

The impacts of exotic species on their neighbors can be better understood by accounting for demographic stochasticity, facilitation, and community composition in fitness models

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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 invasions. Demographic models estimate the strength of species interactions but have several shortcomings, including disregarding facilitation 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 stochasticity and facilitation. Facilitation mediated by exotic species played an integral role in the invaded community, but demographic stochasticity caused many species interactions to vary from facilitative to competitive, 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, and 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 noticeable 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 facilitation of native species by invaders, often by habitat modification. In fact, exotic species have even been used in the restoration of par-

40 ticularly degraded sites to improve conditions for native species when a native alternative is
41 unavailable (for example, fast-growing sterile grasses and nitrogen-fixing shrubs; D’Antonio
42 & Meyerson 2002). Coupling theory and modelling developments to more accurately pre-
43 dict the ambiguous impact of invasions is a critical step towards successful management of
44 ecological communities.

45 While theories of biological invasions have tended to focus on functional or niche-based
46 differences between species, a more recent approach has been to explore the demographic
47 processes that fundamentally drive population growth, species interactions, and ultimately
48 the success and impact of an invasion (Flory *et al.*, 2017; Larios *et al.*, 2017; Mordecai
49 *et al.*, 2018; Thomson *et al.*, 2017; Thomson, 2005). Demographic models that incorporate
50 a species’ intrinsic fitness as well as the competitive effects of one species on the demogra-
51 phy of another can quantify how demography drives species’ performance. These models
52 rely on several important simplifications that have major implications for their efficacy in
53 predicting impacts of invasion. These include 1) plant communities are structured primarily
54 by competitive interactions (Brooker *et al.*, 2008; Bimler *et al.*, 2018), 2) natural variance
55 in demographic rates that can, by chance, alter the strength and direction of species inter-
56 actions is negligible (Shoemaker *et al.*, 2020), and 3) the use of these models to investigate
57 pairwise species interactions rather than natural complex neighborhoods that include the
58 impacts of multiple invaders (Sheppard, 2019; Barabás *et al.*, 2018). While demographic
59 models provide valuable insights into biological invasions (Thomson, 2005; Mitchell *et al.*,
60 2006; McEvoy & Coombs, 1999; Parker, 2000), these simplifications could exacerbate dis-
61 crepancies between predictions and observations of invaded communities, impeding efforts
62 to obtain generalizable models that can more accurately predict the varied impacts of in-
63 vasion across systems. In particular, we propose that a demographic modelling approach
64 to invasion biology would greatly benefit from the inclusion of positive species interactions
65 (facilitation), demographic stochasticity, and stochastic variation in the identity of neighbors

in diverse interaction neighborhoods.

Facilitation plays a large role in driving population dynamics and structuring communities, but is rarely included in models of species interactions (Bruno *et al.*, 2003; Brooker *et al.*, 2008). Facilitation, where one species has a positive effect on another’s growth, reproduction, or survival, has 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 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 facilitative outcomes. For instance by creating micro-climatic conditions that buffer another species 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 ‘invasional meltdown’ occurs (Simberloff & Von Holle, 1999). Native plants have also been found to aid the invasion and growth of exotic species through facilitative impacts such as shading (Bulleri *et al.*, 2008). However, exotic species are less often found (or reported) to facilitate 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 from demographic stochasticity influences the impacts of exotic species. Demographic stochasticity arises from the probabilistic nature of demographic rates and variation in vital rates among individuals within a population (Melbourne & Hastings, 2008). Each process (e.g. births, seed production etc.) can be described by an underlying probability distribution of possible events, which can 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). For example, strong demographic stochasticity could result in

instances of unexpectedly weaker competition or even facilitation between two individuals, which scaled up to the species level, decreases the net competitive outcome of an interaction or increases the variance in the outcomes of species interactions. Stochastic 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 stochasticity (Melbourne & Hastings, 2008; Lande, 1993).

In order to gain greater insights into the importance of facilitation along with demographic and neighborhood stochasticity in mediating the impacts of invading species on resident communities, we use data from the York gum woodland annual plant communities of Western Australia to answer the following questions:

1. Are interactions between native and exotic species' defined mostly by competition, facilitation, or both?
2. How does demographic stochasticity alter the effects of native/exotic species interactions?
3. Do net neighborhood effects differ between native and exotic species?

We hypothesized that facilitation would be a prominent process occurring among species in the York gum woodlands, including between native and exotic species as well as among exotic species (Wainwright *et al.*, 2016). We expected that demographic stochasticity could cause species interactions to shift from competitive to facilitative, blurring the net impacts of interactions on a species' fecundity. We further hypothesized that demographic stochasticity,

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 stochasticity in both intrinsic fitness and interaction coefficients and allows for both facilitation and competition between 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 facilitation to effect both native and exotic species fitness, and the importance of placing these effects within the broader and highly variable neighborhood context.

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: *Arctotheca 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 stochasticity 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.

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 (see Appendix S1 in Supporting Information, 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 species. We incorporated demographic stochasticity 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). We then calculated probability distributions of fecundity, incorporating the net neighborhood effect experienced by each focal

190 species.

191 We used a Bayesian modelling framework to estimate intrinsic seed production and inter-
192 action coefficients with the annual plant fecundity model from Mayfield & Stouffer (2017).
193 This model (Eq. 1) describes seed production (F_i) of a focal individual of species i at the
194 end of the growing season where:

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

195 We recovered posterior distributions of species' density-independent intrinsic fecundity, λ ,
196 and the total direct effects of all intra- and inter-specific neighboring functional groups, G ,
197 from interaction coefficients $\alpha_{i,j}$. Unlike in other common annual plant models (Hallett *et al.*,
198 2019; Levine & HilleRisLambers, 2009), interaction coefficients incorporate both competition
199 (negative values) and facilitation (positive values). Neighboring groups (native forb, exotic
200 forb, exotic grass, and unknown species) are represented by j , with their effect multiplied
201 by abundance of the neighbor group (N) within each neighborhood ring. Interaction effects
202 are summed across all neighboring groups present in a neighborhood ring. Neighbor species
203 were grouped into 'functional groups' based on life form (see Appendix S1, Table S1). These
204 included native annual forb, exotic annual forb and exotic annual grass (native annual grasses
205 are rare in this system). Unidentified neighboring species were grouped into a separate
206 category and included in all analyses and calculations, but are not shown in figures. T.
207 Martyn (Martyn et al. In Review) found in two annual plant systems (including the York
208 gum woodlands), that grouping the effects of neighboring species by functional form and
209 origin was equally as effective as including each neighbor species separately and produced
210 more parsimonious individual fitness models.

211 We incorporated plot-level random effects to account for variability in abiotic factors
212 between plots, where observed fecundity \hat{F}_i was multiplied by a random plot-level parameter,

such that $\hat{F}_i = \epsilon_p F_i$ where p denotes plot identity (Lee *et al.*, 2020). Prior distributions on interaction coefficients were uninformative normal distributions centred on 0 with standard deviations of 1000. For λ , we also used an uninformative prior in the form of a gamma distribution with both shape and rate parameters set to 0.001. For each focal species we ran 3 MCMC chains, sampling 6000 iterations and thinning by two iterations to remove autocorrelations. We assessed convergence of the chains using \hat{R} (Gelman-Rubin convergence diagnostic; assuring the convergence of chains in models for all of our focal species), checking the trace plots for chain mixing. We fit the models in R (Version 3.5.3) using the package rstan (Stan Development Team, 2020) with post-processing in R.

2.3.2 Calculating net neighborhood effect

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

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

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

3 Results

3.1 The relative importance of competition versus facilitation in species interactions

Across all species, competitive interactions were more common than facilitative interactions, though facilitation accounted for just over 25% of interactions among species (Fig. 2). Most interactions however, could not be clearly defined as solely competitive or facilitative (Fig. 2b). Intraspecific interactions were more often competitive than facilitative (competitive 73% of the time; Fig. 2b).

3.2 The role of stochasticity in demography and neighborhood composition

Demographic stochasticity, in some cases combined with relatively weak interaction strength, caused 24% of interaction coefficients to vary between competitive and facilitative, irrespective of abiotic factors (distributions that overlap zero in Fig. 2a). This is 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 stochasticity (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 fe-

cundity ranging from 0.56 to 1.01. Seven of the 11 focal species experienced a range of net neighborhood fecundity encompassing both facilitation and competition 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, despite being found to facilitate the majority of focal species (Fig. 2a). On average, exotic species were facilitated by their neighborhood more often than native species (Fig. 3b), but this average was strongly influenced by *M. monstrosus*, for which we observed strong intraspecific facilitation. All exotic forbs were facilitated in a portion of their observed neighborhoods, while only four of the seven native forbs were sometimes facilitated by their neighborhood (Fig. 3a).

3.3 Differences between native and exotic species

Fully facilitative effects among species were all from exotic neighbors (Fig. 2b). The exotic forbs were found to purely facilitate one of the seven native forbs, and to sometimes facilitate an additional two when demographic stochasticity was considered. Similarly, exotic forbs facilitated two of the four exotic species, and another one when demographic stochasticity was considered. The exotic grass *P. airoides* was found to fully facilitate three out of seven of the native species and two additional native species when demographic stochasticity was considered, highlighting the role of the invasive grass in facilitating a majority of species in the system. *P. airoides* was also found to facilitate two of the exotic forb species, as well as the third exotic forb species when demographic stochasticity was considered. For the native forb species *D. glochidiatus*, *G. tenuifolia* and *M. monstrosus*, intraspecific interactions were not purely competitive (and even often facilitative 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 facilitated by their

surrounding neighbors (Fig. 3b). While all focal species except for the exotic forb *M. mon-*
strosus were, on average, inhibited by their neighborhood, natives were facilitated 5% of the
time while exotics were facilitated 13% of the time.

We compared the net effect of native (Fig. 4a) versus exotic (Fig. 4b) neighbors to the in-
trinsic 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* experi-
encing similar competitive effects on net neighborhood fecundity. In comparison, there was
no identifiable trend between net neighborhood and intrinsic fecundity with exotic neigh-
bors, and many species (both exotic and native) experienced a net facilitative 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 individual-
level variation in fitness will fall within the competitive range. In reality, the ecology of nat-
ural plant communities is much more dynamic, including substantial amounts of variation,
with facilitative and competitive effects both commonly occurring. In invaded communi-
ties, these simplifying assumptions have historically driven the ways in which we look for
mechanisms of invasion, biasing our literature toward the expectation that exotic and native
species compete with each other. By accounting for facilitation, demographic stochasticity,
and observed variation in interaction neighborhoods in models of species performance, our
demographic modelling approach reveals that facilitation and 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, facilitation 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 stochasticity in the effects of pairwise interactions, interactions between exotic-native species pairs ranged from competitive to facilitative 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 competition and facilitation and are highly dynamical both within and among species.

4.1 Facilitation was 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 disregarded in multi-species demographic modelling and have only recently been considered integral to the invasion process (Bulleri *et al.*, 2008). We investigated both competitive and facilitative species interactions between native and exotic species in a highly fragmented, invaded annual plant system and found strong evidence of facilitative patterns both between exotic-exotic and exotic-native species pairs. In our study, the exotic forb *M. monstrosus* was found to facilitate itself and the exotic grass *P. airoides* strongly facilitated 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). However, *P. airoides* also facilitated the majority of the native species in our study, and these native species similarly benefited from the presence of other exotic forbs. The facilitative 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 (Wainwright *et al.*, 2016; Callaway, 2007). 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 stochasticity causes interaction effects to vary from competitive to facilitative

Demographic stochasticity 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). In the context of biological invasions, substantial stochastic variation can account for some of the uncertainty in predicting whether exotic species will successfully invade and their subsequent impacts on native populations. We demonstrate that the effect of one species on another can vary from competitive to facilitative due to demographic stochasticity in the focal species’ demographic rates along with stochasticity 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 stochasticity. 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. Eco-evolutionary novelty has long been hypothesized as important for determining what makes a successful invader. It posits that ‘naive’ communities will be more heavily impacted by species with ecology 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). Further research with increased sample size and diversity of exotic species would help determine whether this trend is a statistical artefact as a result of the typically lower abundance of exotic individuals compared to natives.

4.3 Stochasticity at the interaction neighborhood level

In diverse communities, stochastic variation at the very local, neighborhood level can arise due to the large number of potential neighboring species (Simberloff & Von Holle, 1999; Wiegand *et al.*, 2012; Wang *et al.*, 2016). We aimed to quantify this variability and its impact 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. However, stochasticity 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 facilitative effect a small percentage of the time. Only one exotic forb, *M. monstrosus* experienced a predominantly facilitative net neighborhood effect, driven by strong intraspecific facilitation, although 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 being found to facilitate 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, pairwise interactions rather than considering indirect interactions or higher-order interactions, which could lead to indirect facilitation, another mechanism that 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 fecundity versus intrinsic fecundity. When only native neighbors were considered, there was a trend towards focal species with lower intrinsic fecundity experiencing less competition and/or more facilitation 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 impact on native diversity; a result not necessarily predicted by invasion or competition theory (Gurevitch *et al.*, 2011). 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 be facilitated more often (and by other exotics), yielding a compound effect on the community not predicted when considering single species or single invader effects in isolation. Though exotic species also facilitated natives,

potentially increasing overall densities in the community of both natives and exotics. This highlights 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). Our findings about the impacts of demographic stochasticity and the frequency of facilitation in this system have implications for the allocation of management resources, since removing the exotic species in this system, particularly the exotic grasses, could have unintended consequences such as declines in some native species.

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 stochastic variation and facilitation in demographic studies of diverse communities can yield incorrect conclusions about invasion potential 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 when local invasions are likely and how they may impact native species and other exotics. In this study we demonstrate how the inclusion of demographic stochasticity and facilitation 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

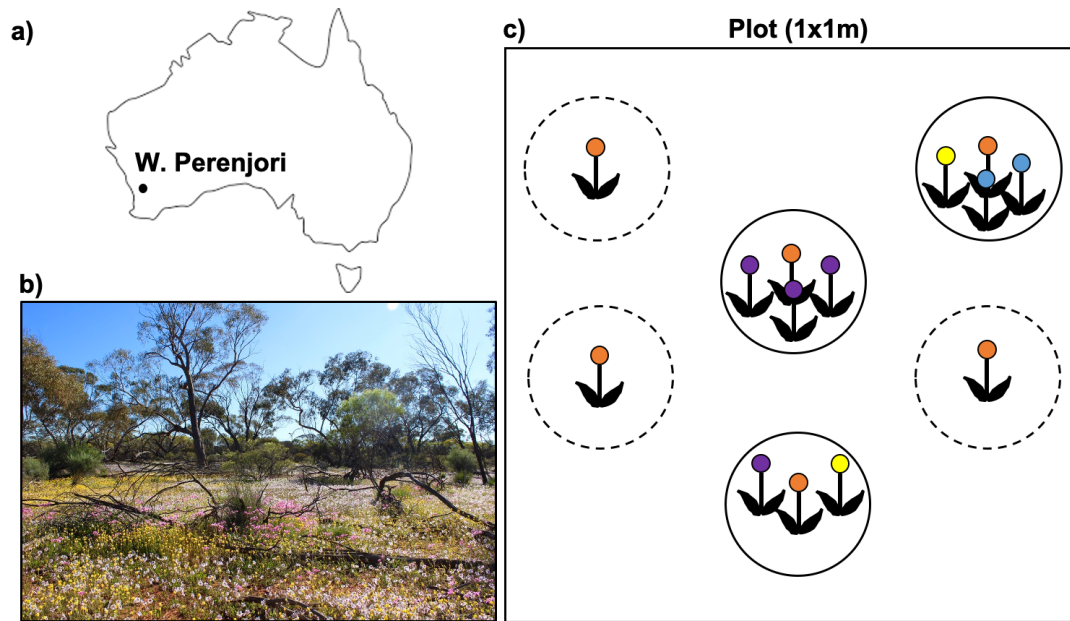


Figure 1: a) Location of West Perenjori Nature Reserve in southwest Western Australia. b) Image of York gum woodlands with annual forb understorey in September 2018. c) Plot design depicting the two types of neighborhood rings which were placed randomly within each plot. In half of the rings all germinants 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.

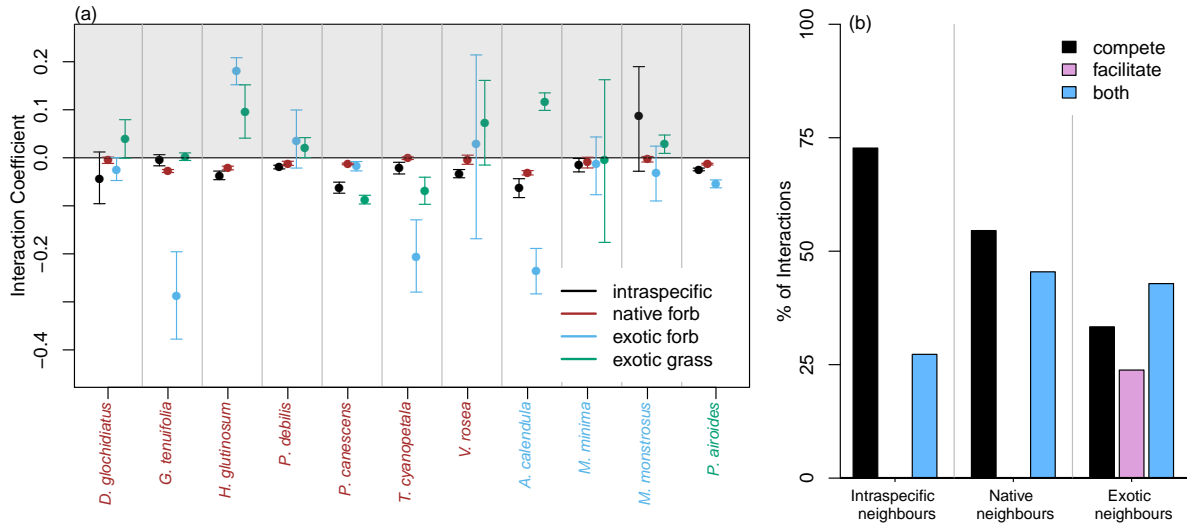


Figure 2: In a) points represent the mean of posterior distributions for interaction coefficients and error bars represent 95% credible intervals. Each focal species is listed on the x-axis. Negative interaction coefficient values represent competition (white background), positive values represent facilitation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

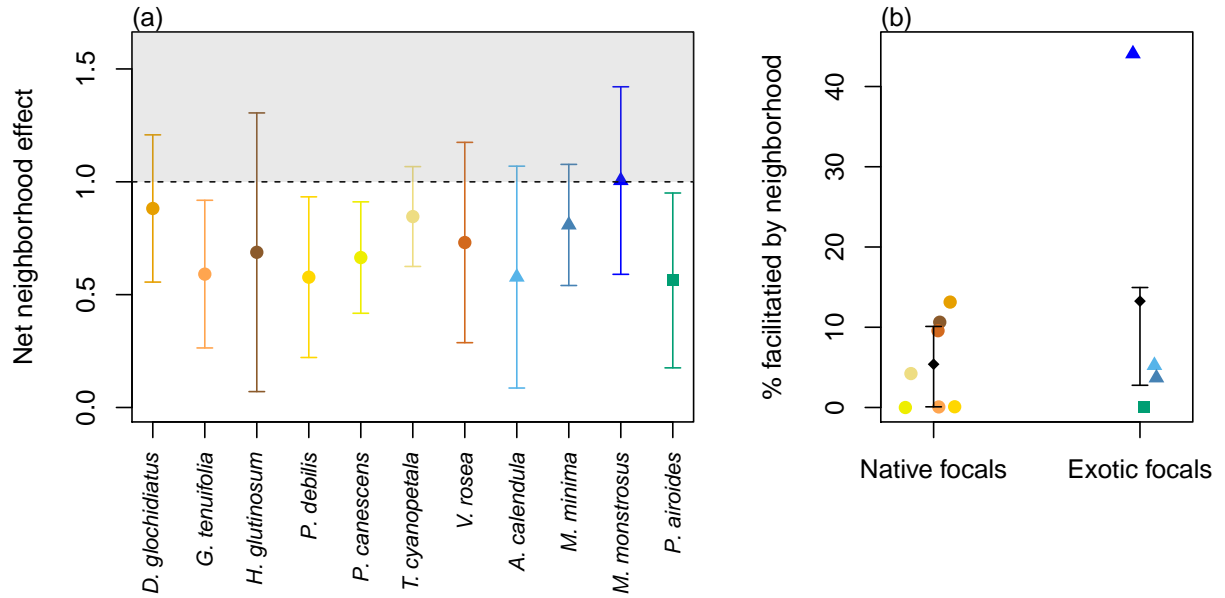


Figure 3: a) Net neighborhood fecundity for each focal species. Values above one represents the focal species experiencing a net facilitative neighborhood effect (grey background). Negative value represents the focal species experiencing a net competitive neighborhood effect. Error bars are 95% credible intervals. b) The percent of focal individuals facilitated by 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.

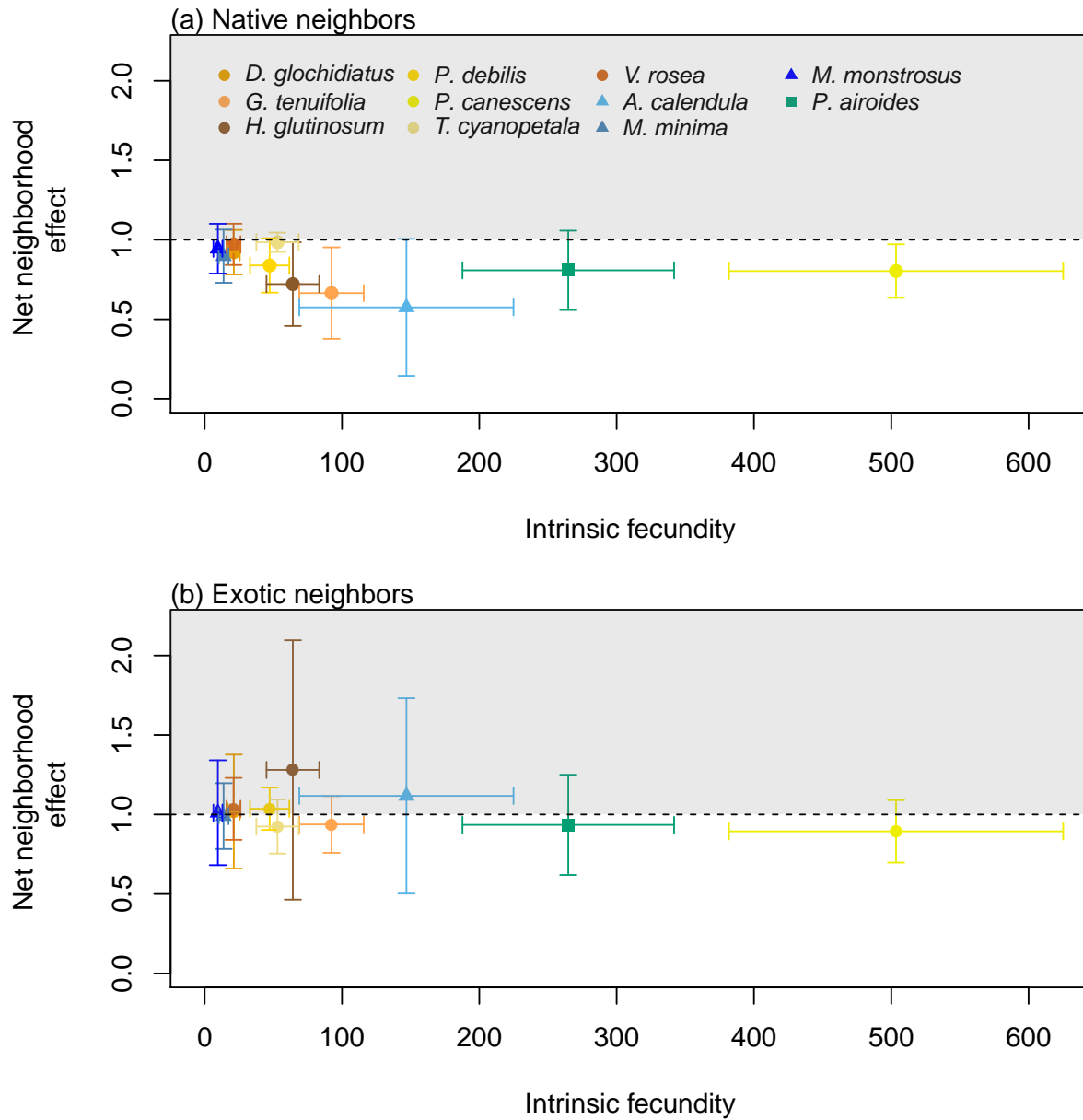


Figure 4: The ratio of net neighborhood fecundity to intrinsic fecundity of focal species. Error bars represent 95% credible intervals. a) Net neighborhood fecundity calculated with native neighbors only, and b) calculated with only exotic neighbors. See Appendix S1, Figure S3 for overall neighborhood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