactions, but are not disentangled from direct effects of climate change on species' vital rates. By contrast, other studies focus on individual species' responses to climate change (e.g., Llorens et al. 2004; Morin et al. 2010; Valencia et al. 2016), and do not address how climate change might alter interaction-driven niche differences. While some empirical studies have examined how interactions in plant communities may be altered by climatic factors (e.g. Dormann et al. 2004; Suttle et al. 2007), few have explicitly examined the implications for coexistence in naturally occurring communities (but see Bimler et al. *in press*; Matias et al. 2018), which requires study of potential changes to both niche and fitness differences (Siepielski & McPeek 2010).

Fortunately, modern coexistence theory (Chesson 2000) provides a useful framework for predicting potential changes in the diversity of plant communities that might arise through the complex interplay of changes to demographic rates and competitive interactions (HilleRisLambers et al. 2012; Fig. 1). Environmental change can affect coexistence in plant communities by simultaneously altering the determinants of both fitness inequalities and stabilizing niche differences among constituent species (Adler et al. 2012; Alexander et al. 2015 & 2016). Addressing how environmental variation affects vital rates influencing fitness inequalities as well as the impacts of interactions on competing species that underlie both fitness and niche differences may reveal whether altered coexistence dynamics are likely, and if so, whether they are generalizable according to the nature of local climate changes or the identities or attributes of competing species (Fig. 1).

To investigate how environmental change affects coexistence dynamics in novel communities (non-historical species combinations), we conducted a field experiment in a diverse semi-arid annual plant system. Specifically, we imposed a water addition experiment in two sites that vary in aridity and associated rainfall. We focused on four common annual plant species and quantified seed production of individuals of these species in density-manipulated plots, so that they experienced a gradient of intra- and inter-specific densities of (potentially) competing neighbours. We used maximum likelihood models to quantify demographic parameters (e.g., no-competition fecundity λ: Fig. 1) and interaction strengths across all watering treatment x site combinations (e.g. intra- and inter-specific interactions α_{ii} and α_{ij} – Fig. 1), and integrated these estimates into pairwise measures of niche and fitness differences (which together determine the potential for coexistence between species pairs – Fig. 1). In total, these results allowed us to determine how water availability influences coexistence dynamics of these focal species and provide insights into whether or not changes to coexistence dynamics induced by environmental variation are generalizable. To achieve these goals, we addressed the following questions:

1) How does variation in water availability alter:
    a. fitness (fecundity - λ) in the absence of competition and
    b. the strength of inter- and intra-specific interactions between species (α_{ii} and α_{ij})?
2) How do changes to demographic rates (i.e. seed production) and interactions (α_{ii} and α_{ij}) induced by environmental change combine to alter fitness differences and niche differences?
3) Does variation in niche and fitness differences with environmental change lead to consistent changes in coexistence dynamics?
4) Are the impacts of environmental change on coexistence consistent by species attributes (e.g. native vs. exotic) or the magnitude of impacts on individual components of coexistence?

Predicted effects of water availability on coexistence in semi-arid plant communities have often been based on the stress gradient hypothesis, which postulates that competitive exclusion is more likely under high resource conditions while facilitation may be more common under environmental stress (e.g., He et al. 2013). However, recent empirical work has demonstrated that relationships between resource availability and coexistence outcomes may not be straightforward. For example, Bimler et al. (*in press*) and Hart et al. (2018) suggest that current coexistence models may not be appropriate in systems where competition intensity and the density of competing individuals are not strongly correlated. Furthermore, Matias et al. (2018) found that among annual plants, experimental drought reduced fitness inequalities, but contrary to expectations, ultimately reduced coexistence relative to control conditions due to increased niche overlap.

We hypothesized that water addition would increase fecundity in the absence of competition relative to ambient conditions. In addition to fecundity, we expected that water addition would release plant communities from an important abiotic resource limitation, and thus, competitive interactions would strengthen relative to ambient conditions. However, the effects of water addition on coexistence are driven by relative changes to vital rates and interaction strengths between species pairs (Fig. 1) that combine to produce stabilizing niche differences and relative fitness differences. Therefore, while we hypothesized water addition would potentially impact individual parameters in predictable ways, we had no *a priori* expectations of how the relative magnitudes of these values, and thus coexistence predictions, would shift among each species pair with water addition.

Materials and methods

Study system

Our study took place in the York gum-jam (*Eucalyptus loxophleba* Benth. and *Acacia acuminata* Benth.) woodland understories in West Perenjori Nature Reserve 29°28'01.3"S 116°12'21.6"E) and Bendering Nature Reserve (32°23'06.1"S 118°22'42.4"E) in southwest Western Australia (Fig. 2). Southwest Western Australia experiences a semi-arid climate typical of Mediterranean-type ecosystems, with mild winters and prolonged summer drought. Like other semi-arid regions, the climate of southwest Western Australia is predicted to become more arid as climate change progresses, with increasing mean annual temperatures and decreasing mean annual precipitation (Suppiah et al. 2007), though heavier individual rainfall events are predicted to become more common (Hope et al. 2015). Previous research by Dwyer et al. (2015) identified regional-scale moisture availability to be one of the strongest drivers of compositional change in annual plant communities throughout the York gum-jam woodland range.

York gum-jam woodlands constitute part of the Southwest Floristic Region, a global biodiversity hotspot (Myers et al. 2000). York-gum woodlands are an open woodland type with sparse canopy cover dominated by *E. loxophleba* and *A. acuminata*. Understories are composed of dense annual forb communities active during the winter-spring growing season (approximately April to November) interspersed with sparse shrubs and perennial grasses (Prober et al. 2011; Dwyer et al. 2015). Soils in this system are highly weathered and historically nutrient-poor, particularly in plant-available phosphorus (Lambers et al. 2008). York gum-jam woodlands have largely been cleared and replaced with agriculture, with an estimated 3% of original extent remaining (Yates et al. 2000). Remnant woodlands have been affected to varying degrees by several aspects of land-use intensification. In particular, many remnants have experienced eutrophication resulting from phosphate fertilizer drift, which is often accompanied by exotic annual grass and forb invasions (Prober and Wiehl 2011; Dwyer et al. 2015). Still, though remnants are often invaded, many retain high native diversity and are composed of species-rich novel communities of native and exotic annuals that co-occur over local spatial scales (< 0.09 m^2; Lai et al. 2015).

West Perenjori Nature Reserve and Bendering Reserve are separated by approximately 381 km and span a regional aridity gradient with West Perenjori Reserve the more xeric (northern) site. The winter-spring growing season precipitation (and associated annual plant phenology) occurs about one month in advance at West Perenjori compared to Bendering; all timing of data collection reflects this staggered phenology. Mean annual maximum temperature for West Perenjori Reserve is 28.2ºC and mean annual precipitation is 285.9 mm (BOM 2018 station IDs 010536 and 010513, 20-year means). Mean annual maximum temperature at Bendering Reserve is 23.8ºC and mean annual rainfall is 303.3 mm. On average it rains (≥1 mm rain) on 42.2 days per year in West Perenjori Reserve and 59.4 days in Bendering (BOM 2018). Both reserves have a high overlap in annual species composition and are dominated by several of the same common species (Dwyer et al. 2015). We chose to examine the responses of four of these common species in our field experiment: native forbs *Trachymene cyanopetala* (F. Muell.) Benth. (Araliaceae) and *Waitzia acuminata* Steetz (Asteraceae), and exotic forbs *Arctotheca calendula* (L.) Levyns (Asteraceae) and *Hypochaeris glabra* L. (Asteraceae) (Supplementary Fig. 1).

Experimental design

Our experiment was designed to investigate the nature of a) inter- and intraspecific competition and b) moisture availability on coexistence potential among our four representative focal species. The composition of competitor species around each focal plant was manipulated by hand weeding within a 50 cm x 50 cm area containing the focal plants early in the 2014 winter growing season (July at West Perenjori and August at Bendering). Moisture availability was manipulated by manually applying a water addition treatment at both reserves, which enabled us to examine species interaction outcomes across reserve-treatment combinations. The four levels (added water plus associated growing season rainfall) of this variable, in order of increasing regional aridity were: Bendering-watered (178.4 mm rainfall), Bendering-control (96.4 mm rainfall), West Perenjori-watered (211.6 mm rainfall), and West Perenjori-control (117.6 mm rainfall). In the year of our study, W. Perenjori received higher winter rainfall than Bendering leading to total realized precipitation (water addition plus ambient rainfall) to be higher at W. Perenjori (Table 1; Supplementary Table 1).

Composition treatment

To start our experiment, we located 50 blocks across the two reserves (West Perenjori n=24, Bendering n=26), each containing at least two of the four focal species (Supplementary Table 2). Blocks were generally less than 15 m^2 in area, which corresponds to soil nutrient turnover rates identified in previous studies (Dwyer et al. 2015). Each block consisted of ten 50 x 50 cm plots, corresponding to one replicate of each possible composition x water treatment combination (Supplementary Table 2; composition treatments explained below). Each 50 cm x 50 cm plot was established to contain one or two focal individuals of two focal species: one individual per 25 x 25 cm quadrant (Fig. 2). In total, data from 916 focal individuals from 298 plots spread across a total of 46 blocks were used for analysis.

To generate a range of densities across which to estimate interaction coefficients, each 50 x 50 cm plot (i.e. all four constituent quadrants) was thinned by hand according to one of five species compositions: 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 unweeded (unmanipulated natural species composition). These treatments reflect our initial interest in examining how interactions depend on native / exotic status; however, we found very little evidence that they did, and thus combined data for analyses. The majority of thinning took place very early in the growing season (once all germinated individuals were identifiable) using small scissors or by hand to minimize effects of root decomposition on remaining plants. Plants were thinned at the soil surface to avoid soil disturbance. Prescribed species compositions were maintained by minimal maintenance weeding at regular intervals throughout the growing season. Resulting interaction neighbourhoods experienced by focal individual ranged in density from one to 328 individuals (mean: 29.41, SE: 0.03, median: 20 individuals).

Watering treatment

To examine how species interactions varied with local moisture availability, the compositional treatments were replicated twice per block, with one subset watered and the other left under ambient conditions (controls). Plots were clustered within blocks according to these watering treatments to prevent runoff into non-watered plots; we henceforth refer to these clusters as ‘sub-blocks’. Water was applied by hand with watering cans.

In total, watered plots at Bendering received an extra 20.5 L of water each (185% ambient rainfall) and watered plots at Perenjori received 23.5 L of rain each (180% ambient rainfall) during the growing season (Table 1; for detailed watering schedule and volumes, see Supplementary Table 1. Each watered plot experienced four watering events throughout the growing season spaced approximately one to three weeks apart. Volume of water addition per plot per watering event was calculated as the volume of rainfall that had occurred in ambient plots in that reserve since the previous watering event (or since the experiment’s implementation in the case of the first watering event). Where the required volume could not be added during one rainfall period, its volume was added to the total volume of the next period. After September 11, 2014, some soils had reached field water capacity, and thus water additions were capped at 1 L per plot.

Data collection

To assess any underlying environmental differences among blocks and plots, we measured percent overhead tree canopy cover at the plot scale, and soil Colwell P (mg/kg) at the sub-block scale. We then analysed pre-treatment differences in these two variables using mixed effects models, with a random effect of block in both models to account for the spatial aggregation of plots.

To quantify the competitive environment of each focal individual, we recorded the identity and abundance of all individuals in the interaction neighbourhood of each focal individual (25 cm x 25 cm quadrant) once compositional treatments had been applied and after all individuals had germinated (24 July 2014 at West Perenjori, 10 August 2014 at Bendering). This interaction neighbourhood size was chosen based on previous research in this system (for example, mean height of tallest individual in an interaction neighbourhood: 12.97 cm; Dwyer et al. unpublished data). Preliminary analyses indicated that origin (native vs exotic) of competitors was a poor predictor of interaction outcomes. Furthermore, pooling species responses and impacts by origin prevented estimation of certain parameters necessary for coexistence calculations (α_{ji}). Therefore, interaction coefficients were calculated among pairs of focal species, and competitive impacts of non-focal species were pooled for all analyses (described in further detail below).

To measure each focal individual's performance in response to various competitor and watering treatments, we counted the number of inflorescences and seeds produced by all focal individuals, including those that did not reproduce. For the two exotic species *A. calendula* and *H. glabra*, many seeds dispersed by wind prior to collection, so we substituted inflorescence count as a response variable. The number of seeds produced is highly correlated with inflorescence count in these two species (*A. calendula* estimate: 33.88 (±2.81) seeds/inflorescence, $p<0.0001$, $r^2 = 0.76$; *H. glabra* estimate: 47.63 (±5.25) seeds/inflorescence, $p<0.0001$, $r^2 = 0.67$), indicating that inflorescence count is a reliable proxy for seed production. Seeds were collected for most of the native focal species, *T. cyanopetala* and *W. acuminata*, but in cases where seeds did disperse (all by wind) prior to collection, we extrapolated total seed production per plant based on inflorescence count. For a given individual where a dispersed inflorescence was found, we multiplied the average seed count from inflorescences collected from that individual, and multiplied this average seed count by the number of dispersed inflorescences. This number was then added to the collected seed count for an estimate of total seed count per individual.

Germination and soil seed survival rates

Field and lab techniques were used to estimate species' vital rates (*g* and *s*). We calculated these vital rates at the reserve level (i.e. they were not subject to experimental watering regimes). Germination and seed viability rates for *A. calendula* were obtained from previous laboratory data collected on seeds obtained from individuals collected from field sites in our study region (Manietta et al. unpublished data). To estimate these rates for *H. glabra*, *T. cyanopetala*, and *W. acuminata* at both of our experimental sites, 30 visibly undamaged and mature seeds of each species were buried in five fine-aperture mesh bags approximately 5 cm beneath the soil surface in December 2013 at Kunjin Reserve (32 °21'19.31"S, 117 °45'42.32"E; 65 km west of Bendering Reserve) and at West Perenjori Reserve (i.e. 150 seeds per species per site). Burial sites in each reserve were chosen in areas representative of intact York gum-jam woodland with minimal soil disturbance and low abundance of exotic species. Bags were excavated in the early winter of 2014 and returned to the laboratory at The University of Queensland. To estimate field germination rates (*g*), all seeds were examined for evidence of germination (e.g., broken seed coat, protruding radicles, etc.). Seeds that were missing were scored as dead and assumed to have been lost to granivory or decomposition. Bags (replicates) in which no seeds germinated were excluded from calculations as past studies of all species have found some germination under field conditions and thus a lack of germination likely reflects the use of sterile seed or infection within specific bags. None of the *H. glabra* seeds deployed at W. Perenjori germinated. As the coexistence model does not permit germination values of zero, and this is likely not a true reflection of germination rates of this species in W. Perenjori, we substituted germination rates for W. Perenjori with those from Kunjin.

To determine survival (*s*) of the ungerminated portion of seeds, ungerminated seeds were imbibed on germination paper with a 400 ppm GA3 solution in a growth chamber and scored for germination over a period of three days. Those that did not germinate in the growth chamber within this period were tested for viability according to methods in the AOSA/SCST Tetrazolium (TZ) handbook (Miller 2010). Survival was thus the sum of lab-germinated and TZ-identified living seeds for each excavated sample.

Annual plant population models

All statistical analyses and model fitting procedures were conducted using R statistical software version 3.2.3 (R Core Team 2015).

We adapted a well-supported annual plant population model (Chesson 2000; Adler et al. 2007; Levine & HilleRisLambers 2009) to calculate the parameters in niche and fitness difference equations described in Fig. 1. First, Maximum Likelihood Estimation (using the ‘optim’ function in R) was used to fit a seed production model following a negative binomial distribution. In all, fitted parameters include per-germinant fecundities in the absence of competition (λ) and interaction coefficients (α) for each of our four focal species. Our model took the general form:

$$F_i = \frac{\lambda_i}{1 + (\alpha_{ii} N_{i,t} + \alpha_{ij} N_{j,t} + \alpha_{ik} N_{k,t} + \alpha_{im} N_{m,t} + \alpha_{in} H_{n,t})}$$

where the number of viable seeds produced per individual of species *i* (F_i) is a function of per-germinant fecundity reduced by intra- and interspecific competition. The term α_{ii} encapsulates per capita intraspecific competition (competitive impact exerted per germinated competitor individual of species *i* ($N_{i,t}$) on focal individual of species *i*) and α_{ij}, α_{ik}, and α_{im} represent analogous per capita interspecific effects on species *i* of the three other focal species *j*, *k*, and *m*. The term α_{in} encompassed the competitive effects of all other non-focal species. In this case, α_{in} was calculated per unit height ($H_{n,t}$) of all non-focal competing individuals rather than per capita, as height is a stronger predictor of potential impact in this system than density alone.

Appropriateness of the height inclusive model was verified with a parsimony analysis of model fit (AICc). Using this approach, we determined that models using height-scaled α_{in} were more parsimonious than those based on a per capita α_{in} applied to the number of germinants summed across all non-focal species ($\Delta\text{AICc} = \text{AICc}_{\text{per capita}} - \text{AICc}_{\text{height}}$): *A. calendula* = 1.69, *H. glabra* = 7.52, *T. cyanopetala* = 7.75, *W. acuminata* = 3.0)).

For each of the four focal species, fitted parameters (described above) were evaluated within each of the four reserve-treatment combinations. Overall, this allowed us to calculate direct intraspecific and interspecific competitive effects on seed production for each focal species combination across each of the four reserve-treatment levels (for R code and data: Wainwright et al. 2018). First, we evaluated null models of mean seed production following either Poisson or negative binomial distributions. The fit of models using negative binomial distributions were superior to those fit with Poisson distributions, and thus negative binomial distributions were used for all subsequent model fitting. We then performed additional model fitting to test whether including competitive interactions substantially improved model fit. Fitted models were more parsimonious than either null model for *H. glabra* and *T. cyanopetala*. For *A. calendula* and *W. acuminata*, the null model following a negative binomial distribution was superior to the full fitted model (*A. calendula* ΔAICc = 11.78, *W. acuminata* ΔAICc = 6.63).

To test how fitted interaction coefficients using the methods above compared to estimates of competitive impacts determined by a traditional regression-like approach, we modelled flower or seed production by focal competitor densities within each reserve-treatment combination using negative binomial generalized linear models (glms) using the ‘glm.nb’ function in R. Importantly, negative binomial glms allow for impacts of competitors to be negative or positive, and have recently been used to estimate direct and higher-order competitor impacts on focal species in this same system (Mayfield & Stouffer 2017). To determine the correspondence between coefficients derived from both of our modelling approaches, we then conducted a Pearson correlation test, for which the interaction coefficients were square-root transformed to improve normality.

Calculation of stabilization and fitness inequalities

We followed well-established methods for calculating stabilization and fitness differences (see detailed explanation in Fig. 1) among each of the six possible species pairs across the four reserve-treatment levels. Previous work suggests that conditions for pairwise coexistence are satisfied when the condition $\rho < \kappa_i/\kappa_j$ is met (Fig. 1), where species *i* is inferior in fitness to species *j*. In addition to fitness differences as a whole, we examined variation in one of its components, the competitive response ratio, in response to watering. By contrast, all pairwise species combinations producing solutions not meeting this condition are consistent with competitive exclusion. Note that we calculated pairwise coexistence values with respect to each individual focal species (i.e. each focal species was set as species *i*, whether or not it was the fitness inferior), which set the range of possible fitness inequality values as $(0, \infty)$ rather than $(1, \infty)$ when fitness inequalities are calculated with respect to species *i* in the role of fitness inferior only.

Results

Pre-existing abiotic differences among treatments

Overhead tree canopy cover did not vary significantly between reserves or among compositional treatments. On average, however, canopy cover was lower in watered plots than in unwatered control plots (41.2% versus 45.3%, p=0.0002; Supplementary Table 3). Though statistically significant, we do not believe this minor difference in canopy cover would have affected our results, and would only have lessened the impacts of watering treatments on soil moisture in watered plots relative to control plots. Soil Colwell P did not vary significantly between reserves or watering treatments (Supplementary Table 4).

No-competition fecundity, germination, and seed survival

Fecundity in the absence of competition (λ) differed among our four focal species by reserve-treatment combination (Fig. 3; Supplementary Tables 5 and 6). For exotic *A. calendula* and native *W. acuminata*, fitted fecundity values exhibited a strong positive response to watering in xeric W. Perenjori, but were not affected by watering at more mesic Bendering. By contrast, exotic *H. glabra* fecundity responded positively to watering at both reserves, particularly in W. Perenjori. For all three of these species, unwatered control plot fecundities did not differ substantially between reserves. Fecundity responses of native *T. cyanopetala* to watering depended on the reserve: at xeric W. Perenjori, watering had a positive effect on fecundity, while the effect of watering on individuals at mesic Bendering was negative relative to individuals in unwatered control plots.

While we did not examine seed survival (*s*) and germination (*g*) values in response to experimental watering, these vital rates did vary with reserve (i.e. regional aridity) among the focal species (Supplementary Table 6; note *A. calendula* not tested in the field). For exotic *H. glabra*, seedbank survival of ungerminated seed was much greater at Kunjin (climate analogue of Bendering) than W. Perenjori. By contrast, native *T. cyanopetala* had higher germination rates at W. Perenjori than Bendering (25.8% and 5.0%, respectively) and similar patterns for seed survival. Native *W. acuminata* also had greater germination at W. Perenjori (15.6% vs 10.8%), though no ungerminated seeds survived in the seed burial bags.

Inter- and intraspecific interaction coefficients

Pairwise per capita interaction coefficients did not vary in consistent ways for the focal species across reserve-treatment combinations (Fig. 3; Supplementary Table 7). Intraspecific competition increased at both reserves with watering for exotic *A. calendula*, and was most intense in the watered xeric plots for this species and exotic *H. glabra*. By contrast, native *W. acuminata* experienced greater intraspecific competition at Bendering, particularly in watered plots, while *T. cyanopetala* did not display a clear trend.

Interspecific competition was highly variable and did not follow consistent patterns among species or among reserve-treatment combinations. The competitive effects of *T. cyanopetala*, however, tended to be stronger within each reserve in watered plots for *A. calendula* and *W. acuminata*, and the competitive impacts of *W. acuminata* on *H. glabra* were strongest in the watered plots at Bendering.

Competitor impacts on focals determined using a negative binomial glm were highly correlated to the impacts determined using the annual plant model ($r = -0.60$, $p < 0.0001$; Supplementary Fig. 2; Supplementary Table 7).

Pairwise niche overlap and fitness differences

Niche overlap (the ratio of pairwise inter- to intraspecific competition experienced by both focal species) was highly variable among focal species pairs among reserve-treatment combinations (Fig. 4; Supplementary Table 8). Stabilizing niche differences, the complement of niche overlap, were generally either near zero (i.e.

approaching neutrality) or one (i.e. completely stabilized). Niche overlap between exotic *H. glabra* and *T. cyanopetala* declined with watering within each reserve, though more strongly so in W. Perenjori. Watering tended to decrease niche overlap between both exotics (*A. calendula* and *H. glabra*) and increase niche overlap between both natives (*T. cyanopetala* and *W. acuminata*). By contrast, pairwise niche overlap between *A. calendula* and either native was not affected by watering, but shifted from high to low between Bendering and W. Perenjori.

Fitness differences did not exhibit consistent responses to watering across focal species pairs (Fig. 4; Supplementary Table 8). Exotic *H. glabra* was always the fitness superior with respect to native *T. cyanopetala*, and exotic A. *calendula* had higher fitness relative to either native species at mesic Bendering. Watering positively affected fitness of native *T. cyanopetala* with respect to native *W. acuminata*, but this only translated to fitness superiority in watered plots at Bendering. Competitive response ratios (the degree to which competition impacts the competitor species compared to the focal) revealed that fitness differences were largely due to differences in species' sensitivities to competition (Supplementary Fig. 3, Supplementary Table 8).

Cumulative effects on coexistence patterns

Out of the 24 possible pairwise focal species and watering treatment level combinations, only 20.8% (five combinations) met the conditions necessary for coexistence ($\rho < \kappa_i/\kappa_j$; Fig 5; Supplementary Fig 4). These coexisting pairs were not distributed in a clear way among reserve-treatment combinations or across species identities (Table 2; Fig 5; Supplementary Fig 4). Notably, the two native species were not predicted to stably coexist in either reserve regardless of watering treatment. By contrast, both natives were predicted to coexist with exotic *A. calendula* in unwatered plots at W. Perenjori.

Discussion

Our results suggest that while some key vital rates and competitive impacts varied due to changes in water availability in predictable ways, coexistence metrics (a function of all vital rates plus interaction strengths – Fig. 1) on average, did not. Specifically, species' fecundities generally increased with watering in this study, but competitive interactions (a component of niche differences), generally did not intensify. We were also surprised to find high variation in interaction strengths among many of the species pairs in this system, which may have made the impacts of watering treatments on niche overlap particularly variable. Interestingly, we found very few cases where stabilizing niche differences outweighed fitness differences (an indication of coexistence) for most of our focal species, despite their common co-occurrence in the field over many years. This negative result implies that the population models we parameterized likely do not capture the key mechanisms of coexistence in this system. In all, our findings point to challenges in operationalizing current coexistence theory for forecasting the impact of global change on diversity dynamics, a finding consistent with other studies of this system (Bimler et al. *in press*). However, our findings also highlight the importance of considering how species responses to water availability are mediated both directly through impacts on population growth as well as indirectly through impacts on interactions with other species in their communities. Given the large number of species on the planet, being able to predict changes in coexistence may be crucial to generalizing community responses to global change.

No-competition fecundity, germination, and seed survival

Patterns of fecundity in the absence of competition (λ) varied consistently with existing autecological knowledge of these species across reserves and watering treatments. For both exotics and native *W. acuminata*, fecundities peaked in watered plots at the xeric site (W. Perenjori), likely because this site received well above-average rainfall in September (when these species typically set seed) of the year of our study. In contrast, fecundity of the native *T. cyanopetala* declined between the mesic and xeric site, but responded positively to watering in the xeric site. The presence of *T. cyanopetala* is known to be positively associated with regional moisture availability in this system (Staples et al. 2016), with individuals grown in the absence of competition producing more seeds under high than low soil moisture conditions (Staples et al. 2016). The fact that *T. cyanopetala* fecundity responded negatively to watering at Bendering may have been due to differential sensitivity to changes in soil microbial communities in continually moist soils.

We believe that direct aridity effects on other unquantified vital rates (germination and seed survival), while likely to influence fitness differences (and thus interpretations of competitive superiority), would not change our conclusions about impacts of aridity on coexistence dynamics overall. Our two native focal species did have higher germination rates in xeric conditions, consistent with Dwyer & Erickson (2016), who found elevated germination rates and seed viability for these species at W. Perenjori. Though including germination and seed viability data from within our experimental plots would have been ideal, it would only have potentially changed coexistence outcomes for a few species pairs, as our model assumes these parameters act on fitness differences only (Fig. 5, y-axis). In this system, increasing temperatures associated with climate change may confer a fitness advantage to native species via increased germination fractions (Dwyer & Erickson 2016). However, these positive direct effects may be tempered by negative effects of shorter growing seasons (e.g., Matias et al. 2018) and increasing environmental stress. Combined, these factors may differentially alter plant growth rates (and thus interaction coefficients) and limit reproductive potential (λ) (Dwyer & Erickson 2016; Lancaster et al. 2017).

Inter- and intraspecific interactions

Interactions were affected by local and regional moisture availability in a variety of ways. As with fecundity in the absence of competition, intraspecific competition was most intense in the watered xeric site for both exotic species. Though plant biomass was not measured in this study, per capita intraspecific competition may have intensified with water addition for exotic species in xeric plots because plants were likely larger in these plots (a conjecture based on personal observation and substantially higher seed production in these plots). As plants grew larger with water addition, a shift may have occurred in the most limiting resource from water to light (Hautier et al. 2009). For native *W. acuminata*, intraspecific competition was greatest in watered plots at the more mesic site, while native *T. cyanopetala* did not display a clear trend.

Unlike previous observations of strong competition in other annual plant systems composed of native and exotic species, our focal species did not experience consistency in direct interspecific competition (e.g., Dyer & Rice 1997; Seabloom et al. 2003; Martorell et al. 2015; Uricchio et al. 2018). Rather, interspecific competition was relatively unpredictable across treatment combinations. An alternative modelling approach revealed that the direct impacts of several of the focal species may be neutral or positive, though these types of impacts did not occur systematically for species pairs across treatments. Indeed, weak interspecific competition has been noted in this system for these species in the past, even in high rainfall years (Wainwright et al. unpublished data). Additionally, our population model does not include facilitative or higher order interactions, which may have buffered the strength of direct competitive effects on these focal species. The contributions of non-competitive and non-additive interactions to coexistence in natural communities warrant greater exploration (Mayfield & Stouffer 2017; Bimler et al. *in press*), and point to challenges in operationalizing current coexistence theory in systems where competitive impacts may not be strongly density-mediated (Hart et al. 2018).

Combined effects on niche and fitness differences

The impact of watering on niche overlap was inconsistent among focal species pairs and between reserves. For example, watering increased niche separation between the exotic species pair, but the reverse was true for the native species pair. In general, most species pairs had either high or very low niche overlap. From a mathematical viewpoint, the clustering of most of our species pairs at these extremes was due to large variation in interaction coefficients among species. While comparisons of interaction sensitivities within species were in several cases interpretable (e.g., competitive response ratios among treatments), among species they varied by orders of magnitude and when combined multiplicatively, produced highly variable outcomes for stabilizing niche differences.

Even though competitive impacts were relatively weak for most species pairs, fitness differences among species were largely driven by differences among species in competitive sensitivity, rather than differences in vital rates. Specifically, the competitive response ratio (which encapsulates the degree to which competition impacts the competitor species compared to the focal) varied more than did the demographic ratio (which encapsulates differences in vital rates; Supplementary Table 8). These findings point to the critical role of interactions both in driving competitive coexistence and competitive exclusion in these systems. For example, exotic *A. calendula* was the least sensitive to competition at the mesic site relative to the sensitivity of its competitors, a fitness advantage that shifted to relative fitness equivalence or inferiority with increasing aridity at the regional scale. This makes sense given the competitive success of this species in high resource, disturbed environments (e.g., under soil eutrophication; McIvor & Smith 1973). By contrast, native *W. acuminata* was competitively superior to all other focals in the xeric site under elevated soil moisture conditions. It is possible that this species, which occurs at relatively high local abundances across a range of climate conditions, is more able to take advantage of pulsed resources in stressful environments relative to its competitors.

Under future climate change and further invasion in this system, competitive interaction outcomes along environmental gradients may be even more unpredictable. Changes in the identities of interacting species (for example, through extinctions and range expansions) can alter multispecies coexistence, and thus long-term patterns of diversity (Alexander et al. 2015). Therefore, current spatial relationships between environmental conditions and community composition may not serve as reliable proxies for impacts of future environmental change, highlighting the need to understand direct and indirect effects of environmental variation on coexistence within non-historical assemblages. We found that competitor impacts were difficult to generalize based on origin, although we examined a relatively small number of species. For example, though exotic *A. calendula* was competitively superior to both natives at the mesic site, exotic *H. glabra* did not competitively impact the native species consistently, in line with previous observations on the competitive impacts of these species (Cal-IPC 2018).

Cumulative effects on coexistence patterns

Rainfall supplementation throughout the growing season did not have any generalizable effects on coexistence in this study across all species. Our model did, however, predict that both native species would stably coexist with exotic *A. calendula* under the most xeric conditions due to reductions in fitness inequalities or stronger stabilization. As these abiotic conditions are the most analogous to those predicted by climate change projections for this region (Suppiah et al. 2007), this result indicates that the likelihood of competitive exclusion of these two natives by this invasive exotic may actually decline as climate change progresses. However, in a different semi-arid system, Matias et al. (2018) demonstrated that drought-induced reductions in fitness differences may be tempered by increased niche overlap (i.e. reduced stabilization), highlighting that these results may be dependent on species identities and local context.

Despite observational evidence that these species do currently coexist in natural settings, coexistence was infrequently predicted by our models. In our study, this pattern was largely driven by fitness inequalities, which were almost always much greater than stabilization. Even in unwatered plots, we found no instances of our native species pairs coexisting according to our models despite seven years of field observations that suggest that they do indeed coexist stably in this system (persistent co-occurrence at neighbourhood scales). This finding is not unique to our system, however. Based on the same models, surprisingly few co-occurring species pairs have been predicted to coexist in grasslands in California (Kraft et al. 2015) and Spain (Matias et al. 2018). There are several potential reasons for this. As noted previously, non-additive (higher order) interactions are also known to be important determinants of individual species performance in this system (Mayfield & Stouffer 2017) but are not evaluated in this model. Other coexistence mechanisms, including temporal storage effects and density-dependent interactions mediated by pathogens or predators operating on seeds or seedlings (e.g. Janzen-Connell effects) are also not accommodated by our experimental design, conducted over one year with competitor densities manipulated at the germinant stage. Spatial coexistence mechanisms operating on scales larger than the plant interaction neighbourhood in a given year may contribute to local co-occurrence patterns, perhaps even more so than local-scale species interactions (e.g., soil heterogeneity and metacommunity dynamics) (Siepielski & McPeek 2010; Kraft et al. 2015). These are issues seldom acknowledged by most local-scale coexistence studies, highlighting common challenges to studying these dynamics empirically.

Conclusion

Climate change is likely to have unanticipated impacts on local patterns of diversity if predictions do not account for indirect effects mediated by environmentally-induced changes in species interactions in addition to direct effects on species' vital rates. Here, we show that environmental variation (change in water availability) has the capacity to affect species both through direct and indirect impacts on all aspects of the fitness and niche differences important for coexistence, and thus, local patterns of community diversity. While the responses of individual components may make intuitive sense and align with theoretical predictions and past experiments, in combination they may not exhibit clear patterns or even accurately predict current coexistence. While modern coexistence theory may be a useful tool for clarifying the potential mechanisms contributing to coexistence, its role as a predictive tool could be limited due to differentially dynamic components of fitness and niche differences. Nevertheless, our findings highlight the importance of considering both direct and indirect impacts of environmental change on communities.

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Author contributions

MMM and JHRL conceptualized the study and designed the field experiments. Data were collected by HRL, XL, and CEW, and were analysed by CEW with assistance from JHRL. The manuscript was prepared by CEW with substantial input from MMM and JHRL. All authors approve of the publication of this manuscript.

Data accessibility

Our data and R code for model fitting are archived at Figshare: doi: 10.6084/m9.figshare.6863711
https://figshare.com/articles/Data_and_R_Code_Wainwright_JECOL_2018/6863711

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Figure legends

Figure 1 - Coexistence under climate change

Figure 2 - A) Location of experimental sites in southwest Western Australia along the regional growing season rainfall gradient (30-year average rainfall quantile data: Australian Bureau of Meteorology 2018). B) Diagram of an example experimental plot containing focal individuals in competitive multispecies neighbourhoods.

Figure 3 – Component results of coexistence models shown across sites and watering treatments. In all panels the x-axis is plotted in by reserve-watering treatment combination: BC = Bendering-control, BW = Bendering-watered, , PC = West Perenjori-control, PW = West Perenjori-watered. Y-axes for rows are as follows: Fecundity (seeds produced per individual) in the absence of competition (λ), impacts of intraspecific competition (interaction coefficients: α, where 0 = no competitive effect on focal species), and impacts of interspecific competition (interaction coefficients: α, where 0 = no competitive effect on focal species). For competition coefficients, points correspond to the response of the focal (columns) with respect to its competitors (denoted by point colour): red = *A. calendula* (ARCA), yellow = *H. glabra* (HYGL), green = *T. cyanopetala* (TRCY), purple = *W. acuminata* (WAAC).

Figure 4 – Niche overlap (ρ) and relative fitness differences among focal species across sites and watering treatments. In all panels the x-axis is plotted in by reserve-watering treatment combination: BC = Bendering-control, BW = Bendering-watered, PC = West Perenjori-control, PW = West Perenjori-watered. Points are jittered horizontally where appropriate (amount = 0.01). For fitness differences, points above the dashed line indicate the focal is superior in fitness relative to its competitor, and points below the line indicate the focal is inferior in fitness relative to its competitor. Points correspond to the response of the focal (columns) with respect to its competitors (denoted by point colour): red = *A. calendula* (ARCA), yellow = *H. glabra* (HYGL), green = *T. cyanopetala* (TRCY), purple = *W. acuminata* (WAAC).

Figure 5 – Stabilization and fitness differences for all pairwise combinations of our four focal species (panels) at Bendering Reserve (circles) and West Perenjori Reserve (squares) in unwatered (empty points) and watered plots (filled points). The grey shaded region indicates combinations of fitness and stabilization satisfying conditions of stable coexistence ($\rho < \kappa_i/\kappa_j$). Competitor identity is denoted by the different colour combinations: red = *A. calendula* (ARCA), yellow = *H. glabra* (HYGL), green = *T. cyanopetala* (TRCY), purple = *W. acuminata* (WAAC).

Table 1 – Historic mean rainfall, ambient rainfall in 2014 (mm), and manual water addition volumes (L) for watered plots during the winter-spring experimental watering period (29 June – 28 September) at Bendering (historically mesic site) and West Perenjori (historically xeric site) in 2014. Historic climate data accessed from the Australian Bureau of Meteorology (www.bom.gov.au) in 2018.

	Mean rainfall (mm)	2014 rainfall (mm)	Watering (L)
Bendering Reserve	140.4	96.4	20.5
W. Perenjori Reserve	96.4	117.6	23.5

Table 2 – Summary of coexistence predictions among pairwise species combinations by reserve (Bendering = mesic, W. Perenjori = xeric) under ambient versus watered conditions. Species identities are as follows: ARCA = *A. calendula* (exotic), HYGL = *H. glabra* (exotic), TRCY = *T. cyanopetala* (native), and WAAC = *W. acuminata* (native). See Supplementary Table 8 for specific parameter values.

Species pair	**Reserve**	**Coexist under ambient conditions?**	**Coexist when watered?**
Native – Native:			
TRCY-WAAC	Bendering	No	No
	W. Perenjori	No	No
Native – Exotic:			
TRCY-ARCA	Bendering	No	No
	W. Perenjori	Yes	Yes
WAAC-ARCA	Bendering	No	No
	W. Perenjori	Yes	No
TRCY-HYGL	Bendering	No	No
	W. Perenjori	No	Yes
WAAC-HYGL	Bendering	No	No
	W. Perenjori	No	No
Exotic – Exotic:			
ARCA-HYGL	Bendering	No	Yes
	W. Perenjori	No	No