Positive interactions of native species melt invasional meltdown over long-term plant succession

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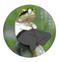

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LETTER

Positive interactions of native species melt invasional meltdown over long-term plant succession

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Abstract

Positive interactions have been hypothesised to influence plant community dynamics and species invasions. However, their prevalence and importance relative to negative interactions remain unclear to understand community change and invasibility. We examined pairwise biotic interactions using over 50 years of successional data to assess the prevalence of positive interactions and their effects on each focal species (either native or exotic). We found that positive interactions were widespread and the relative frequency of positive and negative interactions varied with establishment stage and between native and exotic species. Specifically, positive interactions were more frequent during early establishment and less frequent at later stages. Positive interactions involving native species were more frequent and stronger than those between exotic species, reducing the importance of invasional meltdown on succession. Our study highlights the role of positive native interactions in shielding communities from biological invasion and enhancing the potential for long-term resilience.

KEYWORDS
competition, establishment stages, facilitation, invasional meltdown, plant performance, positive interactions

INTRODUCTION

Biotic interactions can be negative, positive or neutral, and are the primary force shaping community structure, diversity and succession (Bertness & Callaway, 1994; Connell & Slatyer, 1977; Michalet & Pugnaire, 2016). Although the biological significance of positive plant–plant interactions has been appreciated since Darwin (Darwin, 1859), ecological studies have been dominated by classic competition theories, models and experiments (e.g. Gause, 1934; Gross, 2008; Lotka, 1925; Volterra, 1926). This tradition, however, has shifted over the past two decades with increasing experimental evidence pointing to the critical role of positive interactions in community assembly, particularly in extreme environments or degraded systems (Bertness & Callaway, 1994; Callaway, 1995; Cavieres et al., 2006). It is now widely acknowledged that positive plant–plant interactions can improve individual fitness and facilitate population growth (Figure S1a). A large set of field studies support the idea that both positive and negative biotic interactions act simultaneously over succession (Chu et al., 2008; Losapio et al., 2021), and the path of succession depends on the net effects resulting from positive and negative interactions (Callaway et al., 1991; Cavieres, 2021).

Most studies explore the relative importance of positive interactions either by using one or a few species pairs across abiotic gradients (e.g. Greenlee & Callaway, 1996; Wright et al., 2014) or by meta-analyses of scientific literature (e.g. Kuebbing & Nuñez, 2015; Yang et al., 2022). Consequently, understanding the prevalence and relative importance of positive interactions in natural plant communities remains rather limited (Hegland et al., 2009), but is critically important for understanding community change, and especially changes driven by the invasion of exotic species. Ecological invasions are often considered to be limited by competition and other negative interactions, but could also experience positive impacts from other species, causing invasional meltdown (Simberloff & Von Holle, 1999) when these interactions are between exotics.

A series of barriers must be overcome for successful colonisation and establishment of both native and exotic species into a new habitat, for example, overcoming barriers to survival and reproduction for successfully establishing a population (Blackburn et al., 2011; Richardson et al., 2000). Biotic interactions, either positive or negative, can affect components of individual fitness, thereby influencing plant performance, determining when and how native and exotic establishment occur (Goldberg et al., 2001). We argue that in order to understand the effect of species interactions on establishment, it is necessary to disentangle the relative effects of positive and negative interactions for each stage in the establishment process. For example, He et al. (2013) found that plant interactions are often facilitative at the survival stage, but primarily competitive at reproduction. Similarly, Levine et al. (2004) showed that biotic resistance often limits the spread of invading species by constraining their population abundance, but rarely prevents their establishment. These studies suggest that the relative importance of facilitation and competition varies with establishment stage.

Here, we propose a general hypothesis on how biotic effects vary across establishment stages: in early establishment, positive interactions outweigh negative ones, leading to net positive facilitation for the emergence and survival of newly arriving species in a recipient community (Li, Guo, Cadotte, Chen, Kuang, et al., 2015). However, the initial facilitative effect is weakened by the subsequent build-up of negative (competitive) interactions later in establishment, thereby inhibiting population growth and subsequent spread of colonising species (Figure S1a). Assessing differences in the balance between positive and negative interactions throughout the stages of plant establishment will offer an understanding of why some communities are susceptible to invasion while others are not.

Facilitative interactions occur widely among co-occurring native plant species (Callaway & Walker, 1997; Michalet & Pugnaire, 2016). They can also occur between exotic and native plants, for example, exotic species facilitated by natives (Lenz & Facelli, 2003; Madrigal-González et al., 2013) and natives by exotics (Oduor et al., 2018; Svriz et al., 2013). Facilitative interactions among exotic species are of particular interest in biological invasion (Dornbusch et al., 2018; Vitousek & Walker, 1989) as it has been hypothesised that the successful invasion of one exotic species is enhanced when other exotic species are already present in the community (Simberloff & Von Holle, 1999). Facilitation among invasive species would then strengthen the detrimental effects of invaders sufficiently to lead to the invasional meltdown (collapse) of the native community. However, it is not clear how different kinds of species interact (e.g. native on native, native on exotic, exotic on native and exotic on exotic, Figure S1b) to influence community change and particularly invasional meltdown. Specifically, we need to know how the strength of positive interactions among natives changes relative to those among exotic species and whether it is possible for native facilitations to resist invasional meltdown.

To address this need, we used 50 years of vegetation data from the Buell-Small Succession Study (hereafter BSS; Li, Cadotte, Meiners, Hua, Shu, et al., 2015) to analyse pairwise temporal interactions among plant species (including both natives and exotics) over succession. The BSS has a long history of sustained invasion despite compositional turnover of the exotic species with succession (Meiners et al., 2002, 2015), averaging 50% cover over the first 50 years. These plant invasions alter local colonisation and extinction rates of co-occurring species (Li, Cadotte, Meiners, Hua, Shu, et al., 2015; Yurkonis et al., 2005; Yurkonis & Meiners, 2004), reducing local richness. Here, we address the following three questions: (1) How frequent are positive interactions among plant species across a successional gradient? (2) How does the relative frequency of positive interactions change across the plant colonisation process? (3) What is the difference in the frequency and strength of positive interactions between natives in comparison with those of exotic species? Answers to these questions are essential for identifying the contribution of plant interactions, especially facilitation, to the assembly and invasibility of plant communities, and, thereby, for predicting future dynamics and informing invasion management.

MATERIALS AND METHODS

Study site and data collection

The Buell-Small Succession Study (BSS) is a permanent-plot study of abandoned agricultural land in the Piedmont of New Jersey, USA (40°30′ N, 74°34′ W; Pickett, 1982), which consists of 10 abandoned agriculture fields where farming was experimentally ceased in alternate years from 1958 to 1966 (Li et al., 2016; Meiners et al., 2002). The BSS data represent the longest continuous study on plant invasion and post-agricultural succession (Meiners et al., 2002), providing a unique opportunity to test community-level biotic interactions among plant species.

In the BSS, the percentage cover of all plant species present in each permanently marked 0.5 × 2 m plot (48 plots within each field) has been continuously monitored each year from 1958 to 1979 and in alternate years since 1979. For this reason, we condensed the monitoring data into 2-year intervals to maintain even replication over time (Li, Cadotte, Meiners, Hua, Shu, et al., 2015; Li, Guo, Cadotte, Chen, Kuang, et al., 2015). Because the fields varied in abandonment over an eight calendar-year period, the time of our analyses was based on field age rather than calendar year following the most recent research on the Buell-Small Succession Study (Li, Cadotte, Meiners, Hua, Jiang, & Shu, 2015; Xiao et al., 2020). Our analyses were restricted to ages 1–47, as all fields cover this age span.

Statistical analyses

In this study, we selected the 25 most frequent natives and 25 most frequent exotics (originating outside North America) across all fields and years as focal species (see species list in Table S1 in the supporting information). We avoided woody species, because the 0.5 × 2 m plots are not large enough to quantify their demographic parameters. We began by applying presence/absence and percentage cover data for each species across all plots and field ages to hierarchical models (see Figure 1). These models were used to assess the effects of pairwise biotic interactions on the performance of each colonising species in overcoming early (occurrence, survival and colonisation) and late (population growth) barriers when it colonised into the community.

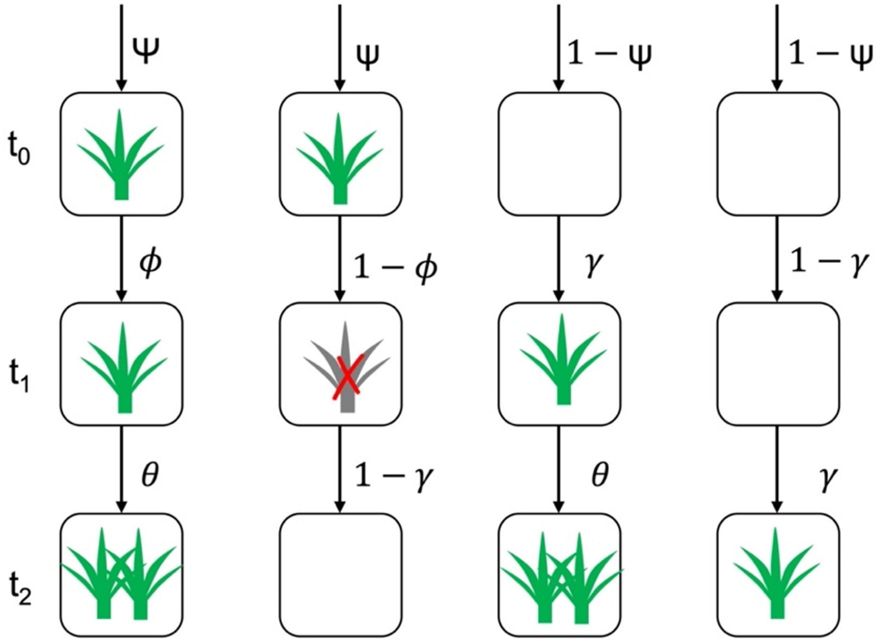

FIGURE 1 Different parameters of the dynamic hierarchical models. The boxes with plants indicate the sites are occupied by the focal species (with an occurrence probabity of ψ), while the blank boxes indicate unoccupied ($1-\psi$). The occupancy state might change due to local extinction (i.e. 1- survival, 1-ϕ) and colonisation (λ) over time. The plants in the box get denser when local population grows (θ). The parameter ψ is the occurrence probability, while ϕ and λ are local survival and colonisation probabilities respectively. θ is the population growth rate.

Model of occurrence probability

Because our interest was to model pairwise interactions of species, we modelled the probability of occurrence of each focal plant species as a function of the percentage cover of another species at each plot *i* in each biennial survey *t*. Let $z_{i,t}$ denote the occurrence state of plot *i* during survey *t*, having possible states 'occupied' ($z_{i,t} = 1$) and 'not occupied' ($z_{i,t} = 0$) by the focal species. The probability of occurrence is ψ, where $\psi = \Pr\left(z_{i,t} = 1\right)$(see Figure 1). The model takes the following form:

$$z_{i,t} \sim Bernoulli\left(\psi_{i,t}\right), logit\left(\psi_{i,t}\right) = a_t + b_1 \times cover_{i,t-1} + c_{field} \tag{1}$$

where $cover_{i,t}$ is the percentage cover of an interacting neighbour species present in the same plot *i* in the survey *t*, b_1 is the effect of pairwise biotic interactions on focal species' occurrence. The terms a_t and c_{field} represent normally distributed random effects for each survey year and abandoned field respectively.

Model of survival and colonisation probabilities

The occurrence state at each plot changes due to local extinction and colonisation over time (Royle & Kéry, 2007). Let ϕ be the probability that an occupied site 'survives' (i.e. remains occupied, thus local extinction probability is 1-ϕ) from period *t* to *t*+1, that is, $\phi_t = \Pr\left(z_{i,t+1} = 1 \mid z_{i,t} = 1\right)$. Let γ be the probability of local colonisation during (t, $t+1$), that is, $\gamma_t = \Pr\left(z_{i,t+1} = 1 \mid z_{i,t} = 0\right)$ (see Figure 1). The occurrence state at $t = 1$ with the initial occurrence probability ψ_1 is $z_{i,1} \sim Bernoulli\left(\psi_1\right)$, whereas, in subsequent surveys, $z_{i,t} \mid z_{i,t-1} \sim Bernoulli\left(\pi_{i,t}\right)$, where $\pi_{i,t} = z_{i,t-1} \times \phi_{t-1} + \left(1 - z_{i,t-1}\right) \times \gamma_{t-1}$, when considering the local extinction and colonisation processes over time. Accordingly, we modelled the pairwise interactions on survival and colonisation probabilities of the focal species as a functions of percentage cover of another plant species in the following form:

$$\begin{aligned} & z_{i,1} \sim Bernoulli\left(\psi_1\right), logit\left(\psi_{i,t}\right) = a_t + b_{2,t-1} \times z_{i,t-1} \\ & + b_3 \times cover_{i,t-1} \times z_{i,t-1} + b_4 \times cover_{i,t-1} \\ & \times \left(1 - z_{i,t-1}\right) + c_{field}, z_{i,t} \sim Bernoulli\left(\psi_{i,t}\right) \end{aligned} \tag{2}$$

where b_3 and b_4 are the effects of pairwise biotic interactions on focal species' survival and colonisation probabilities respectively. The terms a_t and c_{field} represent year-specific and field-specific random effects respectively.

Model of population growth rates

In addition to the occupancy dynamics that focused on species occurrence, survival and colonisation, we also modelled population growth rate of each focal species as a function of pairwise interactions in the following form,

$$growth.rate_{i,t} \sim Normal\left(mu_{i,t}, tau\right)$$

$$mu_{i,t} = a_t + b_5 \times cover_{i,t} + c_{field} \tag{3}$$

where $growth.rate_{i,t}$ is the average annual population growth in terms of cover change in the focal species at plot *i* at survey *t*. b_5 is the effect of pairwise biotic interactions on focal species' population growth rate. The terms a_t and c_{field} represent normally distributed random effects for each survey year and abandoned field respectively.

Following the analyses in models (1), (2) and (3) for all species pairs we selected in the BSS community, we used the 95% credible intervals of parameter estimates (b_1, b_3, b_4 and b_5) to determine the significance and direction (positive or negative) of pairwise interactions on species occurrence, survival, colonisation and population growth rate respectively. Though it is hard to infer plant–plant interactions from correlative relationships alone, we have confidence that they are indicative of the species interactions in our study system to a large extent because: (1) Data used in our dynamic hierarchical models were collected at fine spatial scale (each plot of 0.5 × 2 m), where direct plant–plant interactions are likely to occur (Jin et al., 2020); (2) Model parameters were calculated using 50 years of temporal dynamics, which suggests that the model parameters closely reflect the long-term net effects of plant–plant interactions; (3) The study site in this work is relatively small, with species colonising and growing in relatively homogeneous environmental conditions. In addition, we consider the site and year as random effects in each statistical model. Therefore, it is likely to exclude spatial gradients that might mask or confound the correct inference of interactions from the model parameterisation; (4) Inference was carried out with hierarchical models that describe parameter directions and strengths among plants with a similar or even stronger power to existing models of plant occupancy dynamics (Royle & Dorazio, 2008; Royle & Kéry, 2007).

To understand the prevalence of positive interactions, we first quantified the number of species with significant positive or negative effects on each focal plant species' occurrence, survival, colonisation and population growth rate among all selected plant species (native and exotic) and subdivided by interaction types between native and exotic species (i.e. native on native, native on exotic, exotic on native and exotic on exotic). After assessing the prevalence of positive interactions among all examined plants, we used *t*-tests to assess whether the relative frequency of positive and negative interactions varied with performance indicators (occurrence, survival, colonisation and population growth rate) associated with either early or late establishment stages, and whether the relative frequency and strength of positive interactions varied among interaction types (i.e. native on native, native on exotic, exotic on native, exotic on exotic). To further test whether native facilitations resist invasional meltdown, we evaluated the relationship between the frequency of positive native–native interactions and the number of invasive species in the community over time.

Percentage cover data of each species were centred and scaled to unit standard deviation to fit the models. We used the standard noninformative priors on the parameters a, b, $c \sim$ Normal $(0,10^2)$, $tau \sim$ invGamma (1e-3, 1e-3). Posterior distributions were simulated using Markov chain Monte Carlo (MCMC) in JAGS version 4.3.0 (https://mcmc-jags.sourceforge.io/). All analyses were performed in R version 4.0.2 (R Core Team, 2020).

RESULTS

The prevalence of positive interactions among plant species

Positive biotic interactions were pervasive among the 50 focal plant species across all stages of establishment (Figures 2 and 3). Of the species tested, we found that all had positive effects from at least one other plant species on their occurrence (Figure 3a), survival (Figure 3b) and colonisation (Figure 3c) and 43 species experienced positive effects on their population growth rates from other plant species (Figure 3d). Overall, positive interactions comprised 69.6% of significant interactions for occurrence, 62.0% for survival and 68.5% for colonisation, but only 31.8% for population growth.

When biotic interactions were separated into different types (native on native, native on exotic, exotic on native and exotic on exotic; Figure 4), we observed that positive interactions occurred frequently between exotic species, as well as in other interaction types for all four performance indicators (Figure 4). For example, 24, 25, 23 and 19 species out of the 25 focal exotic species received positive effects from other exotics, respectively, on occurrence, survival, colonisation and population growth rates, accounting for 63.0% (occurrence; Figure 4a-4), 50.0% (survival; Figure 4b-4), 62.0% (colonisation; Figure 4c-4) and 30.9% (population growth rates; Figure 4d-4) of all significant exotic–exotic interactions. Similarly, positive interactions were generally observed in other interaction types for all four performance indicators (Figure 4). The frequency of positive interactions across all examined species strongly supports the prevalence of positive interactions in the BSS plant community.

The relative frequency of positive interactions across establishment stages

Positive and negative interactions acted simultaneously on focal plant species, but the relative frequency of positive

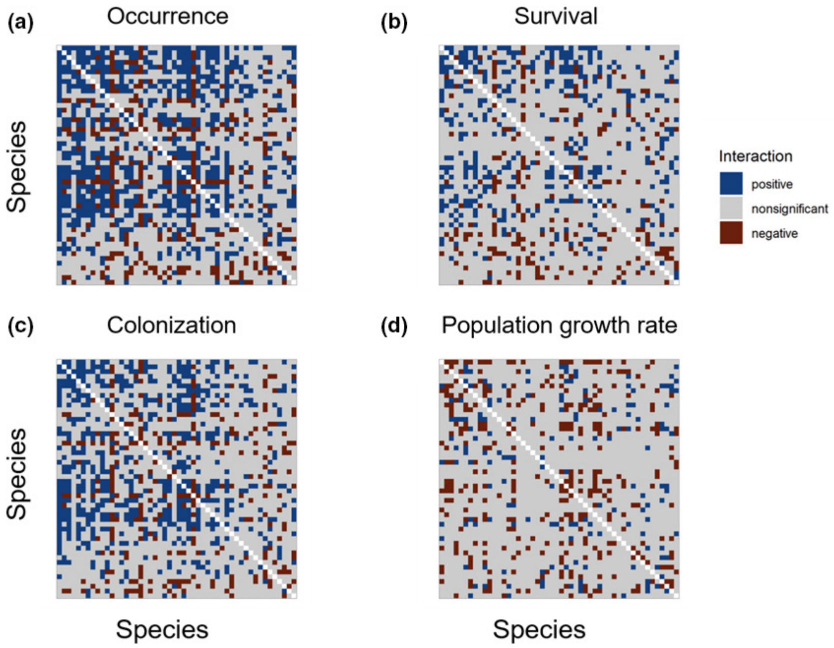

FIGURE 2 Heatmaps showing the interactions estimated with all pairs of plant species for (a) occurrence, (b) survival, (c) colonisation and (d) population growth of each focal species. Each row represents one of the focal plant species, while each column represents one of the interacting neighbour species. The blue, grey and red blocks represent positive, neutral and negative interactions, respectively, and white blocks represent intraspecific integrations, which are not considered in our study.

interactions varied with occurrence, survival, colonisation and population growth (Figure 3 and Figure 4). For the interactions among all species (Figure 3), positive interactions were generally more frequently observed than negative interactions on occurrence (paired *t*-test, $p<0.001$; Figure 3a), survival ($p<0.01$; Figure 3b) and colonisation ($p<0.001$; Figure 3c). However, for population growth rate, positive interactions were less common than negative ones ($p<0.001$; Figure 3d). These results suggest that during the establishment stages, the emergence, colonisation and survival of the colonising species, native or exotic, is likely to benefit from net positive interactions. In contrast, at later stages (i.e. population growth), species might be inhibited by net negative interactions, as hypothesised.

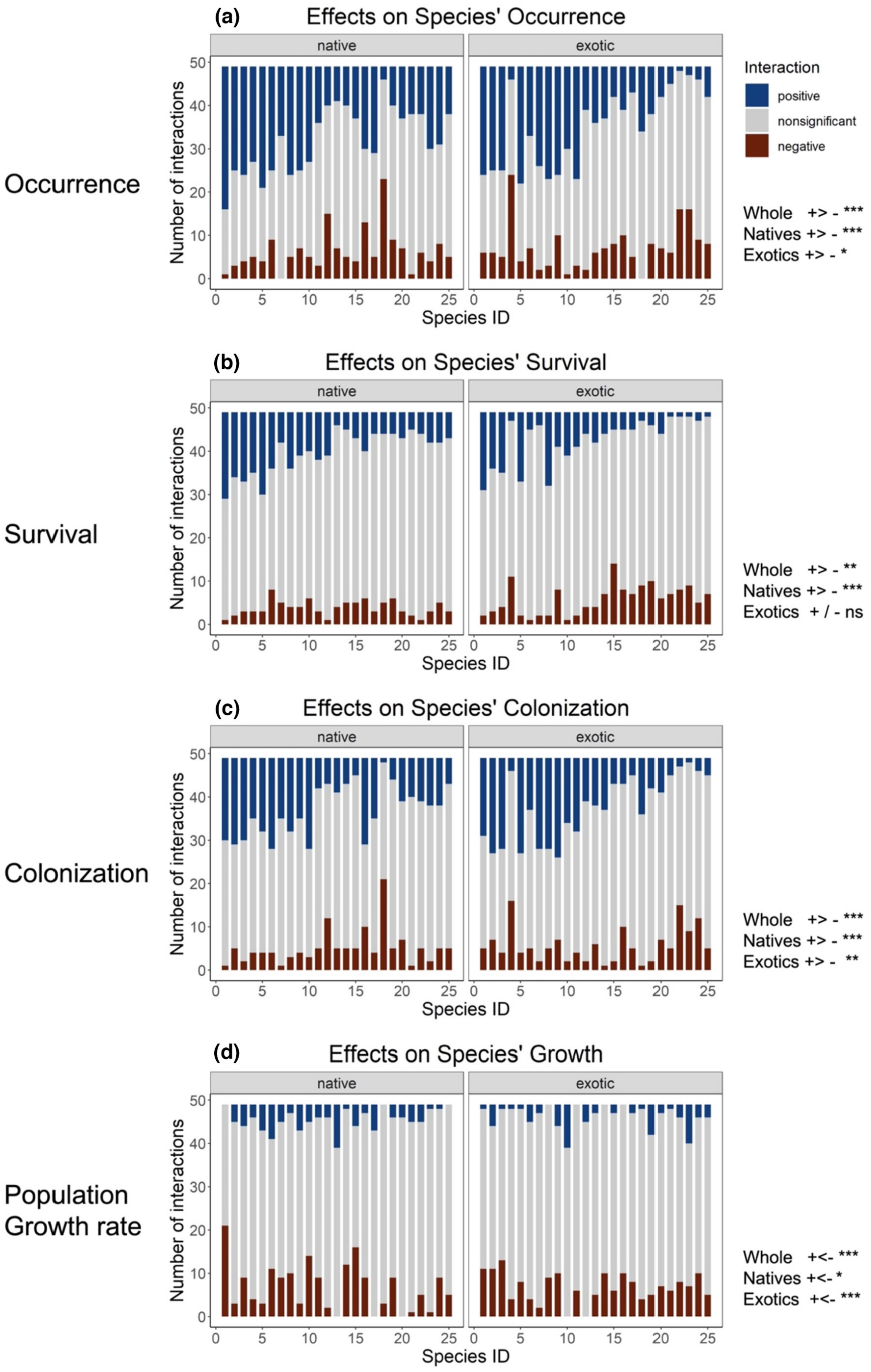

FIGURE 3 The relative frequency of positive and negative interactions on each focal plant species (native or exotic) for the four performance indicators: (a) occurrence, (b) survival, (c) colonisation and (d) population growth. Positive and negative interactions were estimated by coefficients in the dynamic hierarchical models that were used to model the pairwise interactions. The p-values for the paired t-test for the frequency of positive and negative interactions for the whole species, natives or exotics exclusively are shown in each panel, where *** indicates $p<0.001$, **$p<0.01$ and *$p<0.05$

The finding that positive interactions were more common early in establishment and negative interactions were more common later was consistent across all interaction types (Figure 4). The one exception was interactions between exotic species early in the establishment stages, where there was no significant difference between the frequencies of positive and negative interactions on the species' occurrence, survival and

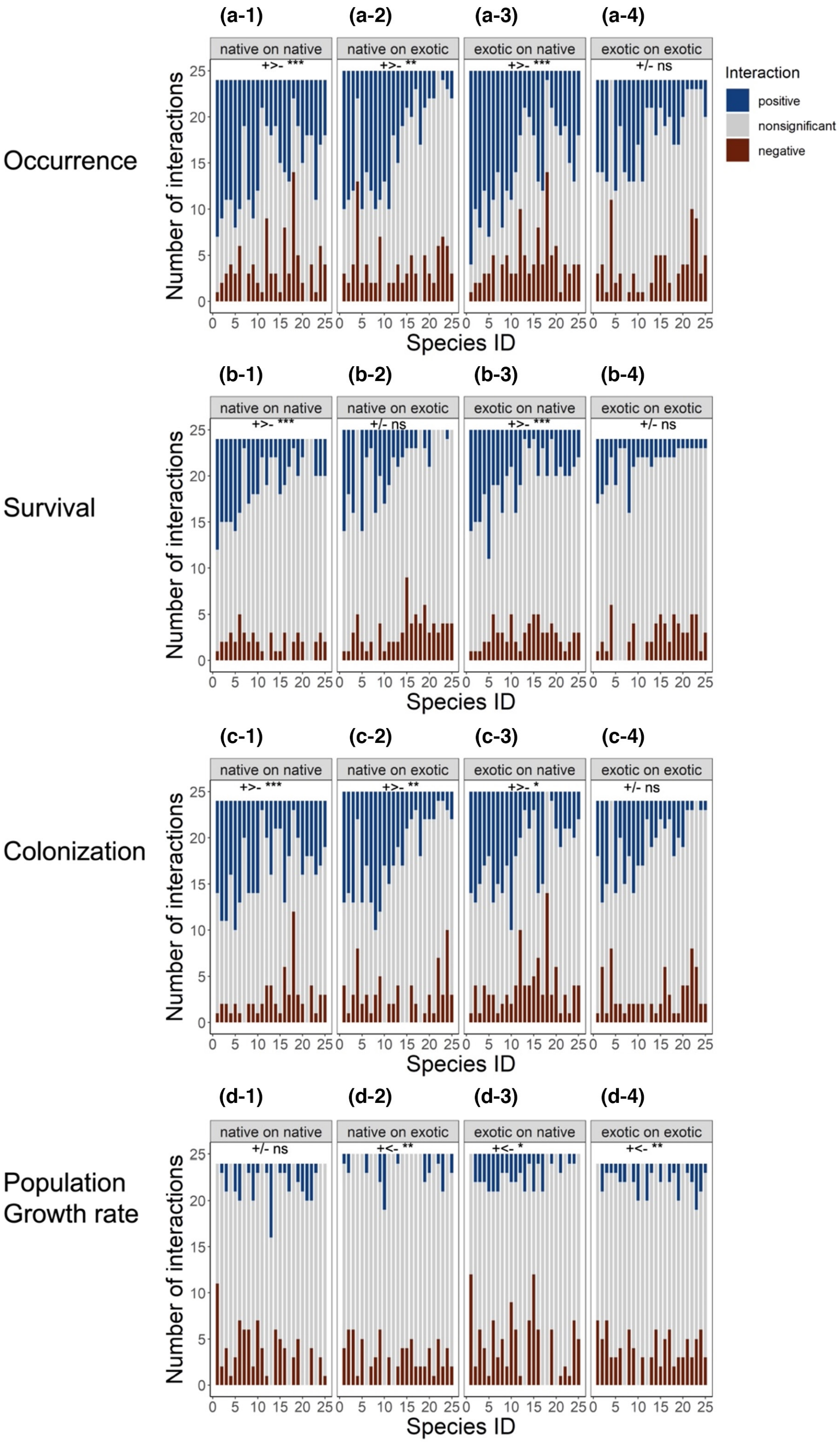

FIGURE 4 The relative frequency of positive and negative interactions within each interaction type (i.e. native on native, native on exotic, exotic on native and exotic on exotic) for the four performance indicators (a) occurrence, (b) survival, (c) colonisation and (d) population growth. Similar to Figure 3, positive and negative interactions were estimated by coefficients in the dynamic hierarchical models that were used to model the pairwise interactions. The p-values for the paired t test for the frequency of positive and negative interactions for each interaction type are shown in each panel, where *** indicates $p<0.001$, **$p<0.01$ and *$p<0.05$.

colonisation (Figure 4a-4, 4b-4 and 4c-4), which suggests that early negative exotic-exotic effects might be counterbalanced by their positive effects.

The relative frequency and strength of positive interactions across interaction types

As stated above, exotic–exotic interactions were equally impacted by positive and negative interactions early in the establishment stages (occurrence, Figure 4a-4; survival, Figure 4b-4 and colonisation, Figure 4c-4). In marked contrast, positive interactions generally outnumbered negative interactions for all other types of interactions (native on native, native on exotic and exotic on native) early in establishment. This was also found late in the establishment stages (population growth rate), but positive interactions were less frequently observed in exotic–exotic interactions (Figure 4d-4), and were comparable to negative interactions in native–native interactions (Figure 4d-1).

In addition to finding more frequent positive effects in interactions involving native species than in exotic–exotic interactions, we also observed that the strengths of positive interactions involving natives were generally, though not significantly, stronger than that of interactions between exotic species for species occurrence, colonisation and population growth rate, but not for species survival (Figure 5). We also found that the frequency of native–native facilitations increased with the number of exotic species in the community over time for occurrence (Figure 6a), survival (Figure 6b), colonisation (Figure 6c) and population growth (Figure 6d), highlighting the importance of positive native interactions in response to biological invasions.

DISCUSSION

By analysing pairwise biotic interactions among plant species, including natives and exotics, using hierarchical models, our work provides strong evidence that positive interactions are pervasive in a diverse and dynamic natural community (Figures 2 and 3). Importantly, other work has highlighted the importance of positive interactions for community assembly in stressed (e.g. arid) ecosystems, with fewer showing them in benign, mesic ecosystems (Callaway, 1995, 2007; Valiente-Banuet & Verdú, 2013), but our work shows that positive interactions are pervasive in a broadly distributed and relatively low-stress ecosystem. Positive and negative biotic interactions simultaneously acted on focal plant species, but the relative frequency of positive interactions varied with demographic processes across establishment stages (Figure 3), and between native and exotic species (Figure 4). Specifically, positive interactions were more frequent early in establishment (occurrence, colonisation and survival), and less frequent later (population

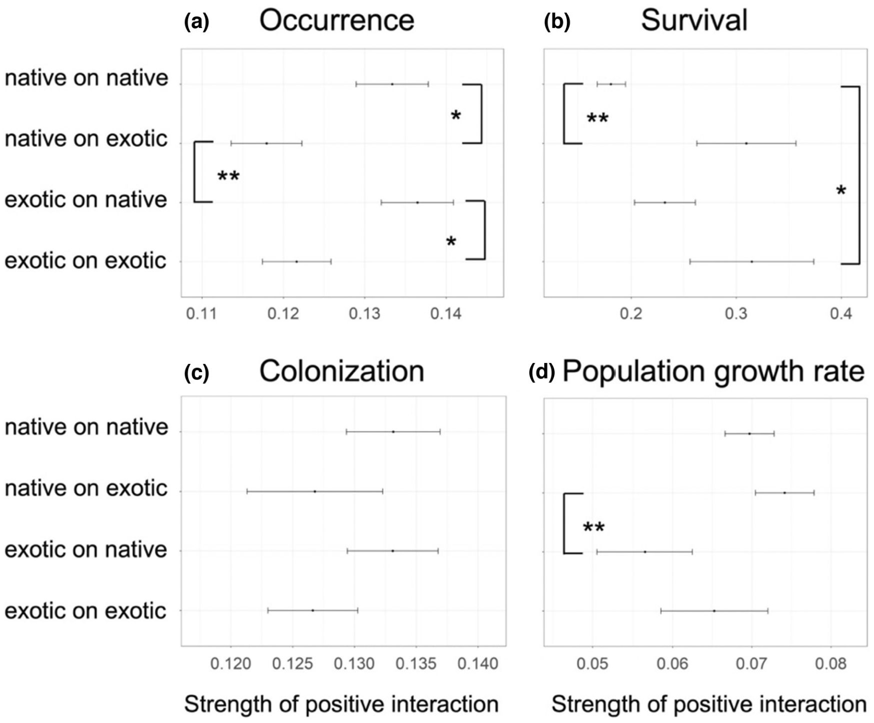

FIGURE 5 The strength of positive interactions across interaction types (native on native, native on exotic, exotic on native and exotic on exotic) for different performance indicators ((a) occurrence, (b) survival, (c) colonisation and (d) population growth rate). Dots and bars represent means and 95% confidence intervals respectively. Interaction strengths were significantly different between two interaction types if '*' signals were labelled in each panel, where ***indicates $p<0.001$, **$p<0.01$ and *$p<0.05$.

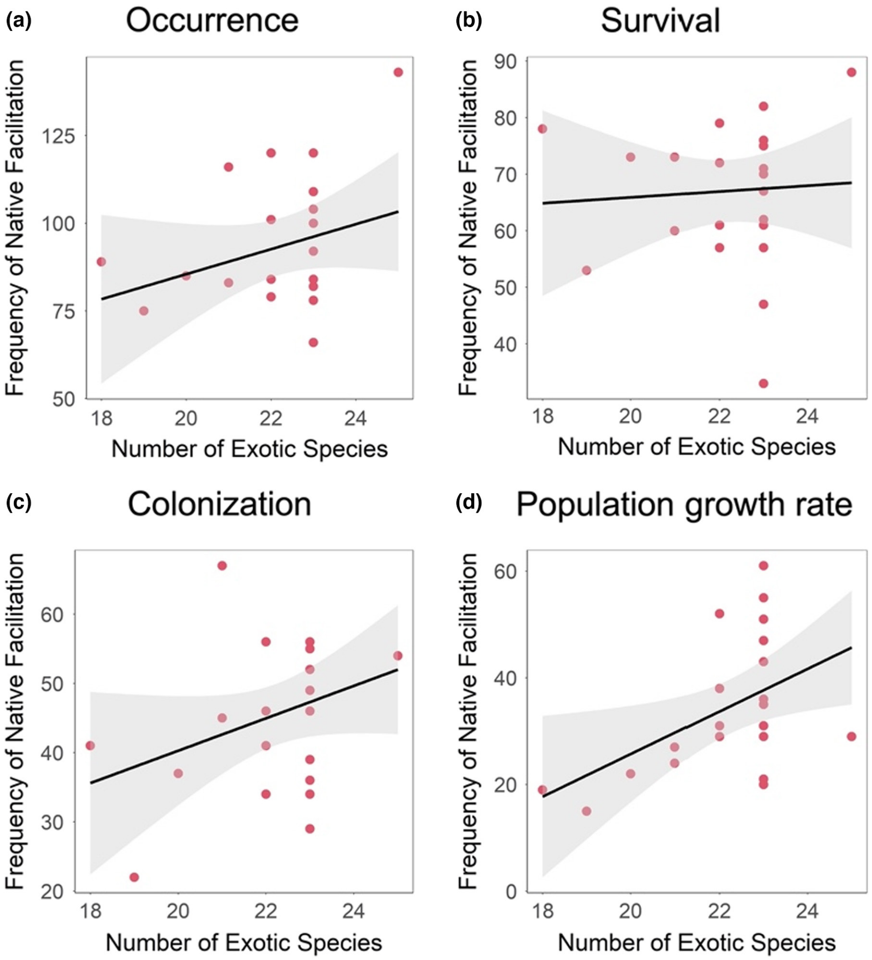

FIGURE 6 The relationship between the frequency of native-native facilitations and the number of exotic species over time for different performance indicators ((a) occurrence, (b) survival, (c) colonisation and (d) population growth rate). Shallow shows the 95% confidence bands.

growth). In addition, the relative frequency of positive interactions (Figure 4), as well as their strength (Figure 5), were generally higher than that of exotic-exotic interactions, counter to the invasional meltdown process. Together with the finding that the frequency of native facilitations increased with the number of exotic species (Figure 6), our study highlights the role of positive interactions involving natives in limiting the impacts of biological invasion and preventing invasional meltdown.

In past decades, the notion that negative interactions such as competition predominantly regulate community composition and species invasion (e.g. Gause, 1934; MacArthur & Levins, 1967; Shea & Chesson, 2002) was supported by a multitude of studies showing negative interactions among plants compared with sporadic reports of positive interactions (Kuebbing & Nuñez, 2015; Yang et al., 2022). This perspective strengthened the view that positive interactions, though potentially important to community structure and dynamics, were not as common as negative interactions (Jackson, 2015; Kuebbing & Nuñez, 2015). Our study, however, provides evidence that positive interactions are at least as pervasive as negative interactions in natural plant communities, if not more common. These results question the long-standing emphasis on the role of negative interactions in determining community dynamics and suggest that the importance of positive interactions likely has been much underestimated in ecology (Bruno et al., 2003; Soliveres et al., 2015). For example, local diversity might facilitate invasion when the importance of competition decreases (Meiners et al., 2004).

The shifting relative frequency of positive to negative interactions between the early and late establishment stages indicates that species' emergence, colonisation and survival benefit from net positive interactions, yet negative interactions are responsible for constraining subsequent population growth (Figure 3). These results support the conclusion of He et al. (2013) that plant interactions are often facilitative for plant survival, but often negative when measuring plant reproduction. The shifting relative importance of positive interactions during establishment argues that incorporation of facilitation into ecological theories and models will not be as simple as changing competition models (e.g. Lotka–Volterra model) into mutualistic ones by switching the signs of coefficients. Instead, ecologists should consider stage-based models that explicitly take population processes into account, for example, stronger effects of positive interactions for species colonisation and survival, while at later stages, competition has a stronger negative effect on reproduction.

The finding that exotic plants experienced fewer positive than negative interactions from other exotics (Figure 4) suggests that their positive effects on invader emergence, colonisation, survival and population growth might often be counterbalanced by negative effects between exotic species. Importantly, net positive effects on exotic species might mainly come from native species, rather than from other exotic species as the invasional meltdown hypothesis suggests (Simberloff & Von Holle, 1999). These results indicate the limited effects of exotic species already present in the community on later invasions of exotics, and a low possibility of invasional meltdown, in spite of the prevalence of exotic–exotic positive interactions (Figure 4). Our study also shows that native species can facilitate rather than compete with invaders, which echoes the conclusions of Meiners et al. (2004) and Cavieres (2021).

Pairwise combinations involving native plants appear to experience more and stronger positive interactions than exotic-exotic plant combinations (Figure 4 and Figure 5). This result suggests that native plants tend to provide more positive effects to other plants but also receive more positive effects from others. These suggest that native plants could mediate biological invasions and community succession by acting as facilitators of other species, thereby preventing the collapse of native communities and thwarting a potential invasional meltdown during plant succession. In addition, the finding that the frequency of facilitations between native species increased with the number of exotic species over time (Figure 6) suggests that exotic species triggered the build-up of positive native interaction to resist invasions. As successional systems are often heavily invaded (Buell et al., 1971; Lepart & Debussche, 1991), we therefore suspected that invasional meltdown might happens in our old-field successional community. This study, however, provides evidence that there is a relatively low propensity of invasional meltdown in our study community, due to the offsetting effects between positive and negative interactions in exotic–exotic interactions, and the multitude of positive native interactions. These findings also imply that native plants probably gain an advantage over exotics as they receive more facilitative interactions, counter to the suggestion that exotic species are competitively superior to co-occurring native species (Gioria & Osborne, 2014; Zhang et al., 2021). For example, the most frequent exotic species, *Daucus carota*, in our study community, was facilitated by 25 out of all 49 other plant species in their occurrence, while the most frequent native species, *Oxalis stricta*, that also occurred at the same time, was facilitated by 33 other species. As we also focused on common natives and exotics in this study, our results support the conclusions of Zhang and van Kleunen (2019) that common exotic plants are not more competitive than common natives, despite the findings that many exotics outcompete natives (Pearse et al., 2019; Vilà & Weiner, 2004).

Our finding that native plants act as stronger facilitators and beneficiaries than exotics could be because native plants might develop traits likely to facilitate or be facilitated over long periods of coexistence with the local abiotic and biotic environment (Coux et al., 2021). It seems more likely that native plants would evolve into ecosystem engineers that modify the environment to the benefit of other plants by influencing nutrient and carbon cycling, fire and hydrological regimes or the physical structure of an ecosystem over the long history (Stachowicz, 2001), thus facilitating other species. Or conversely, could evolve to utilise the environmental conditions imposed by other native species. For example, nitrogen-fixing native plants in nutrient-poor soils often increase available soil nitrogen and facilitate the establishment of other plants (Madrigal-González et al., 2013). Native plants receiving more positive effects than exotics might be associated with a shared mutualist, herbivore or competitor (Kuebbing, 2020), or specific soil conditioning through the release of enzymes or other biochemicals (Li, Guo, Cadotte, Chen, Kuang, et al., 2015). For example, if a shared pollinator benefits natives over exotics or a shared competitor negatively affects exotic species more than the natives, the final result would be that the native species received overall more facilitations than exotic species.

However, our approach is not without limitations. First, environmental conditions, such as light, water and nutrient availability might differentially influence plant performances by favouring some species over others (Gross et al., 2010). Therefore, accounting for field environment as a random effect in our dynamic models, without experimentally testing the interplay between environmental conditions (e.g. drought and biotic interactions) might bias estimates of pairwise biotic effects. The second limitation is that it was beyond our ability to assess the relative importance of positive and negative biotic effects at the population stage prior to species detection (e.g. germination) where both negative and positive interactions could have long-term consequences on plant population dynamics (Li, Guo, Cadotte, Chen, Kuang, et al., 2015).

Understanding how facilitation influences plant colonisation and the relative importance of positive interactions across interaction types are critical to informing invasion management. Our work provides four management implications: (1) Different management actions might be needed at different invasion stages, as net positive effects are more likely to promote the colonisation and survival of exotic species, while net negative effects are more likely to resist reproduction and population growth; (2) Preventing positive interactions between exotic species might not be a top management priority. Although positive effects between exotic species appear pervasive, they might be counterbalanced by the negative effects, and appear to have limited impacts on invasion success; (3) As exotic species can facilitate natives, removal of such exotic species might be ill-advised; (4) Native species appear to be better facilitators and beneficiaries than exotic species, therefore the net community effect would be promotion of native diversity in response to biological invasion. However, generalisation of these implications to other ecosystems should be carefully tested before applications. Although our study provides strong support for these implications, is a single case study of herbaceous invaders over time.

AUTHOR CONTRIBUTIONS

DY and MWC conceived the original idea and designed the study. DY led the analyses and wrote the first draft of the manuscript, and all authors contributed substantially to revision.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

PEER REVIEW

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OPEN RESEARCH BADGES

This article has earned Open Data and Open Materials badges. Data and materials are available at: https://doi.org/10.1111/ele.12476.

DATA AVAILABILITY STATEMENT

All data supporting our results were previously archived in Dryad (https://doi.org/10.5061/dryad.fn5g2). R codes used in this work have been deposited in zenodo (https://zenodo.org/badge/latestdoi/521485437).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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