

The impacts of exotic species can be better understood by accounting for demographic variation, positive interaction outcomes, and community composition

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Abstract

Biological invasions have long fascinated ecologists as they fundamentally alter ecological communities, often in surprising ways. The demography of interacting native and exotic populations are core drivers of invasion impact. Demographic models estimate the strength of species interactions but have several shortcomings, often ignoring positive interactions and focusing only on competition, disregarding individual-level variance in demographic parameters, and focusing on one exotic species at a time. In this study, we investigate the fitness outcomes of eleven native and exotic species from a diverse annual plant community in Western Australia. We use a Bayesian demographic modelling approach that integrates demographic variation. Positive effects of exotic species played an integral role in the invaded community, but demographic variation caused many species interaction outcomes to vary from positive to negative, regardless of abiotic conditions. Our approach reveals variation that could be responsible for the diverse and unexpected impacts of exotic species on recipient communities.

1 Introduction

Biological invasions increasingly alter ecological communities across the globe, leading to the homogenization of landscapes and diminished biodiversity in the novel communities they create (Vitousek *et al.*, 1996; Ricciardi *et al.*, 2013; Gioria & Osborne, 2014). Since Charles Elton’s first articulation of the dynamics of invasive species (Elton, 1958), community ecology has generated multiple theories to guide predictions of invasion impact. Prominent theories highlight the importance of differences between native and exotic species in terms of their niche requirements (Levine & HilleRisLambers, 2009; Shea & Chesson, 2002; Funk & Vitousek, 2007; Leger & Espeland, 2010) and competitive abilities (Shea & Chesson, 2002; Macdougall *et al.*, 2009; Gioria & Osborne, 2014). For instance, classical niche theory predicts that invaders occupying unique niche spaces can successfully invade communities but will have minimal impact on native residents, while modern coexistence theory has been invoked to suggest that only invaders with superior fitness will have strong negative impacts on native resident species. The observed impacts of exotic species, however, are highly variable and in many cases often contradict leading hypotheses derived from these theories. For instance, functionally unique invaders, such as species with the ability to fix nitrogen, have had substantial impacts on recipient communities and even promoted further invasion (Corbin & Antonio, 2004). Conversely, case studies have shown functionally similar invaders to integrate themselves into recipient communities with only weak negative impacts or even positive impacts on native residents. For example, Lai *et al.* (2015) categorised several invasive forbs in the Western Australian York gum woodlands as ‘coexisters’ because they had no detectable impact on native forb diversity. Similarly, Wainwright *et al.* (2016) observed an exotic grass to facilitate a native forb in the same system. Rodriguez (2006) reviewed the much less acknowledged but relatively common promotion of native species survival, growth, and reproduction by invaders, often through habitat modification. In fact,

exotic species have even been used in the restoration of particularly degraded sites to improve conditions for native species when a native alternative is unavailable (for example, fast-growing sterile grasses and nitrogen-fixing shrubs; D’Antonio & Meyerson 2002). Coupling theory and modelling developments to more accurately predict the ambiguous impact of invasions is a critical step towards successful management of ecological communities.

While theories of biological invasions have tended to focus on functional or niche-based differences between species, a more recent approach has been to explore the demographic processes that fundamentally drive population growth, species interactions, and ultimately the impact of an invasion (Flory *et al.*, 2017; Larios *et al.*, 2017; Mordecai *et al.*, 2018; Thomson *et al.*, 2017; Thomson, 2005). Demographic models that incorporate a species’ intrinsic fitness as well as the competitive effects of one species on the demography of another can quantify how demography drives species’ performance. These models rely on several important simplifications that have major implications for their efficacy in predicting impacts of invasion. These assumptions include: 1) plant communities are structured primarily by competitive interactions (Brooker *et al.*, 2008; Bimler *et al.*, 2018), 2) natural variance in demographic rates that can, by chance, alter the strength and direction of species interactions is negligible (Shoemaker *et al.*, 2020), and 3) invasion success and invaders’ effects on native species can be predicted with population or pairwise models. While demographic models provide valuable insights into biological invasions (Thomson, 2005; Mitchell *et al.*, 2006; McEvoy & Coombs, 1999; Parker, 2000), these simplifications may exacerbate discrepancies between predictions and observations of invaded communities, impeding efforts to obtain generalizable models that can more accurately predict the varied impacts of invasion across systems. In particular, we propose that a demographic modelling approach to invasion biology would greatly benefit from the inclusion of positive species interactions, demographic variation, and variation in the identity and density of neighbors in diverse interaction neighborhoods.

Positive effects of neighbor plants on species fecundity plays a large role in driving pop-

ulation dynamics and structuring communities, but are rarely included in models of species interactions (Bruno *et al.*, 2003; Brooker *et al.*, 2008). Positive effects of neighbors on species growth, reproduction, or survival, have been demonstrated to occur in numerous systems including between native and exotic species (Ruesink *et al.*, 2006; Lai *et al.*, 2015; Wainwright *et al.*, 2016). Though competition is often the most common and strongest form of species interaction within plant communities, and must inevitably limit population size, the benefit of neighbors can sometimes substantially outweigh the costs; leading to positive performance outcomes. For instance, neighboring plants have been shown to create micro-climatic conditions that buffer individuals of against abiotic stress (Brooker *et al.*, 2008). Established exotic species have been shown to facilitate the invasion of other exotic species, increasing growth and establishment rates with severe impacts on recipient communities (Wundrow *et al.*, 2012), even to an extent where an ‘invasion meltdown’ occurs (Simberloff & Von Holle, 1999). Native plants have, in other systems, been found to aid the invasion and growth of exotic species through facilitative mechanisms such as shading (Bulleri *et al.*, 2008). Despite evidence of many different relationships between native and exotic plants, exotic species are less often found (or reported) to have positive effects on native species, particularly in plant systems (Richardson & Pyšek 2006; Ruesink *et al.* 2006, but see Wainwright *et al.* 2016).

The varied and often unexpected impacts of invasion beg the question of how strongly individual-level variance influences the impacts of exotic species. Individual-level variance is a result of demographic heterogeneity (differences among individuals in the demographic rates experienced at a given age or stage, for instance seed production (Hart *et al.*, 2016)), and demographic stochasticity (variation due to the random outcome of demographic rates in similar individuals (Melbourne & Hastings, 2008)). We refer to this cumulative individual-level variance as demographic variation. This variation can be described by underlying probability distributions, which can, in turn, inform a quantification of the variability we might expect to see in the interactions between native and exotic species (Hart *et al.*, 2016;

Shoemaker *et al.*, 2020). While numerous recent studies have demonstrated the insights gained when accounting for intraspecific trait variation in demographic and species interaction studies (Siefert *et al.*, 2015)), the focus has been placed on functional traits such as plant height and specific leaf area, or intraspecific variance in responses to the environment (Clark, 2010). This work has led to a now strong understanding that considering only mean trait values per species underestimates the ability of species to respond to neighbors (Ashton *et al.*, 2010; Violle *et al.*, 2012). In a similar way, strong demographic variation may also result in instances of unexpectedly weaker competition or even result in a net positive effect between two individuals (or vice versa), yet studies are currently lacking on this potential effect. Here we fill this knowledge gap by explicitly exploring the importance of intraspecific demographic variation on the outcomes of species interactions.

Variation at the neighborhood-level can also arise in diverse communities due to the large number of potential neighbors, making the identity of nearest-neighbors largely unpredictable (Wiegand *et al.*, 2012). The consequences on species performance in the neighborhood-level spatial arrangement of species has been examined primarily in diverse rainforests from both Asia and the Americas (Punchi-manage *et al.*, 2020). Incorporating this multi-layered variation in species fitness outcomes may be important for accurately predicting the impacts of exotic species, especially early in the invasion process where low invader population sizes heighten the effects of demographic variation (Melbourne & Hastings, 2008; Lande, 1993).

In this study, we aimed to gain greater insights into the importance of positive interaction effects along with demographic and neighborhood variability on fecundity in mediating the impacts of established exotic species on resident communities. We do this using a phenomenological Bayesian modelling framework (i.e. a statistical approach that allows us to model species interactions based on individual demographic responses to one another) applied to data from the annual plant communities from the York gum woodlands of Western Australia to answer the following questions:

1. Do native and exotic focal species tend to experience net negative or positive effects on fecundity from the presence of native and/or exotic neighbors?
2. How does demographic variation alter the effects of native/exotic species interactions?
3. Do net neighborhood effects differ between native and exotic species?

We hypothesized that positive effects of neighbors on focal species' fecundity would be a prominent process occurring among species in the York gum woodlands, including between exotic-exotic and native-exotic species pairs (Wainwright *et al.*, 2016; Dwyer *et al.*, 2015). We expected that demographic variation could cause species interactions to shift between net competitive to positive, blurring the overall impacts of species interactions on a species' fecundity. We further hypothesized that demographic variation, along with the high variation in neighbor identity in this diverse system, would reveal greater variability in native and exotic species' performance at the neighborhood level. To test these hypotheses, we investigated the fitness outcomes of eleven commonly co-occurring native and exotic annual plant species, using a flexible Bayesian demographic modelling approach. Our approach integrates demographic variation in both intrinsic fitness and interaction coefficients and allows for both positive and negative effects on neighbors on focal species. We then calculated probability distributions for the net neighborhood effect experienced by individuals from each focal species. This highlighted the importance of considering the potential for positive species interactions to effect the fitness of both native and exotic species, and the importance of placing these effects within the broader and highly-variable context of naturally diverse plant neighborhoods.

2 Methods

2.1 Study system

Data collection was undertaken from July to October in 2018 in the annual plant understory of the York gum woodlands in West Perenjori Nature Reserve (29°47'S, 116°20'E). West Perenjori Reserve is located at the northern extent of the York gum woodlands in southwest Western Australia (Fig. 1a). York gum woodlands occur on infertile, sandy loam soils and have an extremely low canopy density composed primarily of York gum (*Eucalyptus loxophleba*) and jam (*Acacia acuminata*) trees. These woodlands are located in the agricultural region known as the western Wheatbelt, a highly fragmented landscape consisting of small York gum woodland remnants scattered throughout an agricultural matrix (primarily wheat, canola and sheep farming), with exotic annual plant invasion exacerbated by fertilizer run-off (Dwyer *et al.*, 2015). The region experiences a Mediterranean climate with hot, dry summers and cool, wet winters. Winter rainfall triggers the germination of a diverse array of annual forb species, with an average of 7 distinct species of native and exotic annual forbs and grasses within a 15 cm diameter circle (Fig. 1b).

We chose a mixture of common annual native (7) and exotic (4) species as focal species for our field experiments and demographic modeling. The seven native species were: *Daucus glochidiatus*, *Gilberta tenuifolia*, *Hyalosperma glutinosum*, *Plantago debilis*, *Podolepis canescens*, *Trachymene cyanopetala* and *Velleia rosea*. The four exotic species were: *Arc-totheca calendula*, *Medicago minima*, *Monoculus monstrosus*, and *Pentameris airoides*. All of these species are annual forbs, except for *P. airoides* which is an annual grass. There are no native annual grasses common to this system, which is why none were considered. To investigate the inter- and intraspecific interactions between these focal species and their neighbors, we manipulated the local interaction neighborhood around focal individuals and recorded fecundity for each (total seed set per individual) as described below.

2.2 Study design

In a spatially nested design, we established 16 plots (1x1 m) for each of our 11 focal species. We located plots throughout a study area of approximately 12 ha within West Perenjori Reserve covered in York gum woodland vegetation. Within each plot, we placed six non-overlapping 15 cm diameter ‘neighborhood rings’ centered on a focal individual or ‘phytometer’ of the relevant species (Fig. 1c). Half of the rings within a plot were un-manipulated (with the abundance and identity of all individuals around the phytometer recorded), while the other half had all germinants except the focal phytometer carefully removed by hand at the beginning of the growing season. Any delayed germinants were subsequently removed during periodic checks of each neighborhood ring throughout the growing season. This design allowed us to isolate the demographic variation of seed production (fecundity) in both the presence and absence of interacting individuals. This design also allowed us to differentiate between intrinsic fecundity versus intra- and inter-specific interactions when fitting demographic models. Total seed production was collected for each focal phytometer at the end of the growing season. Seeds were transported back to the Mayfield laboratory at the University of Queensland for counting. We treated all focal individuals that died prior to seed production as having a seed production of zero. We conducted a test of the seed counting process itself to demonstrate the very small amount of sampling error that could be expected (see Appendix S1 in Supporting Information, Table S2).

Neighborhood ring diameter was chosen to capture the local interaction neighborhood of the phytometer plants, following protocol from Mayfield & Stouffer (2017). Plot size was sufficiently small that plants experience near identical abiotic conditions within the plot region (Dwyer *et al.*, 2015). Within each plot we quantified the key abiotic conditions shown to alter vegetative community composition: canopy cover, soil phosphorous, and litter (Dwyer *et al.*, 2015). We measured plot-level canopy cover percentage by taking a wide-angle digital photograph from the center of each plot, and processed the images in

ImageJ (Abràmoff *et al.*, 2004). A 70 mm deep soil core was collected from each plot and analysed for extractable phosphorus (mg/kg) at the School of Agriculture and Food Sciences, the University of Queensland. Percentage leaf litter cover was also estimated for each plot by taking digital photographs, overlaying a 100-point grid, and counting ‘hits’. We found little effect of these three recorded environmental variables on demographic rates across focal species (Appendix S1, Figure S1 and S2), and hence these specific variables were not included in the fecundity modelling described below.

2.3 Statistical analysis

2.3.1 Annual plant fecundity models

To test our hypotheses, we fit Bayesian models of annual plant fecundity for each of our eleven focal species. We incorporated demographic variation and estimated posterior distributions of intrinsic fecundity and interaction coefficients from the major groups of neighbors (native/exotic annual forbs and an exotic annual grass). Using a Bayesian approach allowed us to fully characterize the variation in these coefficients and propagate that variation forward to better understand its influence on community dynamics. We did this by calculating the net neighborhood effects on fecundity to understand the interaction between demographic variation and neighborhood variation (variation in nearest-neighbor identity).

We estimated intrinsic seed production and interaction coefficients with the annual plant fecundity model from Mayfield & Stouffer (2017). This model (Eq. 1) describes seed production (F_i) of a focal individual of species i at the end of the growing season where:

$$F_i = \lambda_i e^{\alpha_{i,i} N_i + \sum_{j \neq i}^G \alpha_{i,j} N_j} \quad (1)$$

We recovered posterior distributions of species’ density-independent intrinsic fecundity, λ , and the total direct effects of all intra- and inter-specific neighboring functional groups, G ,

212 from interaction coefficients $\alpha_{i,j}$. Unlike in other common annual plant models (Hallett *et al.*,
 213 2019; Levine & HilleRisLambers, 2009), interaction coefficients incorporate both positive and
 214 negative values (i.e. an increase or reduction in fecundity in the presence of neighbors, re-
 215 spectively). Neighboring groups (native forb, exotic forb, exotic grass, and unknown species)
 216 are represented by j , with their effect multiplied by abundance of the neighbor group (N)
 217 within each neighborhood ring. Interaction effects are summed across all neighboring groups
 218 present in a neighborhood ring. Neighbor species were grouped into ‘functional groups’ based
 219 on life form (see Appendix S1, Table S1). These included native annual forb, exotic annual
 220 forb and exotic annual grass (native annual grasses are rare in this system). Unidentified
 221 neighboring species were grouped into a separate category and included in all analyses and
 222 calculations, but are not shown in figures. T. Martyn (Martyn *et al.* In Review) found in
 223 two annual plant systems (including the York gum woodlands), that grouping the effects of
 224 neighboring species by functional form and origin was equally as effective as including each
 225 neighbor species separately and produced more parsimonious individual fitness models.

226 We incorporated plot-level random effects to account for variability in abiotic factors
 227 between plots, where observed fecundity \hat{F}_i was multiplied by a random plot-level paramete-
 228 ter, such that $\hat{F}_i = \epsilon_p F_i$ where p denotes plot identity (Lee *et al.*, 2020). This allows us to
 229 isolate the effect of demographic variation from potential effects of underlying environmen-
 230 tal heterogeneity. Prior distributions on interaction coefficients were uninformative normal
 231 distributions centred on 0 with standard deviations of 1000. For λ , we also used an uninfor-
 232 mative prior in the form of a gamma distribution with both shape and rate parameters set
 233 to 0.001 and $\epsilon_p \sim \text{gamma}(\sigma, \sigma)$ with $\sigma \sim \text{gamma}(0.001, 0.001)$ (Lee *et al.*, 2020). For each
 234 focal species we ran 3 MCMC chains, sampling 6000 iterations and thinning by two iterations
 235 to remove autocorrelations. We assessed convergence of the chains using \hat{R} (Gelman-Rubin
 236 convergence diagnostic; assuring the convergence of chains in models for all of our focal
 237 species), checking the trace plots for chain mixing. We fit the models in R (Version 3.5.3)

238 using the package rstan (Stan Development Team, 2020) with post-processing in R.

239 **2.3.2 Calculating net neighborhood effect**

240 From the posterior distributions for intrinsic fecundity and interaction effects, we calculated
241 the percentage of negative versus positive effects that conspecific versus exotic or native
242 species had on all focal species. We then calculated the net neighborhood effect experienced
243 by a focal species (F_N), incorporating observed variation in neighborhood functional group
244 diversity and density:

$$F_N = F_i / \lambda_i = e^{\alpha_{i,i} N_i + \sum_{j \neq i}^G \alpha_{i,j} N_j} \quad (2)$$

245 If F_N is greater than 1, the focal species experiences an overall positive effect from their
246 neighborhood. If F_N is less than 1, the focal species experiences an overall competitive
247 effect. If F_N is equal to 1, the focal species experiences no net neighborhood effect (i.e. the
248 focal species' fecundity in the presence of neighbors is equal to the focal species intrinsic
249 fecundity).

250 **3 Results**

251 **3.1 The relative importance of positive versus negative species** 252 **interactions**

253 Across all species, net negative effects of neighboring species were more common than net
254 positive effects. However, net positive effects accounted for just over 25% of interactions
255 among species (Fig. 2). Most interactions however, could not be clearly defined as solely
256 negative or positive (Fig. 2b). Intraspecific interactions were more often negative than
257 positive (negative 73% of the time; Fig. 2b).

3.2 The role of variability in demography and neighborhood composition

Demographic variation, in some cases combined with relatively weak interaction strength, caused 24% of interaction coefficients to vary between negative and positive, irrespective of abiotic factors (distributions that overlap zero in Fig. 2a). This was especially strong for interspecific interactions; for both native and exotic neighboring species, where nearly 50% of interactions had posterior distributions that crossed zero (Fig. 2b). The underlying variability in interaction coefficients - as quantified from the spread of the distributions - differed dramatically between native and exotic species. Interactions with native forbs tended to be precisely estimated, with tight posterior distributions, while species responses to exotic neighbors generally had much wider distributions and a larger range in the strength of these interactions, despite both commonly occurring as neighbors (Fig. 2a).

Demographic and neighborhood variability (variation in neighborhood composition, including species' identities and densities) generated a high amount of variation in focal species responses to their interaction neighborhood, with the mean net neighborhood fecundity ranging from 0.56 to 1.01. Seven of the 11 focal species experienced a range of net neighborhood fecundity encompassing both positive and negative effects from their neighborhoods - a higher proportion than when we consider solely the sign of interspecific interactions ($\alpha_{i,j}$ without considering neighborhood composition; comparing Fig. 2b and Fig. 3a). In particular, the invasive grass *P. airoides* was strongly inhibited by its neighborhood (Fig. 2a). On average, exotic species were positive impacted by their neighborhood more often than native species (Fig. 3b), but this average was strongly influenced by *M. monstrosus*, for which we observed strong positive effects on conspecifics. All exotic forbs experienced positive neighbor effects in a portion of their observed neighborhoods, while only four of the seven native forbs experienced positive effects from their neighborhood (Fig. 3a).

3.3 Differences between native and exotic species

Fully positive effects among species were all from exotic neighbors (Fig. 2b). The presence of exotic forbs was found to have purely positive effects on one of the seven native forbs, and to have an occasional positive effect on an additional two when demographic variation is incorporated into our analyses. Similarly, exotic forbs had positive effects on two of the four exotic species, and another one when demographic variation was considered. The exotic grass *P. airoides* was found to have fully positive effects on three out of seven of the native species and two additional native species when demographic variation was considered, highlighting the potential role of the invasive grass in facilitating a majority of species in the system. *P. airoides* was also found to have a positive effect on two of the exotic forb species, as well as the third exotic forb species depending on demographic variation. For the native forb species *D. glochidiatus*, *G. tenuifolia* and *M. monstrosus*, intraspecific interactions were not purely competitive (and even often positive in the case of *M. monstrosus*; Fig. 2a).

The net effect that each focal species experienced from their local interaction neighborhood differed between exotic and native species, with exotics more often positively impacted by their surrounding neighbors (Fig. 3b). While all focal species except for the exotic forb *M. monstrosus* were, on average, inhibited by their neighborhood, natives experienced net positive effects 5% of the time while exotics 13% of the time.

We compared the net effect of native (Fig. 4a) versus exotic (Fig. 4b) neighbors to the intrinsic fecundity of each focal species, examining how net neighborhood effects might covary with species' underlying intrinsic fecundity. Species with lower intrinsic fecundity tended to experience less competition from native neighbors, but this trend plateaued at higher values of intrinsic fecundity with the exotic grass *P. airoides* and native forb *P. canescens* experiencing similar competitive effects on net neighborhood fecundity. In comparison, there was no identifiable trend between net neighborhood and intrinsic fecundity with exotic neighbors, and many species (both exotic and native) experienced a net positive effect from the exotic

neighbor species, regardless of their intrinsic fecundity.

4 Discussion

Ecological theory leads us to assume that the diversity found in natural communities is strongly influenced by competition between species, and thus that cross-species and demographic variation in fitness will fall within the competitive range. In reality, the ecology of natural plant communities is much more dynamic, including substantial amounts of variation, with positive and negative effects both common occurrences. In invaded communities, these simplifying assumptions have historically driven the ways in which we look for impacts of invasion, biasing our literature toward the expectation that exotic and native species compete with each other. By accounting for positive species interactions, demographic variation, and observed variation in interaction neighborhoods in models of species performance, our demographic modelling approach reveals that positive neighbor effects and demographic variation are key drivers of the diverse and often unexpected impacts of exotic species on invaded communities. Specifically, we found that in a species rich, invaded annual plant system, net positive interactions played an integral role in native species' fitness and was common both among exotic-native and exotic-exotic species pairs. We also found that due to large amounts of demographic variation in the effects of pairwise interactions, interactions between exotic-native species pairs ranged from strongly negative to positive in the same community - often for individuals of the same focal species. This result indicates that variation in species responses to one another can and do encompass both negative and positive impacts and are highly dynamic both within and among species.

4.1 Net positive interactions were common between native and exotic species

Positive intra- and interspecific interactions have been demonstrated in many annual plant systems (Leger & Espeland, 2010; Sheley & James, 2014; Bimler *et al.*, 2018), but are typically regarded in multi-species demographic modelling as relatively minor and are rarely been considered integral to invasion impacts (Bulleri *et al.*, 2008; Northfield *et al.*, 2018; Gross *et al.*, 2015; Sheley & James, 2014).

We investigated both negative and positive performance results of species interactions between native and exotic species in a fragmented, highly invaded annual plant system and found strong evidence of positive effects on fecundity both between exotic-exotic and exotic-native species pairs. In our study, the exotic forb *M. monstrosus* was found to positively influence conspecifics, and the exotic grass *P. airoides* to have strong positive net effects on other exotic species, indicative of an invasional meltdown whereby exotic species promote the establishment of each other (Simberloff & Von Holle, 1999; Wundrow *et al.*, 2012). Indeed, in our study, natives experienced a positive net effect from their surrounding neighborhood only 5% of the time, while exotics experienced a positive effect 13% of the time. However, the presence of the exotic grass *P. airoides* also appeared to have positive effects on the majority of the native species in our study, and these native species similarly benefited from the presence of other exotic forbs. The positive effects of *P. airoides* have been observed previously in the York gum woodlands and are hypothesized to be the result of reduced environmental stressors, such as decreased evaporation in dense plant patches, outweighing the competitive effects of intraspecific aggregation, though further experiments are required to isolate this mechanism (Wainwright *et al.*, 2016; Callaway, 2007). Phenomenological estimates of species interactions are a common, efficient, and generalisable approach for quantifying and understanding species interactions in ecology (Letten & Stouffer, 2019).

Phenomenological models provide insights about the net outcomes of species interactions and can function as well to expand our understanding of the range of outcomes in species performance we can expect between native and exotic species. These insights can be used further to identify interactions of interest for further mechanistic modelling. While positive effects of interactions could be a signature of facilitation, our study was not designed to determine the underlying mechanism behind these signatures. They could be the result of direct pairwise facilitation, or diffuse competition (i.e. the net result of multiple neighbor effects; Mitchley (1987)). Future work combining manipulative studies with mechanistic models would be beneficial for determining the underlying mechanisms for the interactions of interest uncovered in this study.

Across systems exotic species have occasionally been found to facilitate native species, but these effects are much less studied or reported on than competition. For example, Pec & Carlton (2014) also found an exotic grass species to promote the growth and reproduction of certain native forb species by preventing early establishment of woody shrubs after disturbance from fires in Californian coastal sage brush. Such findings support a typically overlooked management strategy of using the knowledge of novel niche requirements or micro-habitat modifications of exotic species to aid the recovery of native populations (D’Antonio & Meyerson, 2002).

4.2 Demographic variation causes interaction effects to vary from negative to positive

Demographic variation can create variability in species vital rates and their response to one another that can drive unexpected outcomes of species interactions (Vellend *et al.*, 2014; Hart *et al.*, 2016; Shoemaker *et al.*, 2020). While previous studies have tended to focus on the importance of environmental variation, here we highlight that substantial demographic

variation can, separately from environmental variation, account for some of the uncertainty in the observed impacts of established exotic species on natives in the community. We demonstrate that the effect of one species on another can vary from negative to positive due to demographic variation in the focal species' demographic rates along with variability in the identity and density of neighbors. This finding strongly suggests a link between individual and local scale variation and invasion success or failure. Our results also allow us to gain important insights from the shape of the probability distributions of species' interactions due to demographic variation. We saw that native species had consistently small effects on most of our 11 focal species, with tight distributions centred around zero. The effect of exotic species on the majority of focal species, however, was much more varied with substantially higher variation (even when informed with sufficient data), showing wider distributions and a greater range of interaction strengths across the same community. These stronger and more varied impacts of exotic compared to native species could be a result of their eco-evolutionary novelty (Levin *et al.*, 2020). Eco-evolutionary novelty has long been hypothesized as important for determining the impacts of exotic species. It posits that 'naive' communities will be more heavily impacted by species with dynamics that they have not experienced in their evolutionary history. For instance, exotic invaders may have novel forms of attack, defense and competition (Pearse *et al.*, 2019). While the results presented here are consistent with predictions based on eco-evolutionary novelty, it would be important to investigate these patterns across a wider range of abiotic conditions and spatial grain as well as investigating differences in functional traits to see if this trend is truly the result of eco-evolutionary novelty (Levin *et al.*, 2020).

4.3 Variability at the interaction neighborhood level

In diverse communities, variation in neighbor identity at the very local neighborhood level arises due to the large number of potential neighboring species, and this variation in nearest

nearest neighbors can increase the uncertainty in specific species demographic rates at the population level (Simberloff & Von Holle, 1999; Wiegand *et al.*, 2012; Wang *et al.*, 2016). We aimed to quantify this variability and its impact on fitness outcomes by calculating the net neighborhood effect experienced by each focal species. The average of, and variance for, the net neighborhood effect for both native and exotic species was remarkably similar, with the majority of species having their fecundity inhibited by their nearest-neighbors, as expected from theory (Macarthur *et al.*, 1967). However, variability in each species' intrinsic fitness and response to neighbor abundance and identity meant that the majority of both native and exotic species experienced a net positive effect in some cases. Only one exotic forb, *M. monstrosus* experienced a predominantly positive net neighborhood effect, driven by apparent strong effects on itself; this finding is likely due to this species not being at high enough local abundances to experience negative frequency dependence. Interestingly, the invasive grass *P. airoides* exclusively experienced net competitive effects despite its presence having positive impacts on the majority of the other focal species. Since we only considered 11 of the most common species in this highly diverse system, it is possible that we missed a species involved in a positive feedback loop with *P. airoides*. Also, we only focus here on direct interactions rather than considering indirect interactions or higher-order interactions, which could lead to indirect facilitation, which may help to maintain species' populations in diverse communities (Mayfield & Stouffer, 2017; Levine *et al.*, 2017). Looking to the future, network analyses also pose a promising approach for further investigating the positions that species hold within local interaction neighborhoods and may be able to better explain the complex dynamics that our results hint at here.

To further explore the local neighborhood-level effects of these exotic-native species interactions, we calculated the ratio of the net effect of all native versus exotic neighbors on focal species realized versus intrinsic fecundity. When only native neighbors were considered, there was a trend towards focal species with lower intrinsic fecundity experiencing

less negative and/or more positive neighbor impacts and species with higher intrinsic fecundity experiencing stronger competition. This trend matches predictions where species with high seed production must be more limited by their neighbors in highly-diverse ecosystems. However, this trend eroded when considering exotic neighbors, again likely a result of the eco-evolutionary novelty of many exotic invaders and their novel interactions (Pearse *et al.*, 2019).

Exotic species can integrate themselves into plant communities with minimal impacts on native diversity; a result not necessarily predicted by invasion or competition theory (?). In this system, the large variation in both competitive strength and intrinsic fecundity could limit the more common exotic species (*A. calendula* and *P. airoides*) from becoming dominant. Likewise, while *M. monstrosus* was the only species observed to facilitate itself, it was also likely self-regulated by its comparatively low intrinsic fecundity. However, we saw that exotics tended to experience positive effects on fecundity in the presence of other exotic species, yielding a compounding effect on the community not predicted when considering single species or single invader effects in isolation. Though exotic species also had positive effects on natives, potentially increasing overall densities in the community of both natives and exotics. These findings highlight the need to consider the combined impacts of multiple exotics at a neighborhood level, ensuring that the overall impact of all exotic species in a community is not overlooked (Sheppard, 2019). Overall, our findings point to a wide range of questions about biological invasions for which more accurate findings may be possible by including demographic variation and positive interactions. In providing a novel framework through which such details can be applied to a range of models and questions we see great potential to expand our understanding of exotic species dynamics, community resilience, invasion meltdowns, and invasion control. Our findings and potential applications of our framework to the study of invasion ecology have potential implications for the allocation of management resources. Removing exotic species in this system and others like it, could have

unintended consequences such as declines in some native species that may be struggling more than in the past due to other factors such as fragmentation, climate change or soil eutrophication.

4.4 Conclusion

The use of multi-species demographic models in applied ecology and invasion biology can greatly improve predictions and generalizations across systems. We show that ignoring variation and positive outcomes of species interactions in demographic studies of diverse communities can yield incorrect conclusions about the impacts of exotic species on resident communities at local scales. Though we still have much to understand about how multiple species interact simultaneously within diverse communities, our demographic modelling framework provides a feasible approach for adding meaningful biological realism to the study of biological invasions, moving towards a generalizable framework for understanding how invasions may impact native species and other resident exotics. In this study we demonstrate how the inclusion of demographic variation and positive species interactions into classic demographic models of plant fecundity reveals variation in species responses to one another that could be responsible for the diverse and often unexpected impacts of invading species on existing communities.

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Table 1: Estimated fecundity (seed production) and net neighborhood effect of each focal species

Focal species	Intrinsic fecundity (λ)	Estimated fecundity (F_i)	Neighbor effect (F_N)
Native forbs			
<i>D. glochidiatus</i>	21.21	18.71	0.88
<i>G. tenuifolia</i>	92.37	54.59	0.59
<i>H. glutinosum</i>	64.20	44.16	0.69
<i>P. debilis</i>	47.34	27.33	0.58
<i>P. canescens</i>	503.49	334.51	0.66
<i>T. cyanopetala</i>	53.03	44.87	0.85
<i>V. rosea</i>	21.00	15.35	0.73
Exotic forbs			
<i>A. calendula</i>	146.93	84.89	0.58
<i>M. minima</i>	13.76	11.13	0.81
<i>M. monstrosus</i>	9.62	9.67	1.01
Exotic grass			
<i>P. airoides</i>	264.79	149.07	0.56

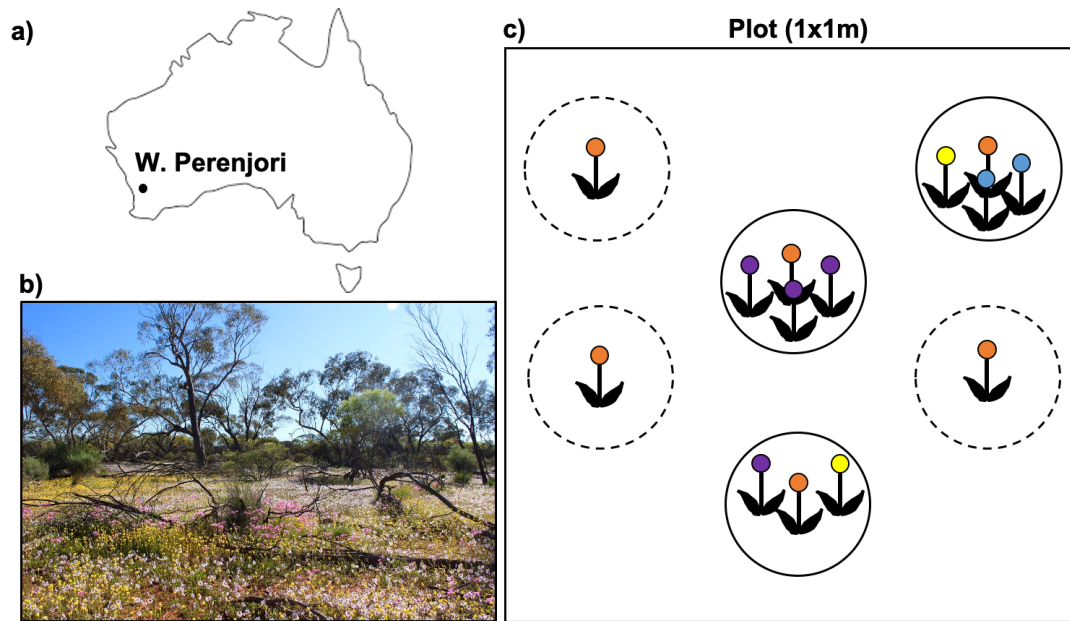


Figure 1: a) Location of West Perenjori Nature Reserve in southwest Western Australia. b) Image of York gum woodlands with annual forb understorey in September 2018. c) Plot design depicting the two types of neighborhood rings which were placed randomly within each plot. In half of the rings all germinants around the focal plant were thinned (dashed circles) to inform intrinsic fecundity estimates and the other half were left unmanipulated (solid circles) to assess the impacts of neighbors on focal individuals.

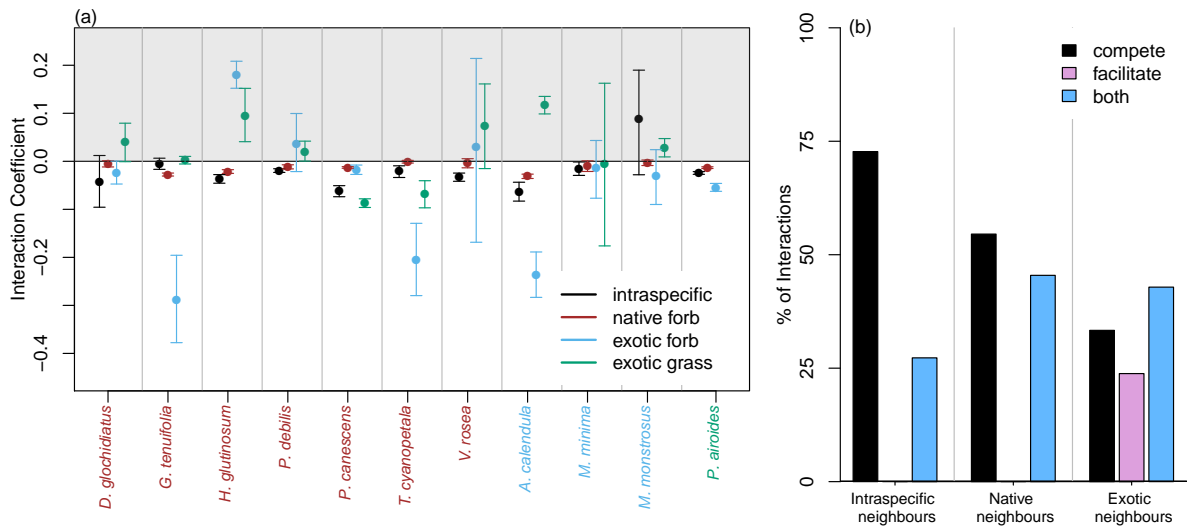


Figure 2: In a) points represent the mean of posterior distributions for interaction coefficients and error bars represent 95% credible intervals. Each focal species is listed on the x-axis. b) Summarizes the total percentage of intraspecific interactions and interactions with native versus exotic neighbors that are negative, positive, or both across the whole study.

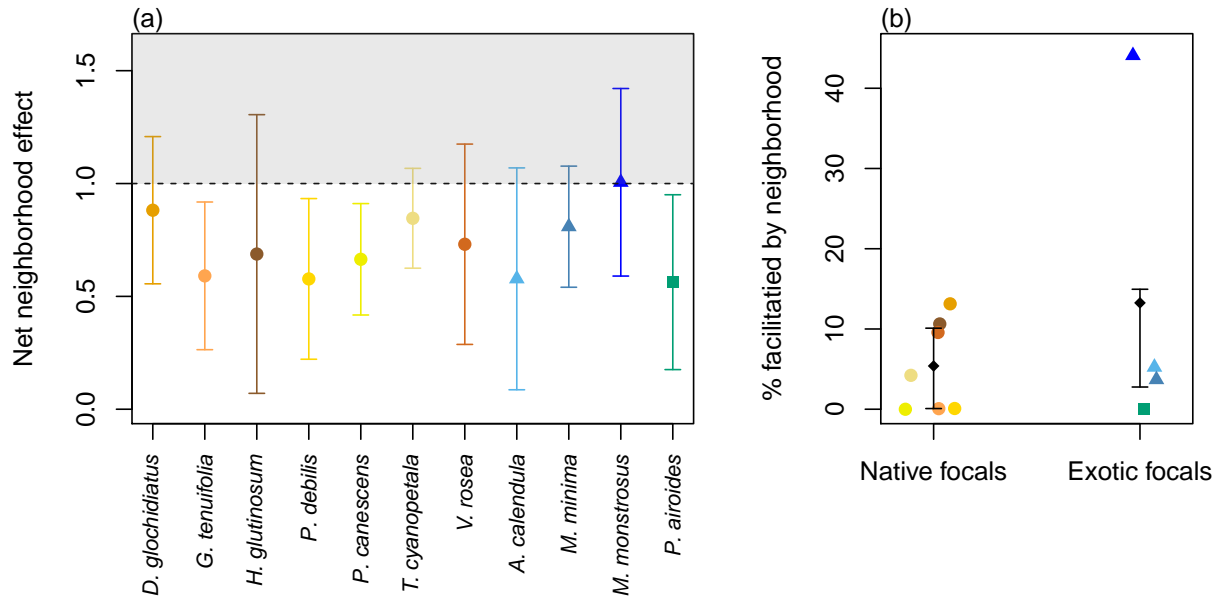


Figure 3: a) Net neighborhood fecundity for each focal species. Values above one represents the focal species experiencing a net positive neighborhood effect (grey background). Negative value represents the focal species experiencing a net competitive neighborhood effect. Error bars are 95% credible intervals. b) The percent of focal individuals that experience net positive effects from their neighborhood, separated by native versus exotics. Points represent percentage for each species. Dot colours in b match those in panel a to allow species comparison. Black diamonds represent mean for native versus exotic focal species, and error bars show interquartile range.

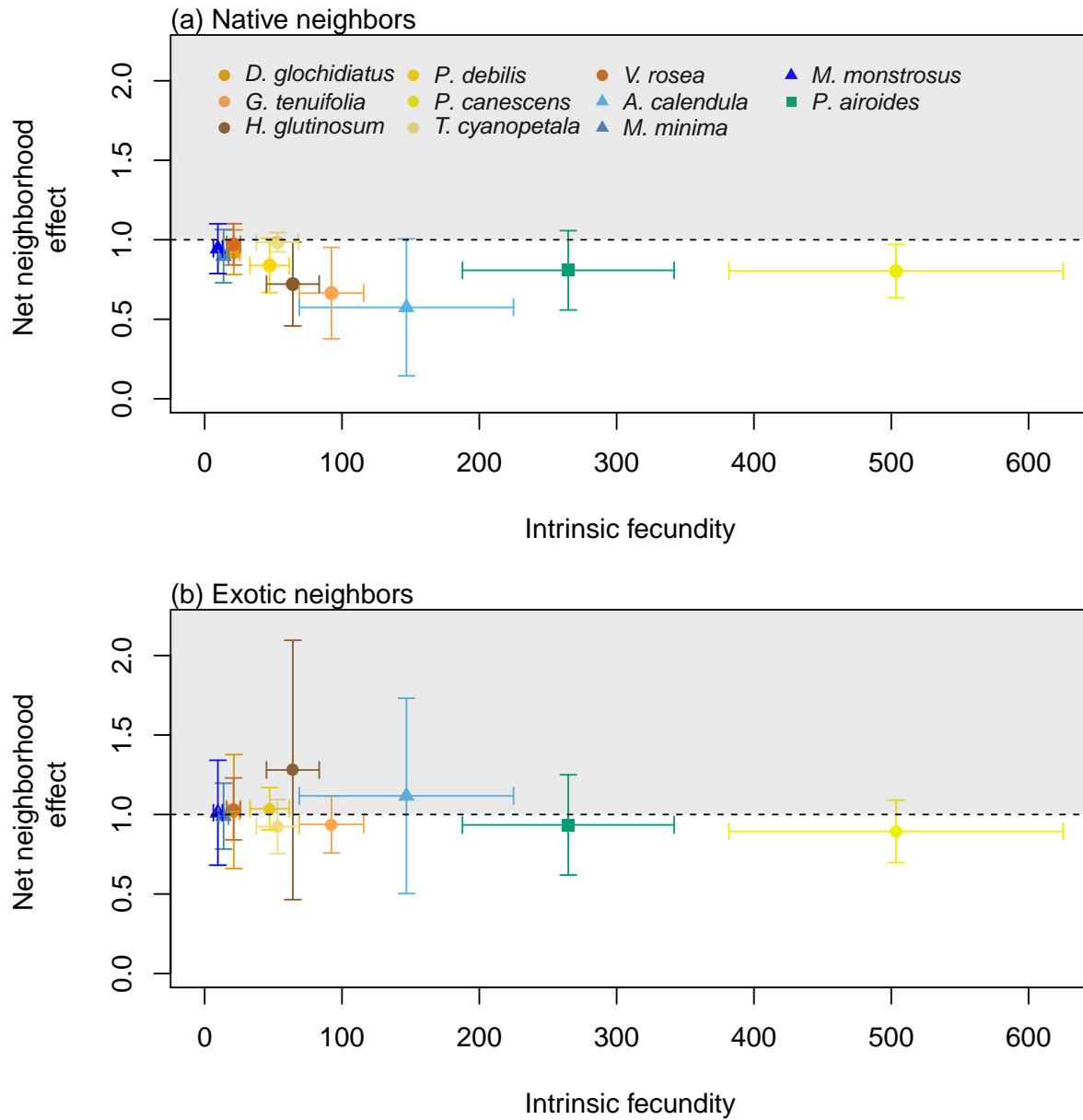


Figure 4: The ratio of net neighborhood fecundity to intrinsic fecundity of focal species. Error bars represent 95% credible intervals. a) Net neighborhood fecundity calculated with native neighbors only, and b) calculated with only exotic neighbors. See Appendix S1, Figure S3 for overall neighborhood effect.