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Positive effects of exotic species dampened by neighborhood heterogeneity

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Abstract

It is well known that species interactions between exotic and native species are important for determining the success of biological invasions and how influential exotic species become in invaded communities. The strength and type of interactions between species can substantially vary, however, from negative and detrimental to minimal or even positive. Increasing evidence from the literature shows that exotic species have positive interactions with native species more often than originally thought. Gaps in our theory for how population growth is limited when interactions are positive, however, restrict our understanding of the mechanisms by which exotic "facilitators" contribute to diversity maintenance in invaded systems. Here, we quantified interactions between seven native and four exotic (established nonnative) common annual plant species in the highly diverse, York Gum woodlands of Western Australia. We used a Bayesian demographic modeling approach that allowed for interaction coefficients to be positive or negative, and explored key sources of variation in species responses to native and exotic neighbors at per capita (individual) and neighborhood levels. We observed positive per capita effects from exotic neighbors on exotic focal species as well as on several native focal species. However, all focal species were, on average, inhibited by their interaction neighborhood, when the variance in identity and abundance of observed neighbors was considered. At the neighborhood scale, exotic species were found to suppress all focal species, particularly those with high intrinsic fecundity. Our study demonstrates that within-neighborhood heterogeneity can regulate per capita positive effects of invaders, limiting runaway population growth of both natives and exotic invaders.

KEYWORDS
alien species, Bayesian modeling, invasion ecology, positive interactions, species interactions, variance, York gum woodlands

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INTRODUCTION

Extensive research has shown that exotic species can have a wide range of effects on the performance of native species, ranging from strongly negative to positive effects on native survival, growth, and reproductive performance (Ferenc & Sheppard, 2020; Gross et al., 2015; Hulme et al., 2013; Lenda et al., 2019; Liancourt et al., 2005; Suding et al., 2003). Quantifying the strength of interactions within and among native and exotic plant species has been a key approach in invasion biology. For instance, this information can help determine the impacts of exotic species on plant communities in studies both focused on the per capita scale (interactions between individuals) and at the local interaction neighborhood scale (Mouquet & Loreau, 2003; Spasojevic & Suding, 2012).

While positive interactions between species pairs have been demonstrated in numerous systems, particularly plants, it remains less clear how such positive outcomes are restricted, a necessary outcome to avoid runaway population growth (i.e., species A indefinitely facilitating the population growth of species B) (Brooker et al., 2008; Soliveres et al., 2015). The uncertainty about how positive outcomes end in natural systems often drives researchers to ignore these interactions altogether, deciding to only consider competitive effects when modeling interactions between species and predicted changes in species abundances and community properties through time. This practice, though of great practical appeal, misses the important fundamental question of what limits population growth in natural communities in which positive interaction outcomes are prevalent? Here we explore how within-neighborhood heterogeneity, a critical source of ecological variation that is defined as variation in the identity and abundance of observed neighbors (hence an average individual experiences interactions with multiple species), may limit population growth in the context of an invaded annual herbaceous wildflower community in the York gum woodlands, Western Australia. This system is known to involve substantial numbers of positive species interactions, specifically between exotic and native species pairs (Bimler et al., 2018; Lai et al., 2015; Wainwright et al., 2019).

The varied effects of exotic species on natives have been linked to differences in terms of their niche requirements (Funk & Vitousek, 2007; Leger & Espeland, 2010; Levine & HilleRisLambers, 2009; Shea & Chesson, 2002), their competitive abilities (Gioria & Osborne, 2014; Shea & Chesson, 2002) or both (Gross et al., 2013; Macdougall et al., 2009). Variation in the identity and density of neighbors in diverse communities ("within-neighborhood heterogeneity"), though less explored in the literature, may also play a key role in how populations are affected by interactions with specific established exotic species (Ferenc & Sheppard, 2020; Lenda et al., 2019). Variation in species' performance can arise at the neighborhood-level, especially in diverse communities, due to the large number of potential neighbors and variation in the density of different neighbor species (Wiegand et al., 2012). The consequences of this neighborhood level variation on species' performance have been examined primarily in diverse rainforests from both Asia and the Americas (Punchi-Manage et al., 2020). However, similar effects are likely to occur across other ecosystems, including annual plant communities, where individual neighborhoods are highly variable in their densities and compositions (Martorell & Freckleton, 2014).

This neighborhood variation may play an important role in how multiple exotic species interact with each other and on how exotic species affect resident natives. For instance, it is possible that the collective neighborhood effect masks the positive effect that a particular neighboring species has on a focal species. Understanding the sources of variance in the response of native species to established exotics is particularly important for managers faced with multiple co-occurring exotic species exhibiting distinct effects on the native community (Ferenc & Sheppard, 2020; Lenda et al., 2019; Sheppard, 2019). For instance, in cases where managers are seeking to create species mixes that positively impact the success of native species, or help suppress population growth of an exotic species, it is important to know which species combinations result in positive interactions and their net effect in diverse communities.

Here we used a demographic Bayesian modeling framework to estimate interaction coefficients between native and exotic species. We applied this to fecundity (seed production) data from neighbor removal treatments for seven native and four exotic annual plant species from the invaded understory of the York Gum woodlands in southwest Western Australia. We investigated the strength and direction of species interactions between natives and exotics, comparing across functional groups (grass and forb). We quantified the net neighborhood effect that each focal species experienced, determining whether these species were inhibited or promoted by their neighborhood. We asked two questions: are exotic species promoting or inhibiting the per capita seed production of native species and other exotic species, and are exotic species suppressing the seed production of each other and native neighbors at the neighborhood level? We hypothesized that positive effects of neighbors on the per capita seed production of focal species would be common between exotic-exotic and native–exotic species

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pairs, as has been demonstrated through pairwise segregation (Lai et al., 2015) and linear models (Wainwright et al., 2016) in this system. However, we expected that these per capita positive effects of exotic species on native species' fecundity may not be strong enough to lead to a net promotion of fecundity at the interaction neighborhood level, thereby controlling population growth, even in the presence of species with positive effects (Qian & Akcay, 2019).

METHODS

Study system

Data were collected between July and October in 2018 in the annual plant understory of the York gum woodlands in West Perenjori Nature Reserve (29°47′ S, 116°20′ E), located at the northern extent of the York gum woodlands in southwest Western Australia (Figure 1a,b). 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 with exotic annual plant establishment in remnants exacerbated by fertilizer run-off (Dwyer et al., 2015). The region experiences a Mediterranean climate where winter rainfall (May–October) triggers the germination of a diverse array of annual forb and a few grass species.

We chose a mixture of dominant and co-occurring annual native (seven) and exotic (four) species (three forbs and one grass) that are all either gravity or wind dispersed as the focal species for our field experiments and demographic modeling. The seven native forb 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* (the only grass). There are no native annual grasses common to this system, which is why none were considered.

Study design

In a spatially nested design, we established 16 plots (1 × 1 m) for each of our 11 focal species. We located plots throughout a study area of ∼12 ha within West Perenjori Reserve. We allocated plots in a haphazard, but targeted, way that focused on areas where each focal species was growing. This ensured we captured the wide extent of variation in neighborhood composition and local environments experienced by each focal species. In doing so we captured a gradient of experienced inter- and intraspecific interactions for each focal species. Within each plot, we placed six 15 cm diameter "neighborhood rings" centered on a focal individual or "phytometer" of the relevant species (Figure 1c). Focal individuals were chosen by haphazardly tossing metal rings on the ground

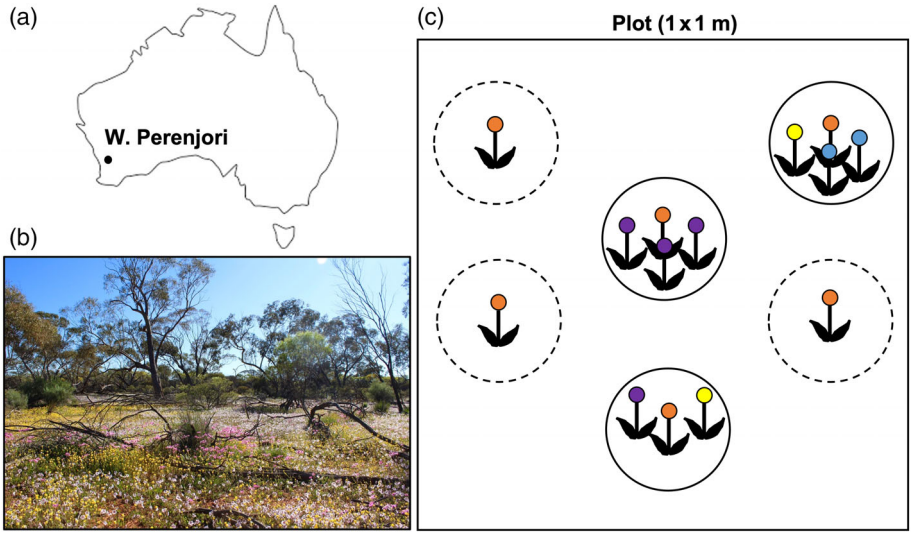

FIGURE 1 (a) Location of West Perenjori Nature Reserve in southwest Western Australia. (b) Image of York gum woodlands with annual forb understory in September 2018. (c) Plot design depicting the two types of neighborhood rings (15 cm diameter) that were centered around a randomly chosen focal plant 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 effects of neighbors.

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as each plot had the focal species in them. Then we selected the individual of the relevant species nearest to the center of the ring to be the focal plant. If no individual of the relevant focal species was in the ring, we repeated ring placement. No rings overlapped to cover the same neighborhood. Half of the rings within a plot were randomly assigned an un-manipulated treatment (with the 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 from the cleared plots during periodic checks throughout the growing season.

We tracked the survival to reproductive maturity and seed production of each focal plant. To assess seed production, we placed thin mesh bags over immature fruiting bodies as these fruiting bodies were produced, minimizing disturbance to each plant and any loss of seeds. For most species, the target individual's total seed production was counted by hand, excluding seeds that were unfilled. In the case of *Pentameris airoides*, the number of florets was recorded and then multiplied by two as a measure of fecundity as florets of this species contain two seeds on average. As focal plant survival was generally high (99.8%), 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 (using the same seeds collected for this study) to demonstrate the very small amount of observation error (<6%) expected (see Appendix S1: Table S3).

Neighborhood ring diameter was chosen to capture the local interaction neighborhood of the phytometer plants, following protocol from Mayfield and Stouffer (2017). Plot size was sufficiently small that plants experience minimal abiotic variation within a given plot (Dwyer et al., 2015). Within each plot, we quantified the key abiotic conditions previously shown to alter vegetative community composition: canopy cover, soil phosphorus, 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 at the beginning of the growing season, to best represent nutrient content prior to annual plant uptake. These samples were then air-dried and analyzed for extractable phosphorus (mg/kg) by the School of Agriculture and Food Sciences, the University of Queensland. Percent leaf litter cover was also estimated for each plot by taking digital photographs, overlaying a 100-point grid, and counting the number of litter "hits." We found little effect of these three key environmental variables on demographic rates across focal species (Appendix S1: Figures S1 and S2), and hence these specific variables were not included in our final fecundity models described in *Measuring Abiotic Varation*.

Statistical analysis

Annual plant fecundity models

To test our hypotheses, we fit Bayesian models of annual plant fecundity for each of our 11 focal species, incorporating intrinsic seed fecundity along with conspecific and heterospecific density dependence. We estimated posterior distributions of intrinsic fecundity and interaction coefficients from the major groups of neighbors (native/exotic annual forbs and an exotic annual grass). Bayesian analysis estimates a "posterior" probability distribution for demographic rates (e.g., seed production and species interaction coefficients; Ellison, 2004), rather than a typical point estimate and standard error from a frequentist framework.

We estimated intrinsic seed production and interaction coefficients with the annual plant fecundity model from Mayfield and Stouffer (2017). This model (Equation 1) describes expected seed production ($\widehat{F}_i$) of a focal individual of species i at the end of the growing season where

$$\widehat{F}_i = \lambda_i e^{\alpha_{ii}N_i + \sum_{j \neq i}^{G} \alpha_{ij}N_j}. \quad (1)$$

For each of our 11 focal species, we calculated posterior distributions for each model parameter: species' density-independent intrinsic fecundity λ_i, intraspecific interaction coefficients α_{ii}, and interspecific interaction coefficients α_{ij} between the focal species i and neighborhood group j (with a total of four groups; $G = 4$) of neighbor abundance N. Unlike in other common annual plant models (Hallett et al., 2019; Levine & HilleRisLambers, 2009), interaction coefficients in this model incorporate both positive and negative values (i.e., an increase or reduction in fecundity in the presence of neighbors, respectively). Neighbor species were grouped into four "functional groups" based on life form (see Appendix S1: Table S1). These included "native annual forb," "exotic annual forb," "exotic annual grass," and "other." Note that the exotic annual grass category only includes *Pentameris airoides*, as it is the only annual grass commonly found in this system. Unidentified neighboring species were grouped into the "other" category and included in Bayesian model fits (though not shown in figures) but not in net neighborhood calculations as their posterior distributions were all broad and uninformative. Martyn et al. (2021) found in two annual

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plant systems (one of which was the York gum woodlands) that models that included groups of neighboring species by functional form and origin fit as well as or better than those that included each neighbor species separately. Interaction effects were based on the total abundance of all species within a functional group that were present in the relevant neighborhood ring.

We incorporated a random plot-level effect in each focal species' model to account for variability in abiotic factors between plots, where expected fecundity $\widehat{F}$ was multiplied by a random plot-level parameter, ε_p where p denotes plot identity (Lee et al., 2020). Observed fecundity (F) was thus modeled as $F \sim \text{Poisson}\left(\varepsilon_p \widehat{F}\right)$. This allowed us to isolate the effects of biotic variation from potential effects of underlying environmental heterogeneity across plots. Plot-level random effects did not vary systematically across environmental gradients (Appendix S1: Figures S1, S2) but were included to allow us to remove this source of variation and focus on biotic effects in downstream analyses.

Prior distributions on interaction coefficients were uninformative normal distributions centered on 0 with standard deviations of 1000, leaving the posterior distributions to be largely shaped by the data rather than prior assumptions of their value. For I, we also used an uninformative prior in the form of a gamma distribution with both shape and rate parameters set to 0.001. Plot-level random effects were given priors $\varepsilon_p \sim \text{gamma}(\sigma,\sigma)$ with $\sigma \sim \text{gamma}(0.001, 0.001)$ (Lee et al., 2020).

For each focal species, we ran three MCMC chains, sampling 6000 iterations and thinning by two iterations to remove autocorrelation. We assessed convergence of the chains using $\widehat{R}$ (Gelman-Rubin convergence diagnostic, assuring the convergence of chains in models for all our focal species) and by visually checking the trace plots for chain mixing. We fit the models in R (Version 3.5.3) using the package Rstan (Stan Development, 2020) with post-processing in R.

Calculating net neighborhood effect

To examine how the density and identity of neighborhood individuals alter species' fecundity, we calculated the net neighborhood effect experienced by each focal species F_N as

$$F_N = \ln\left(\frac{\widehat{F}_i}{\lambda_i}\right) = \alpha_{ii}N_i + \sum_{j \neq i}^{G} \alpha_{ij}N_j. \quad (2)$$

If $F_N > 0$, the focal species experiences an overall positive effect from their neighborhood. If $F_N < 0$, the focal species experiences an overall competitive effect. If $F_N = 0$, 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). For the net neighborhood effect, we included the interaction coefficients for conspecific, native, and exotic neighbors, but not for the "other" category since posteriors were broad and uninformative (i.e., $G = 3$ in Equation 2).

We further explored if net neighborhood effects covaried systematically with each species' intrinsic fecundity, examining covariation patterns across both focal-species and neighbor identity and providing insight into the role of exotic species in the community. To do this, we calculated Spearman's rank correlation coefficients between net neighborhood effect (partitioned for native/exotic neighbors) and intrinsic fecundity across focal species, giving us a distribution of correlations between net neighborhood effects and intrinsic fecundity. We expected to see a negative correlation between net neighborhood effect and intrinsic fecundity, i.e., species with higher intrinsic fecundity should experience a greater net inhibition of fecundity by their neighborhood.

RESULTS

Exotic neighbors had positive effects on focal natives and other exotics, while native neighbors did not

Exotic species accounted for all strictly positive per capita effects (i.e., those with positive 95% credible intervals not including zero) observed in the community (Figure 2). The exotic grass (*Pentameris airoides*) had a strictly positive effect on the fecundity of three of the seven native forbs and two of the four exotic species (Figure 2a). The presence of exotic forbs as a group had a strictly positive effect on the fecundity of one native species (Figure 2a). In the remaining cases where exotic neighbors had a positive effect on average on native species, the credible interval for the posterior distribution overlapped zero (Figure 2a), giving some probability (from 4% to 42% across species) that per capita effects were negative.

Interaction coefficients were strictly negative for 73% of conspecific and native neighbor interactions, but only for 29% of exotic neighbor interactions (Figure 2b). 24% of exotic neighbor interaction coefficients were strictly positive (Figure 2b). The remaining 27% of conspecific and native neighbor interaction coefficients and 48% of exotic neighbor interaction coefficients had posterior distributions overlapping zero (Figure 2b). In addition to exotic neighbors accounting for all strictly positive

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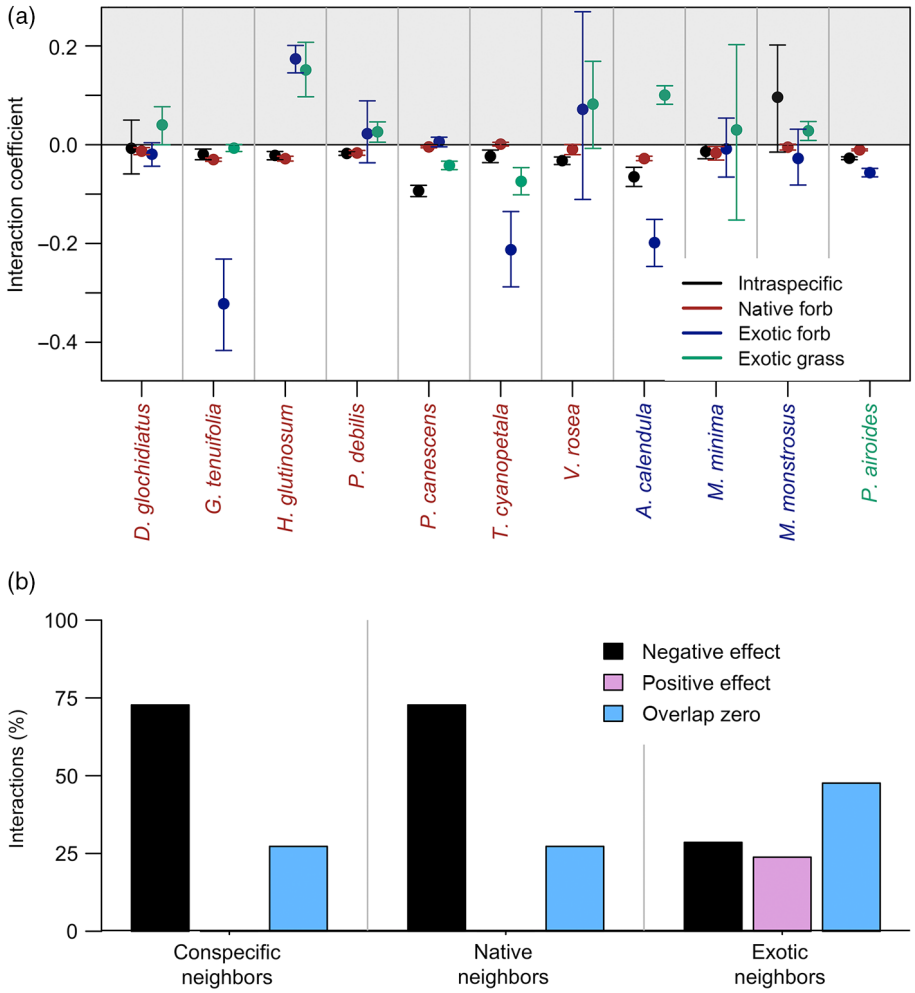

FIGURE 2 In (a), points represent the mean of posterior distributions of per capita interaction coefficients and ranges show 95% credible intervals. Each focal species is listed on the *x*-axis, color coded by its functional group (*Daucus glochidiatus*, *Gilberta tenuifolia*, *Hyalosperma glutinosum*, *Plantago debilis*, *Podolepis canescens*, *Trachymene cyanopetala*, *Velleia rosea*, *Arctotheca calendula*, *Medicago minima*, *Monoculus monstrosus*, and *Pentameris airoides*.) Panel (b) summarizes the total percentage of intraspecific interactions and interactions with native versus exotic neighbors that are negative, positive, or not strictly either across the whole study.

interactions, the percentage of interactions with probability distributions overlapping zero and therefore exhibiting a probability of either positive or negative interactions, was also highest for exotic neighbors (49%) compared to native neighbors or conspecifics (27%) (Figure 2b). This was the case for the effect of exotic forbs on *Plantago debilis* (29% probability of being negative) and *Velleia rosea* (42% probability of being negative), and for the effect of the exotic grass, *Pentameris airoides*, on *Goodenia rosea* (though with only 4% probability of exhibiting a negative effect in this case). In only one out of three cases, the exotic grass's effect on an exotic forb (*Medicago minima*) had a credible interval for the posterior distribution overlapping zero (Figure 2a; 43% probability of being negative).

Across focal species, interactions were strongly reflective of the observed data, with narrower ranges than our uninformative prior normal (0, 1000) and with changes in mean parameter estimates from our prior.

Neighborhood level effects were predominantly negative

When considering variation in neighborhood composition, all neighborhoods on average, inhibited focal species (Figure 3a). The bounds of the credible intervals for posterior distributions of net neighborhood effects across focal species ranged from −2.33 (*Arcotheca calendula*) to 0.51 (*Hyalosperma glutinosum*) (Figure 3a). Probabilistically, all species were most likely (82% for exotics, 94% for natives) to be inhibited by their full neighborhoods (Figure 3b). Posterior distributions of the neighborhood effects that

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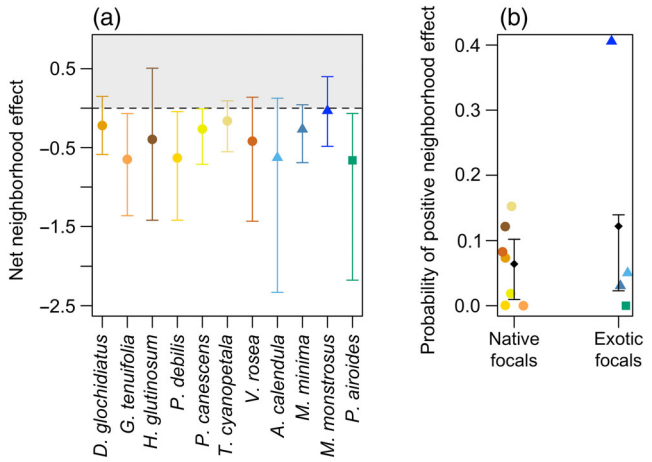

FIGURE 3 (a) Net neighborhood effect (from conspecific, exotic, and native neighbors) for each focal species (each represented by a different color). Positive values represent focal species experiencing net positive neighborhood effect (gray background). Negative values represent focal species experiencing net competitive neighborhood effect. Ranges represent 95% credible intervals. (b) Proportion of credible intervals greater than zero for each focal species separated by native versus exotic focal species. Points represent percentage for each species and match colors in panel (a). Black diamonds represent mean for native versus exotic focal species, and bars show interquartile range.

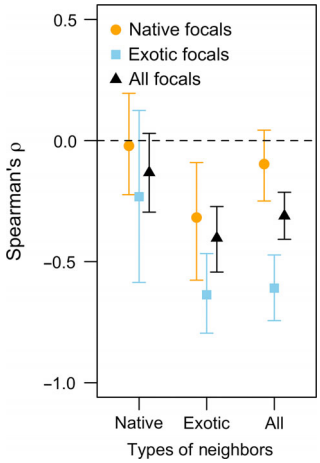

FIGURE 4 Correlation coefficients between net neighborhood effect and intrinsic fecundity across focal species, grouped by origin (native or exotic), each also including intraspecific interaction effects in the "All" calculations). The 95% credible intervals and mean of distributions are shown.

each focal species experienced did not differ substantially between native and exotic species (Figure 3a).

Negative correlation between intrinsic fecundity and net neighborhood effect, particularly when exotic neighbors were present

Negative Spearman's ρ values indicate that species with higher intrinsic fecundity were more strongly limited by their neighbors. We found this negative correlation at the community level, when we considered the aggregate effect of all neighbors (ρ values for native focal species, −0.1; exotic focal species, −0.61; all focal species, −0.31; Figure 4). Partitioning the effects of native versus exotic neighbors revealed this pattern to be strongly driven by the effects of exotic neighbors, regardless of focal species (exotic neighbors generating ρ values of −0.32 for native focal species; −0.63 for exotic focal species; −0.4 for all focal species; Figure 4).

DISCUSSION

Our study suggests that the collective impacts of diverse neighborhoods on the outcomes of species interactions can prevent positive interactions between species pairs from yielding "run-away" population dynamics. The diversity of neighboring individuals' identities and densities maintains a net competitive outcome despite strong positive interactions from exotic species. We found that positive effects on seed production of both native and exotic focal species were observed from exotic neighbors, particularly when that neighbor was the exotic annual grass *Pentameris airoides* (Figure 2). However, all focal species were, on average, inhibited by their full interaction neighborhood (Figure 3a). At the neighborhood scale, exotic species as a group were found to suppress all focal species, particularly those with high intrinsic fecundity (regardless of whether they were native or exotic; Figures 3 and 4). These results highlight the importance of considering within- neighborhood heterogeneity and taking a community-level approach when deciding how best to manage invaded systems (Sheppard, 2019).

Positive per capita effects on fecundity were only from exotic neighbors

We found evidence of positive per capita effects on fecundity between both exotic-exotic and exotic–native species pairs (Figure 2). The exotic grass *Pentameris airoides* was found to have strictly positive effects on two of the four exotic species, and three of the seven native species. Exotic forbs, as a group, were also found to have a strictly positive effect on one of the seven native species. Positive effects of

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neighbor plants on species fecundity can play a large role in driving population dynamics and structuring communities (Brooker et al., 2008; Bruno et al., 2003). Positive effects of neighbors on species growth, reproductive output, and survival have been demonstrated to occur in numerous systems including between native and exotic species, often through micro-habitat modification (Lai et al., 2015; Ruesink et al., 2006; Wainwright et al., 2016). As such, 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 have been used to improve soil characteristics to promote the survival and growth of natives seeded in later succession stages (D'Antonio & Meyerson, 2002).

In a neighborhood context, exotics exhibiting a positive effect on other exotic species can result in an "invasional meltdown" whereby exotic species promote the establishment of each other, causing drastic community reassembly (Flory & Bauer, 2014; Simberloff & Von Holle, 1999; Wundrow et al., 2012). When considering the overall neighborhood context, we found little evidence of this type of effect, despite observing several per-capita positive exotic–exotic species interactions. In fact, exotic species strongly suppressed the fecundity of each other when in multispecies communities (Figure 3), despite having positive pairwise interaction coefficients (Figure 2). While one exotic forb, *Monoculus monstrosus*, was observed to exhibit positive per capita effects on the fecundity of conspecifics, this finding is likely due to this species not being at high enough local abundances to experience negative frequency dependence (Towers et al., 2020).

The positive effect of the exotic grass, *Pentameris airoides*, on native species fecundity has been observed previously in the York gum woodlands (Wainwright et al., 2016). Though no direct mechanism of this effect has been identified, it is thought to result from *P. airoides* reducing environmental stress on natives, perhaps by decreased evaporation in dense plant patches, which benefits plant performance and outweigh the competitive effects of interspecific aggregation. Further experiments are needed, however, to isolate the exact mechanism of this effect (Callaway, 2007; Wainwright et al., 2016). Pec and 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).

Positive outcomes of interactions can arise from a variety of underlying reasons such as 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 causes of the interactions uncovered in this study. Further, while our experiment adopted a commonly used design to capture the effects on fecundity from species interacting for resources (water, light, and nutrients) we recognize the potential for other important interactions to be occurring within our neighborhood rings and at larger spatial scales, for instance through dispersal of herbivores and pathogens, and interactions with belowground microbial communities.

Net neighborhood effects suppressed positive per capita effects

The net neighborhood effect on both native and exotic focal species was remarkably similar, both in terms of the mean and variance (Figure 3). On average, all species were inhibited by their interaction neighborhood, despite the observed positive per capita interaction coefficients between many species (Figure 2). This result suggests that within-neighborhood heterogeneity (causing the average individual to experience interactions with multiple species) is a key factor limiting species' population growth and suggests that caution is needed from inferences based on pairwise species interactions only. Rather, aggregated community effects may stabilize dynamics and limit run-away dynamics that can occur in pairwise models of facilitation.

These findings highlight the need to study multiple co-occurring exotic species within a system and explore both their per capita interactions as well as the cumulative effect of interactions with the observed neighborhood, particularly as this neighborhood can vary hugely in diverse plant communities (Kuebbing et al., 2013). This has implications for management of invaded systems, as for instance, if certain exotic species were targeted for removal from this system, the fecundity of many native species may be reduced, even as others may be released from strong competition. Further, since native species were all found to suppress each other, removing exotics may more strongly stress rarer native species. Simulating the addition/removal of particular species in this system could help to disentangle

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these relationships and further guide management decisions.

Conversely, if some exotics, such as the grass *Pentameris airoides*, were to increase in abundance, species dynamics within the system could become highly unstable (i.e., unlimited population growth of facilitated species), due to an intensification of its positive effects. However, it may be likely that the benefits of neighbors may outweigh competitive effects at low densities, but not high densities. Wainwright et al. (2019) found evidence of such trends with different combinations of interacting species from the York gum woodlands. Increased associated pathogen or herbivore persistence at higher densities may also limit population growth of species that experience interspecific facilitation (Connell et al., 1971; Janzen, 1970). The fact that we saw exotic species experiencing the strongest negative correlation between intrinsic fecundity and net neighborhood effect, does, however, suggest that the exotics are unlikely to grow to dominance in this system.

Exotic species appear to be self-regulated within the community

We found that the exotic species in this study had the strongest negative correlation between their intrinsic fecundity and net neighborhood effect (negative Spearman's ρ values in Figure 4), suggesting that their abundance (particularly of exotic species with high intrinsic fecundity such as *Arctotheca calendula* and *Pentameris airoides*) is regulated by community dynamics.

The exotic neighbors also played a key role in limiting the fecundity of the native species with high intrinsic fecundity, contrary to several recent studies that found competition between multiple exotic species to alleviate competition with natives (Ferenc & Sheppard, 2020; Lenda et al., 2019). While exotic species had positive per capita effects on some focal species, this strong negative correlation indicates that positive effects from exotic species were more likely to occur for species with low intrinsic fecundity. This suppression of native species by exotics could be due to the typically higher magnitude of the negative per capita effects of exotic neighbors than those of native neighbors (Bimler et al., 2018). It is also important to note that these trends were observed using data from a single year and future work should examine these relationships both immediately following establishment of an exotic and in the long-term, incorporating possible interannual variability.

Future directions

The variation we observed in this study comes in part from variation in the composition of species grouped within our "exotic forb" and "native forb" categories. A next step would be to design an experiment that allowed sources of variation to be partitioned in different ways, including at the species rather than functional group level. Future work linking uncertainty and observed variation in demographic rates to functional traits and controlling for genotypes may also represent interesting approaches for differentiating biological sources of variation and for extrapolating the importance of this variation to the community level (Carboni et al., 2018; Ferenc & Sheppard, 2020; Gross et al., 2009). The outcomes of interactions observed in our study may also be due to nonadditive effects. Mayfield and Stouffer (2017) found several annuals in the York gum woodlands experience buffering effects against competition via nonadditive higher-order interactions (HOIs). Teasing apart how additive versus nonadditive effects influence the net neighborhood effect in these scenarios is an important avenue for future work. However, heavy data requirements of nonadditive models can limit their efficacy in applied ecology, and such models are also limited by the number of interactions (i.e., higher powers than two- or three-way interactions) that they can reasonably include.

CONCLUSION

We found that comparing outcomes of species interactions at both the per capita and neighborhood levels improve our understanding of how native and exotic species interact in invaded ecosystems. Such understanding has the potential to improve efforts to manage such systems. For instance, we can identify where an exotic species may generally be promoting a native species, but also what circumstances may lead to suppression of this net positive outcome and hence the prevention of runaway population growth. We also identified within-neighborhood heterogeneity as a potential mechanism for buffering positive interaction outcomes in natural systems, where diverse neighborhoods maintain population stability despite numerous positive pairwise interactions.

AUTHOR CONTRIBUTIONS

Catherine H. Bowler, Lauren G. Shoemaker, and Margaret M. Mayfield developed the idea for this study. Catherine H. Bowler and Isaac R. Towers

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designed and conducted the field study with help from Margaret M. Mayfield. Catherine H. Bowler, Lauren G. Shoemaker, and Christopher Weiss-Lehmans created and analyzed models. Catherine H. Bowler wrote the paper with extensive help from Lauren G. Shoemaker, Christopher Weiss-Lehman, and Margaret M. Mayfield.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Towers et al., 2020) are available at https://doi.org/10.1002/ecy.3185. Model code (Bowler, 2022) is available on Zenodo at https://doi.org/10.5281/zenodo.6588674.

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