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RESEARCH ARTICLE

Asymmetric sharing of generalist pathogens between exotic and native plants correlates with exotic impact in communities

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Abstract

1. As exotic plants invade into a new range, they can escape from specialist enemies. However, they may support generalist enemies, including both native and introduced fungal pathogens, which creates the potential for spillover and apparent competition from exotic to native plants in communities.
2. To assess the potential for spillover of putatively pathogenic, root-associated fungi (hereafter, 'pathogens') in communities invaded by exotic plants, we conducted a two-phase plant–soil feedback experiment: a monoculture experiment with native and exotic plants grown alone and a multi-species, community-level experiment that ranged in the extent of exotic dominance. We used next-generation sequencing to characterise sharing of pathogens between native and exotic plants in communities.
3. Exotic plants outperformed natives in communities, despite harbouring higher relative abundance of generalist pathogens. The higher generalism of pathogens supported by exotic plants made them more prone to be shared with natives. The proportion of pathogens shared between exotic and native plants in communities correlated with reduced competitive ability of native compared with exotic plants.
4. *Synthesis*: These data suggest that exotic plants host more generalist pathogens that are shared with native plants, which may confer an indirect benefit to exotic over native plants through apparent competition.

KEYWORDS
apparent competition, enemy release, exotic species, fungi, generalist pathogens, indirect interactions, invasion ecology, pathogens, spillback, spillover

1 | INTRODUCTION

Despite evidence that many plant pathogens are generalists and interact with multiple hosts in the community (Parker & Gilbert, 2007; Semchenko et al., 2022), interactions between plants and pathogens are typically studied in isolation of the wider community (but see Hawksworth, 2001). In invaded communities, exotic plant species can benefit from supporting and tolerating

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generalist pathogens that are shared with native species (i.e. accumulation of Local Pathogens Hypothesis, Eppinga et al., 2006; Mitchell et al., 2010; Semchenko et al., 2022; Visscher et al., 2021), resulting in pathogen-mediated apparent competition between plants (Holt, 1977; Holt & Bonsall, 2017, also known as disease-mediated invasion, Strauss et al., 2012). Exotic plants may benefit from influencing pathogen communities in native plant communities through various pathways: (1) pathogens that are compatible with resident plants are introduced with exotic hosts and integrate into native plant-pathogen networks (Bufford et al., 2020), (2) novel pathogens are introduced with exotic plants and make a host jump following a lag phase (Gilbert & Parker, 2010) or (3) exotic plants may amplify native or exotic pathogens that are already present in the environment (Eppinga et al., 2006; Malmstrom et al., 2005; Strauss et al., 2012). The importance of pathogen spread from exotic plants to native plants in invaded communities is difficult to quantify experimentally and marks an important gap in our knowledge of plant community dynamics (Flory & Clay, 2013; Goss et al., 2020).

Research in simplified crop and cultivated systems has shown that exotic invaders can serve as 'reservoir hosts' (asymptomatic or mildly symptomatic plants, also known as amplification hosts), spreading pathogens to agricultural plants (Linde et al., 2016; Wisler & Norris, 2005). However, demonstrating that exotic plants may act as reservoir hosts in more complex, multi-host, multi-pathogen natural systems has proven to be more challenging (Paull et al., 2012). Studies that do adopt a microbial community approach often examine plant–soil feedbacks (Bever et al., 1997), comparing the influence of different plants on and their response to pathogen communities in soils. However, plant–soil feedback experiments rarely involve more than 1–2 plant hosts or characterise specific microbial functional groups, thereby failing to determine whether effects of soil biota are due to pathogens or parasitic mutualists (e.g. mycorrhizal fungi, Klironomos, 2003). Furthermore, these tests cannot distinguish between the Enemy Release (Keane & Crawley, 2002) and Accumulation of Local Pathogens Hypotheses, as the absence of a growth depression from antagonistic soil biotic communities could indicate that plants have either escaped or are simply tolerating pathogens. Finally, it remains unclear whether plant–soil feedback effects observed in monoculture translate to a community, where the sharing of interaction partners may result in influential indirect interactions (Allen, 2020).

Several characteristics of exotic plants could make them more competent hosts for pathogens compared to native species. For instance, many exotic invaders exhibit "quick-return" strategies, such as faster growth and high nitrogen in tissues (Leishman et al., 2014; van Kleunen et al., 2010), and "quick-return" plants are generally more competent hosts for antagonists, including pathogens, than "slow-return" species (Allen et al., 2021; Cappelli et al., 2020; Cronin et al., 2010; Fahey et al., 2022; Strauss & Agrawal, 1999). Second, many exotic plants can tolerate damage from enemies with minimal impact on plant fitness (Ashton & Lerdau, 2008; Goss et al., 2020; Roy & Kirchner, 2000), and/or can replace lost tissues faster than slow-growing species (Allen et al., 2021; Gianoli & Salgado-Luarte, 2017). Third, exotic plants can attain high local abundance, increasing opportunities for pathogen establishment and spread (Burdon & Chilvers, 1982; Gilbert, 2002). Thus, communities with a majority of tolerant, exotic host biomass likely experience maximum transmission rates by pathogens (Parker & Gilbert, 2004). Considering that many exotic plants possess quick-return strategies, exhibit disease-tolerance, and occur at high abundance, they are likely to meet these criteria for acting as reservoir hosts.

To examine whether exotic plants host more generalist fungi that are shared with native plants, we conducted a single-species and a community-level plant–soil feedback experiment. We characterised fungal communities in the roots of native and exotic plants growing together in the 8-species communities ($n = 80$), spanning a range of exotic dominance from 0% to 100%. Our focus was on soil-borne fungi, as they represent the most common and damaging pathogen group affecting plants (Delgado-Baquerizo et al., 2020). We restricted our analyses to include only fungal taxa previously recognised as "probable" or "highly probable" pathogens/pathotrophs in the FUNGuild database (Nguyen et al., 2016). We quantified the relative abundance of pathogens in plant roots, calculated the proportion of operational taxonomic units (OTUs) shared between native and exotic plant hosts, assessed the generality of associations for both plants and fungi (relative to other species in the community) and analysed the frequency at which generalist fungi are shared with other plants. We addressed the following research questions: (1) Do exotic plants and exotic-dominated communities host more generalist pathogens than native plants and native-dominated communities? (2) Given their higher generalism, do exotic plants share a greater proportion of putative fungal pathogens with natives than do other native plants? (3) Does pathogen sharing between native and exotic plants correlate with exotic plant dominance in communities? (4) Do plant–soil feedbacks in monoculture predict feedbacks in communities?

2 | MATERIALS AND METHODS

2.1 | Study site and plant–soil culturing

We initiated this study in 2016, first in a glasshouse and then in large mesocosm pots set in a fallow field at Lincoln University (Lincoln, New Zealand. 43.6434°S, 172.4678°E, elevation 10 m, no permits were required for fieldwork), and completed it in 2019 (Waller et al., 2020).

In the first phase of the experiment, we cultured 39 species-specific microbial communities by growing 19 native and 20 invasive, exotic plant species individually in live, field-collected soil (species details listed in Table S1 and Supplementary Methods). To accomplish this, we collected approximately 1 m^3 of topsoil from each of eight sites across Canterbury, New Zealand in June 2016. We mixed

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the live soil in a 1:2 ratio with a pasteurised background media (50:50 mineral soil: sand that had been steamed twice for 60 min at 100°C internal temperature) and then added it to 10 L pots. Individual seedlings were grown from seed and cuttings in trays containing a sterile 50:50 mixture of vermiculite and perlite and then transplanted into the pots (12–20 replicates per species). After 9–10 months of growth, we harvested and discarded aboveground material from each pot, but retained and chopped the roots finely and reincorporated them into the soil. After combining replicates of each species, we had soils from each of the 39 plant species that could be used as "home" (i.e. cultured by a conspecific) or "away" (i.e. cultured by a heterospecific) soil.

To establish the single-species plant–soil feedback experiment, we grew 20 individuals of each of the 39 plant species in 10 L pots containing 7 L of freshly pasteurised soil: sand mixture (using the same methods, seeds and source-cuttings as described above), with 10 individuals receiving 2.5 L of "home" soil and the other 10 receiving 2.5 L of "away" soil (one of 10 different randomly chosen heterospecific species). After approximately 10 months of growth, we harvested all above and belowground plant material and determined the dry weight of all individuals.

To establish the community-level plant–soil feedback experiment, we designed 20 communities, each containing eight unique plant species taken from the pool of 39 species and grown in 125 L pots (575 mm dia.). Prior to out-planting, seeds and cuttings were started in the glasshouse in trays using the same methods, seeds and source-cuttings as in the first phase, but were transplanted into 1 L pots containing live soil inocula after plants had at least one true leaf. We staggered the timing at which we started the different species based on our previous knowledge of germination time and growth rates so that all individuals would be the same size at out-planting. Communities varied orthogonally in their proportion of exotic plant species (0%–100%) and woody plant species (0%–63%). We grew each 8-species community in pots containing a bottom layer of 22 L of gravel, covered with 88 L of pasteurised soil: sand mixture and topped with 12 L of the live inoculum soil created in the first round of feedback. Each of the 20 plant communities was replicated four times (80 pots total). Plant communities received one of two soil treatments, referred to as "home" or "away". To prepare the "home" soils, we mixed soil from each of the resident species in that community in equal parts. "Away" soils were mixtures of eight species occurring in one of the other 19 plant communities (a different community where none of the residents occurred). After approximately 1 year of growth, we recorded the realised plant species richness of each mesocosm community, harvested all above and belowground plant material, and determined dry weight of all individuals.

The experimental design included an additional 80 pots with an herbivore addition treatment (reported in Allen et al., 2021, 2023; Waller et al., 2020). However, that treatment was not relevant for our hypotheses, and so was excluded from the current analysis.

2.2 | Molecular sequencing and bioinformatics

DNA was extracted from a total of 491 root samples harvested from individual plants from all 80 mesocosms at the end of the experiment, using MoBio PowerSoil (QIAGEN) extraction kits. Root samples were taken from each individual plant using a sterile razor blade, cutting approximately 10–15 fine-root fragments from random places on the washed root ball, then bundling the roots together and slicing a 0.5–1.0 cm cross section piece from the bundle. Root samples were immediately placed into a 96 well plate from the extraction kit and frozen at −80°C as soon as a plate was full. We characterised the fungal communities by amplifying the internal transcribed spacer (ITS) of the ribosomal RNA (rRNA) operon using polymerase chain reaction (PCR) with the barcoded primers fITS7/ITS4 (Ihrmark et al., 2012; PCR conditions are described in the Supplementary Methods). Amplicons were sequenced on an Illumina MiSeq analyser using the 600-cycle Reagent Kit V3, delivering 2 X 300 base pair reads/sequence (Illumina, San Diego, California, USA).

Sequences were paired, putative chimeras removed, and clustered into operational taxonomic units (OTUs) at 97% sequence similarity using Vsearch (Rognes et al., 2016). Quality and barcode filtering resulted in 6,093,371 reads with a median length of 225 bases.

We assigned functional attributes to OTUs using the FUNGuild database (Nguyen et al., 2016) and retained only the taxa assigned as "probable" or "highly probable" plant pathogens for subsequent analyses (details about taxa from FUNGuild are listed in Data S1). We restricted our inclusion of taxa to those that receive most of their nutrients by harming host cells (defined as "pathotrophs" by FUNGuild) and excluded taxa with mixed strategies from our analyses (i.e. "pathotroph-saprotroph"), as many of these taxa are primarily saprotrophs and only occasionally pathogens. We acknowledge that by limiting our pathogen assignment in this way we have likely excluded many taxa that may be pathogens in some environments, so our results represent a conservative analysis of the pathogen communities hosted by our plants. Moreover, the taxa listed here are putative pathogens (hereafter referred to simply as "pathogens"), as we rely on commonly accepted life history descriptions rather than performing real-time functional assays for each plant-fungal interaction.

2.3 | Fatty acid extraction and quantification

As an independent measure of fungal biomass, we quantified phospho- and neutral lipid fatty acids (PLFA and NLFA, respectively) from approximately 10 g of freeze-dried soil from each mesocosm pot. Briefly, lipids were extracted by a commercial laboratory (Microbial ID, Newark, DE, USA), using methods described in Frostegård et al. (2011) and Waller et al. (2020). We used the PLFA fungal biomarker 18:2ω6 to assess biomass of fungi, excluding arbuscular mycorrhizal (AM) fungi. We used the NLFA biomarker 16.1ω5 for AM

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fungi, (Frostegård et al., 2011), as PLFA 16:1ω5 can sometimes indicate bacteria (Olsson & Johnson, 2005).

2.4 | Data analysis

Here we present a condensed version of the data analysis, with an expanded version in the supplement. We used generalised linear mixed-effects models (GLMMs) with the package lme4 (Bates et al., 2014) in R version 3.2.3 (R Core Team, 2019) for all models, unless specified otherwise (see Table 1 for final models). We used the emmeans package (Lenth, 2020) in R to calculate estimated marginal means and conduct post-hoc tests. Chi-square tests and *p*-values were calculated using the Anova function in the package car (Fox & Weisberg, 2019). Normalised degree of plants was modelled using a normal error distribution, pathogen relative abundance with a binomial distribution and normalised degree of pathogens and closeness centrality with a Gamma distribution (Zuur et al., 2009). We used the logit link function in the binomial models and the log link function in all other models.

We calculated a range of metrics of pathogen diversity and sharing. We calculated fungal pathogen richness and relative (proportional) abundance of pathogens in individual plant roots and plant communities. To study partner sharing, we calculated the species-level interaction network metrics normalised degree and closeness centrality (weighted closeness) using the R package bipartite (Dormann, 2011). High closeness centrality indicates that a plant species tends to share partners with many species or with particular species that share with many others. Given this sharing, here we used closeness centrality as an indicator of how much influence

TABLE 1 Structures and results of generalised linear mixed-effects models measured at the community and individual plant-level.

Response variable	Community- level	χ^2	*p*	Individual-level	χ^2	*p*
a. Pathogen richness	Exotic	1.05	0.30	Provenance	0.84	0.36
	Soil	2.67	0.10	Soil	2.26	0.11
	Exot.×Soil	1.89	0.17	Prov.×Soil	1.28	0.26
b. Pathogen relative abundance	Exotic	5.17	**0.02**	Provenance	1.31	0.25
	Soil	0.27	0.60	Soil	2.62	0.11
	Exot.×Soil	3.31	0.07	Prov.×Soil	1.28	0.26
c. Plant normalised degree	Exotic	37.97	**<0.001**	Provenance	21.80	**<0.001**
	Soil	0.37	0.54	Soil	0.19	0.67
	Exot.×Soil	0.04	0.85	Prov.×Soil	1.82	0.18
d. Plant weighted centrality	Exotic	15.68	**<0.001**	Provenance	36.57	**<0.001**
	Soil	2.06	0.15	Soil	2.89	0.09
	Exot.×Soil	1.86	0.17	Prov.×Soil	0.74	0.39
e. Pathogens shared	Exotic	6.37	**0.01**			
	Soil	3.08	0.08			
	Exot.×Soil	0.05	0.82			
f. Fungal biomass (PLFA)	Exotic	0.16	0.69			
	Soil	0.41	0.52			
	Exot.×Soil	1.80	0. 81			
g. Pathogen normalised degree	Exotic	45.12	**<0.001**			
	Soil	0.36	0.55			
	Exot.×Soil	0.04	0.83			
h. Plant biomass (PSF)	Provenance	20.07	**<0.001**	Provenance	4.98	**0.03**
	Soil	2.41	0.12	Soil	31.21	**<0.001**
	Prov.×Soil	2.64	0.10	Prov.×Soil	48.81	**<0.001**
i. Relative interaction intensity (RII)	Exotic	0.49	0.48			
	Path. shared	3.74	**0.05**			

Note: Response variables a-g were tested as a function of the proportion of exotic plants planted in experimental communities, ranging from 0%–100% (i.e. exotic is tested at the community-level), the soil treatment (home or away) and their interaction. Random factors were mesocosm (pot 1–80) nested in plant community (community 1–20). Response variable h (plant biomass, as a measure of plant–soil feedback [PSF]) was tested as a function of plant provenance, the soil treatment and their interaction. Response variable i was tested as a function of the proportion of exotic plants and the proportion of pathogens shared between native and exotic plants. Response variables a-d were also tested as a function of plant provenance, native or exotic (i.e. provenance is tested at the individual-level), the soil treatment and their interaction. Random factors were the same as above plus plant species. Significant variables ($p < 0.05$) are designated in bold.

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a plant could have in a community through its ability to indirectly affect other species by spreading pathogens; an antagonistic equivalent to previous findings that species with high closeness centrality confer indirect benefits in belowground mutualisms (Tylianakis et al., 2018).

To test whether exotic plants host more generalist fungal pathogens than native plants (Question 1) and how the generality of pathogens and the potential for interactions to be shared changed along the exotic plant gradient (Questions 1 and 2), we quantified how pathogen richness, relative abundance, normalised degree and closeness centrality changed as a function of the proportion of exotics planted into the community (ranging from 0% to 100%), soil treatment (home or away) and their interaction as fixed effects, with mesocosm (pot 1–80) nested in plant community (community 1–20) as random effects.

To test whether native and exotic plants differ in the proportion of fungal pathogens they share (Question 2), we modelled pathogen sharing between native and exotic plants in each mesocosm community as a function of the proportion of exotics planted, soil treatment and their interaction, with random factors as described above (and in Table 1). We excluded communities containing both 100% native and 100% exotic plants from this analysis (i.e. retained communities with 25%, 50% and 75% exotic) because there could be no sharing by provenance if there were only natives or only exotics. To confirm the robustness of our results, we ran all models again, replacing the proportion of exotics planted with the proportion realised at the end of the experiment; results were consistent between these two approaches (Table S2). To calculate the proportion of pathogens that were shared (or not) between native and exotic plants in a community, we calculated the number of pathogenic fungal taxa that were identified from (1) only native plant roots, (2) only exotic plant roots, or (3) both native and exotic plant roots in each mesocosm pot. We then calculated the proportion of pathogenic fungal OTUs that were shared between natives and exotics in a mesocosm by dividing the number of shared pathogen OTUs by the total pathogen OTU richness in each mesocosm.

To determine whether exotics shared pathogens with natives more than would be expected by chance in each community, we simulated a null model showing how much sharing (as calculated above) we would expect along the full realised exotic gradient by chance (see Supplemental Methods). We used polynomial regression and fitted a curvilinear line to model the relationship between pathogen sharing and exotic dominance.

To test whether pathogen sharing between native and exotic plants correlates with exotic plant impact in communities (Question 3), we calculated a relative interaction intensity index (RII, Armas et al., 2004) for native and exotic plants and quantified its relationship with the proportion of pathogens shared between native and exotic plants in the community. The relative interaction intensity index quantifies the relative change in plant biomass from an assumed initial equal biomass (0.125) to what was realised at the end of the experiment, using the formula ((realised proportional biomass − 0.125)/(realised proportional biomass + 0.125)) and thus provides a measure of the deviation from the expected performance of native versus exotic plants in communities. RII is bounded between 1 and −1, with positive numbers indicating over performance and negative numbers indicating underperformance in communities. We modelled RII as a function of the proportion of shared pathogens and the proportion of exotics, with mesocosm nested in plant community as random effects.

To understand how natives vs exotics performed when grown in mixed versus pure communities, we also present the difference in native and exotic biomass that was realised from what was expected based on their planted proportions. We would expect more competitive species to grow larger than expected and less competitive species to grow smaller than expected. To calculate the expected biomass in the 100% native and exotic communities, we used the mean biomass of all mesocosms. To calculate the expected biomass value in mixed communities, we calculated 25%, 50% and 75% of the mean biomass.

To test whether plant–soil feedbacks when grown alone in monoculture predict feedbacks in a community (Question 4) we evaluated whether plant–soil feedbacks (i.e. the difference in biomass of a given species in home vs. away soils) differed between native versus exotic plants (i.e. interaction effect between soil treatment and plant provenance) and whether this difference was influenced by whether a plant was grown alone in monoculture or a community. In monoculture, we tested this by modelling plant biomass from the monoculture experiment as a function of plant provenance, the soil treatment and their interaction as fixed effects, with plant species as a random effect. In communities, we modelled how plant biomass changed as a function of plant provenance, the soil treatment and their interaction as fixed effects, with plant species and mesocosm nested in plant community as random effects. While others have presented response ratios to evaluate plant–soil feedbacks (Brinkman et al., 2010), we were unable to calculate a response ratio in communities due to differential plant mortality across treatments.

3 | RESULTS

From the 5482 OTUs classified to be fungal, 3851 were assigned functional attributes in FUNGuild. Of these, 364 OTUs (9%) were identified as being probable or highly probable pathogens of plants (listed in Data S1).

3.1 | Exotic plants host more generalist fungal plant pathogens

Fungal pathogen richness did not differ between native and exotic plants ($\chi^2 = 0.84$, $p = 0.36$), with individual plants hosting approximately 8 OTUs (±0.4 S.E.) identified as pathogenic on average. Fungal pathogen richness did not change with the proportion of exotic plants planted in the community or differ in home versus away soil (proportion of exotics: $\chi^2 = 1.05$, $p = 0.30$; soil treatment: $\chi^2 = 2.67$,

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$p = 0.10$, Table 1). Fungal pathogen relative abundance did not differ between native and exotic plants ($\chi^2 = 1.31$, $p = 0.25$, Table 1), but pathogen relative abundance increased along the exotic gradient, when exotic and native plants were evaluated at the community-level ($\chi^2 = 5.17$, $p = 0.02$, Table 1, Figure 1a). The soil treatment had no effect on pathogen relative abundance in communities ($\chi^2 = 0.27$, $p = 0.60$) and no interaction with the proportion of exotics ($\chi^2 = 3.31$, $p = 0.07$, Table 1). Total fungal biomass (using phospholipid fatty acid [PLFA] biomarkers) did not change along the exotic plant gradient ($\chi^2 = 0.16$, $p = 0.69$, Table 1), but exotic-dominated communities saw sharp reductions in AM fungal biomass (using neutral lipid fatty acid [NLFA] biomarkers, as reported in Waller et al., 2020).

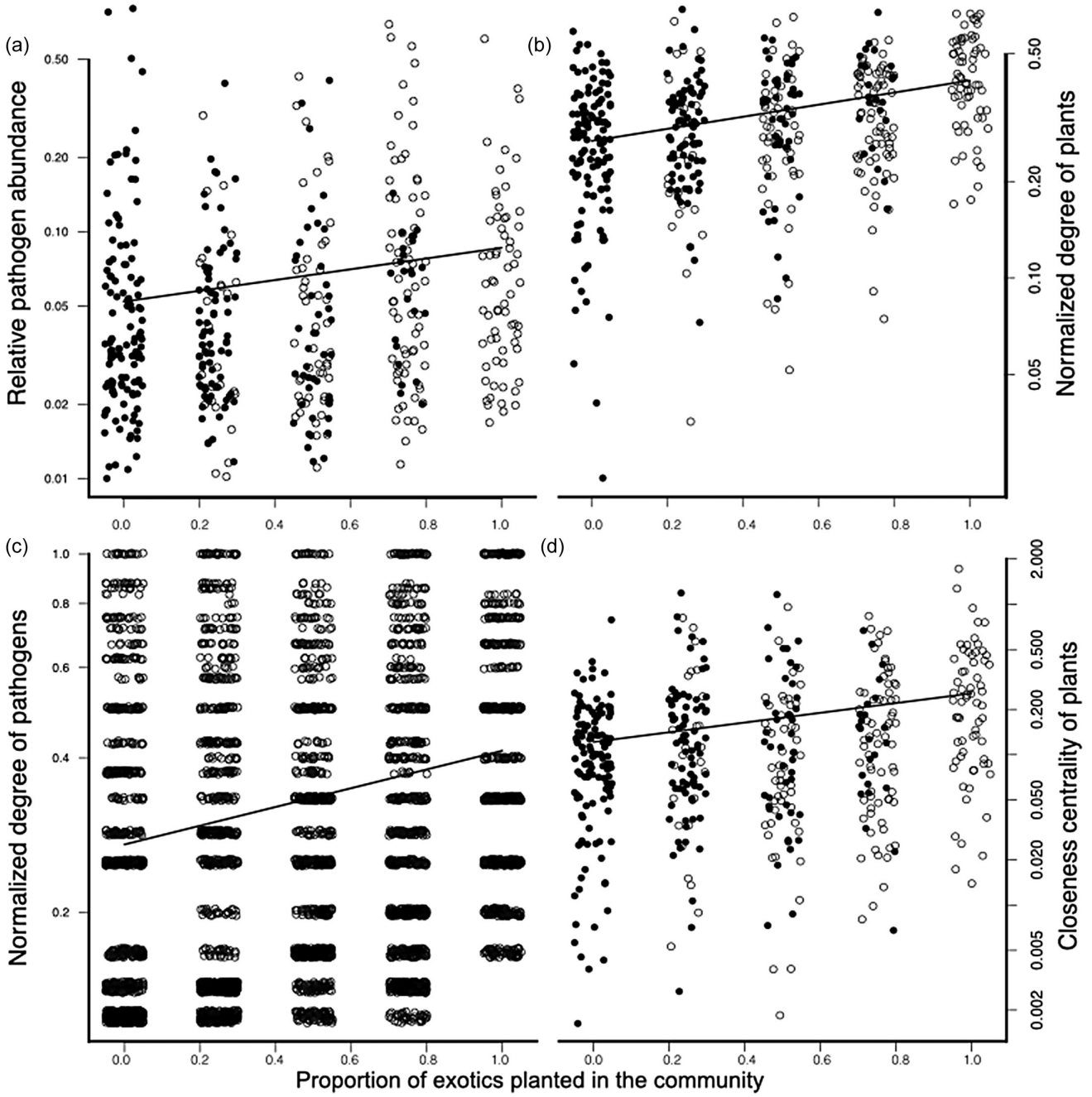

FIGURE 1 Relationship between the proportion of exotic plants planted in the experimental community and (a) relative abundance of sequences identified as plant pathogens in plant roots (pathogen sequences/total sequences); (b) normalised degree of plants (measures the generality of interactions by plants with pathogens); (c) normalised degree of pathogens (measures the generality of interactions by pathogens with plants); (d) closeness centrality of plants (measures the frequency at which plants share generalist pathogens with other plants). Closed circles represent native plants and open circles represent exotic plants in (a, b and d). Response variables were modelled on a log scale. A slight jitter was added to the points on the *x*-axis for ease of viewing. All interactions were tested but dropped from the models based on AIC.

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On average, plants interacted with an increasing proportion of available fungal pathogens along the exotic plant gradient, as indicated by plant-normalised degree ($\chi^2 = 37.97$, $p < 0.001$, Table 1, Figure 1b). Likewise, more generalist pathogens inhabited the roots of plants in exotic-, compared with native-dominated communities, as indicated by the normalised degree of fungal pathogens ($\chi^2 = 45.12$, $p < 0.001$, Table 1, Figure 1c). When growing in communities with only native or only exotic plants (i.e. in 100% native or 100% exotic mesocosms), exotic plants were more generalist than native plants in their interactions with pathogens, as indicated by normalised degree ($\chi^2 = 21.80$, $p < 0.001$, Table 1, Figure 2a). Exotic plants were also more central in their respective networks, as indicated by mean closeness centrality values for natives versus exotics ($\chi^2 = 36.57$, $p < 0.001$, Table 1, Figure 2b).

3.2 | Exotic plants share putative fungal pathogens with native plants

We found asymmetric sharing of pathogens between native and exotic plants along the exotic gradient (Figure 3). The relationship between shared pathogens and exotic dominance in mixed communities (Figure 3a) deviated significantly from null expectations (Figure 3b). Communities dominated by exotic plants shared a greater proportion of pathogen OTUs between native and exotic plants than would be expected by chance, compared with communities dominated by native plants, which shared fewer pathogen OTUs than our null model predicted (Figure 3). Native and exotic plants also shared 4% more pathogens in home compared with away soils ($\chi^2 = 6.37$, $p = 0.01$, Table 1). The observed proportion of shared pathogens appeared to reach a peak when the community contained approximately 60% exotic plants, while it was lowest in communities with 25% exotic plants (excluding communities with no exotic plants present; Figure 3). Further, the efficiency at which plants shared pathogens with other plants increased with the proportion of exotic plants in the community, as indicated by increasing values of closeness centrality with increasing exotic dominance ($\chi^2 = 15.68$, $p < 0.001$, Table 1, Figure 1d).

3.3 | Pathogen sharing between native and exotic plants correlates with exotic plant impact in communities

Relative interaction intensity (RII) increased as the proportion of pathogens shared between native and exotic plants increased, irrespective of the proportion of exotics initially planted (RII ~ shared pathogens + proportion exotics + (1|community/mesocosm); pathogen shared: $\chi^2 = 3.74$, $p < 0.05$; proportion exotics: $\chi^2 = 0.49$, $p > 0.05$, Figure 4a, Table 1). When modelled as a function of realised exotics (RII increased both as the proportions of pathogens shared increased and the proportion of realised exotics increased, pathogen shared: $\chi^2 = 7.88$, $p < 0.005$; proportion exotics: $\chi^2 = 12.47$, $p < 0.001$, Table S2). In fact, the proportional native plant biomass from the beginning to the end of the experiment was consistently reduced in every community where exotic plants shared 30% or more of their pathogens with them (Figure 4a). In contrast, the correlation between pathogen sharing and exotic plant success was not significant (Figure 4b); rather, exotic plants overperformed in nearly every mixed community they grew (Figure 5), making up a greater proportion of community biomass compared to that which they were initially planted.

Native plants over-performed when grown in purely native communities, but under-performed when grown in mixed communities (Figure 5). In contrast, exotic plants under-performed when grown with only exotic plants, but only when grown in home soil (Figure 5). However, when grown in mixture, exotic plants benefited, out-competing native plants, regardless of higher pathogen loads (Figure 5).

3.4 | Plant–soil feedbacks in monoculture do not predict feedbacks in a community

Plant–soil feedbacks in monoculture did not predict feedbacks in communities. When grown in monoculture, exotic plants showed strong negative feedback when grown in their home soils, whereas natives benefitted from their home soil (provenance × soil interaction: $\chi^2 = 45.91$, $p < 0.001$, Figure 6A, Table S3). Exotic plants grown in away soil were over 20% larger on average than exotics grown in home soil, whereas native plants grown in away soil were 12% smaller than natives grown in home soil. However, the apparent benefit of plant–soil feedbacks to natives in monoculture disappeared when plants were grown in communities. In communities, exotic plants were approximately 9 times larger than native plants (provenance: $\chi^2 = 19.14$, $p < 0.001$, soil: $\chi^2 = 3.07$, $p > 0.05$, provenance × soil interaction: $\chi^2 = 2.60$, $p > 0.05$, Figure 6B, Table S3 and Figure S1). As reported in Waller et al. (2020), total plant community biomass across all mesocosms was reduced in home soil, but these soil effects did not differ with the proportion of exotics planted in the community.

4 | DISCUSSION

Our experiment revealed that exotic-dominated plant communities supported a higher relative abundance of fungal pathogens, and on average, those pathogens tended to be more generalist than those supported by plants in native-dominated communities. We observed a pattern of pathogen sharing congruent with asymmetric spillover, whereby exotic plants shared more pathogens with natives than were shared between natives. Moreover, exotic plants showed strong potential to indirectly reduce the biomass of co-occurring native plants by spreading pathogens, whereas native plants had less influence (closeness centrality) over shared pathogen interactions. These findings suggest that exotic plant hosts have a high potential to be reservoirs for generalist fungal pathogens, which

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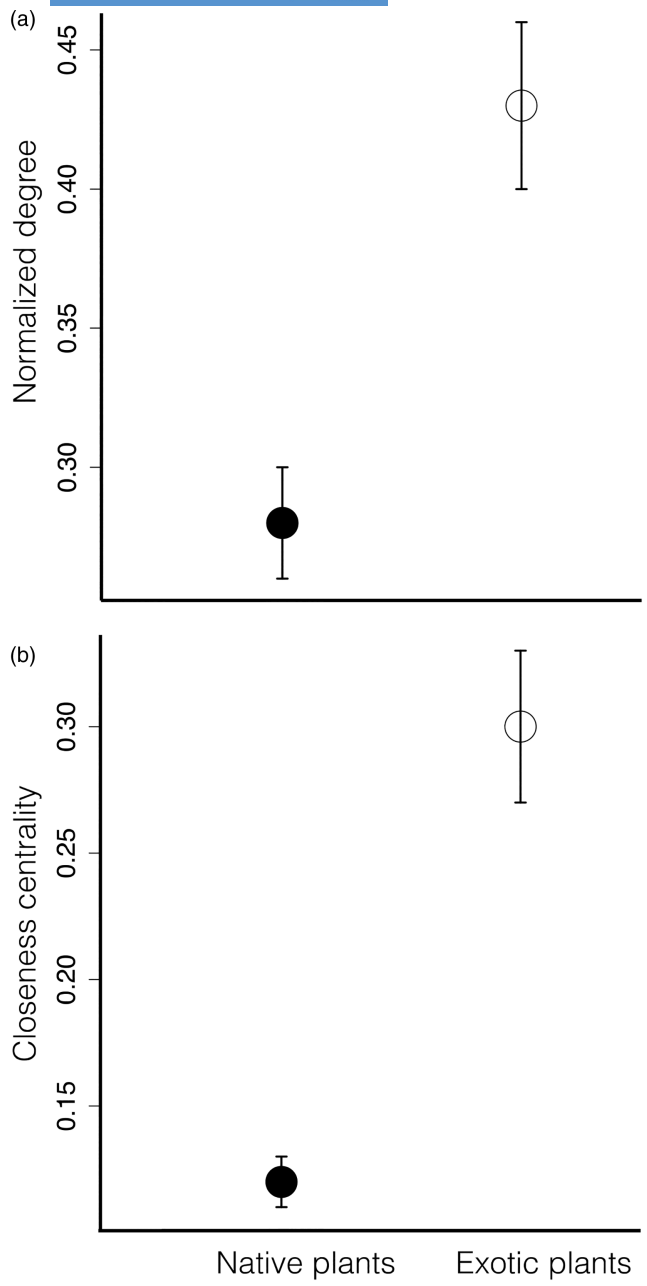

FIGURE 2 Estimated marginal means (±S.E.) of (a) normalised degree (measures the generality of interactions by plants with pathogens) and (b) closeness centrality (measures of the frequency at which plants share generalist pathogens with other plants) of plants growing in communities of only native plants (i.e. 100% native communities, closed circles) and only exotic plants (i.e. 100% exotic communities, open circles).

could constitute a feedback that increases exotic plant dominance in mixed communities of native and exotic plants.

We observed declines in native plant performance consistent with pathogen-mediated apparent competition between plants. Native plants were strongly impacted by the presence of exotics in this experiment, as illustrated by significantly reduced native biomass when grown with exotics. In particular, the greater the level of pathogen sharing, the worse native plants fared in competition. Exotic plants underperformed when grown with only exotic neighbours and in home soil, presumably due to the accumulation of pathogens in exotic-dominated soils, yet overperformed and also outperformed native plants in almost all mixed communities. These results suggest that exotic plants have a tolerance to fungal pathogens that allows them to persist in monoculture, albeit in a somewhat diminished capacity compared with their performance in mixed communities (consistent with a reservoir host, being weakly symptomatic or asymptomatic). These correlations may or may not be causal, as it is possible that the same traits that allow exotic plants to tolerate pathogens, such as faster growth (Cronin et al., 2010), also increase their ability to compete directly against native plants (Allen et al., 2021). However, pathogen relative abundance and pathogen sharing among plants (indicated by our network metrics) was highest in communities with 100% exotic plants, despite maintaining high biomass in those communities (i.e. no net change in community biomass along the exotic gradient, as reported in Waller et al., 2020), suggesting that exotic plants had higher tolerance to fungal pathogens compared with native plants.

Conducting plant–soil feedback experiments in monoculture and in communities allowed us to compare results between the different contexts. While native plants showed positive feedback and exotics negative feedback in monoculture, these patterns disappeared in mesocosm communites (Figure 6). The negative effects that exotics had on themselves disappeared when grown in competition with natives, an example of apparent competition (Holt, 1977; Holt & Bonsall, 2017) supporting the concept of disease-mediated invasion (Strauss et al., 2012). Our results suggest that the ability of PSFs in monoculture to predict community PSFs may depend on the community context.

Our findings indicate that exotic plants are contributing to higher generalist pathogen loads, as seen by an increasing relative abundance of pathogens and increased generalism of pathogens, with no change in total fungal biomass. We cannot determine whether the pathogen sharing between native and exotic plants constituted co-introduced non-native pathogens ("spillover", e.g. Bufford et al., 2016) or native pathogens ("spillback", e.g. Borer et al., 2007; Levine et al., 2004), as we do not know the provenance of the pathogens in this study. Either scenario can increase exotic plant success (Dickie et al., 2017; Power & Mitchell, 2004), though spillback may be more common in plant invasions (Strauss et al., 2012). Non-native pathogens in New Zealand ecosystems tend to be more generalist compared with native pathogens (Bufford et al., 2020), so it would not be unreasonable to assume that many of the pathogens from our experiment were non-native. Spillover of non-native pathogens may also increase the probability of emerging novel pathogens on native hosts, with consequences for conservation and functioning of indigenous ecosystems. Regardless, our results show that exotic plants are more generalist in their associations with resident pathogens, driving asymmetric sharing from exotic to native plants.

AM fungi, which are known for their beneficial effects on plant growth and for their pathogen suppression ability (Sikes et al., 2009), had significantly lower biomass in exotic-dominated communities

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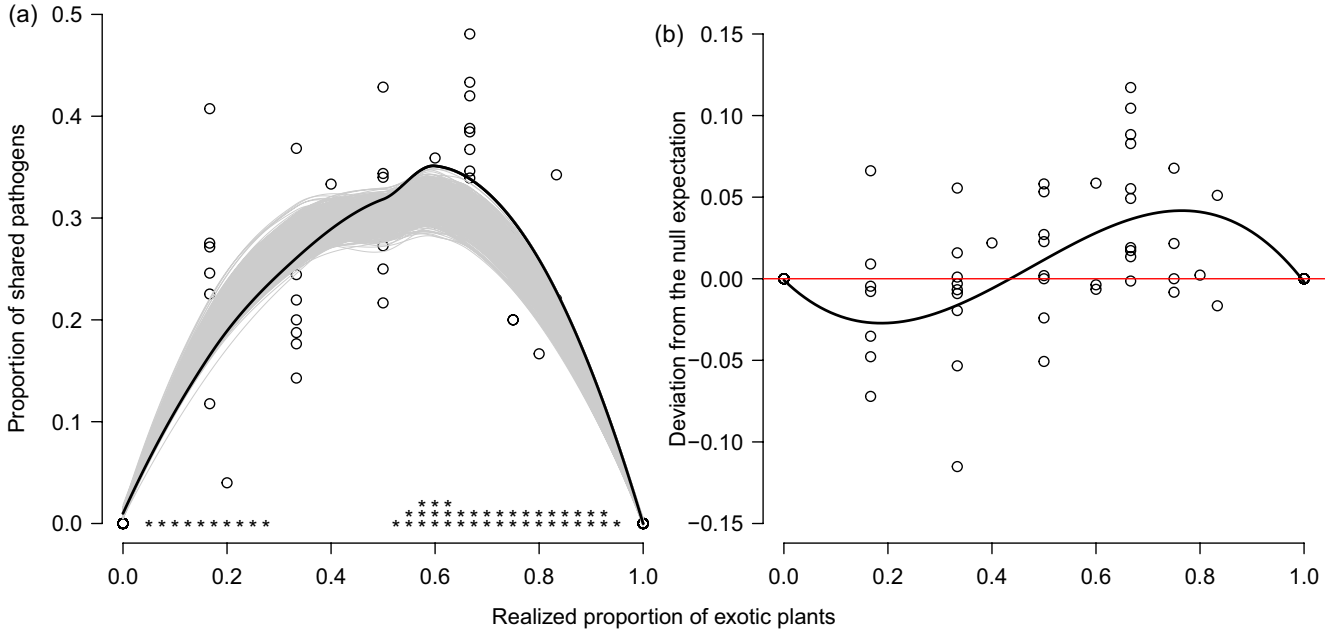

FIGURE 3 Relationship between the realised proportion of exotic plants in communities at harvest time and the proportion of putative fungal pathogens that were shared between native and exotic plants. (a) Asymmetric sharing of pathogens between native and exotic plants in communities. The black line is fitted through the observed data (points) from the community experiment showing the proportion of putative fungal pathogens that were shared as a function of the realised proportion of exotic plants in communities at harvest time, and the grey lines represent 999 simulations of a null model of random sharing. Note that proportions of 0 and 1 must have zero sharing of pathogens between native and exotic plants by definition. Stars indicate p values <0.05 for the fitted model versus the 999 simulations. (b) Deviation between the observed (points) and the null expectation (red line) of putative fungal pathogen sharing between native and exotic plants, showing the 3rd order polynomial fit ($F_{3,76}=8.57$, $p<0.001$, $R^2_{adj}=0.22$). Together, (a) and (b) show that communities with few exotic plants have lower than random sharing of pathogens, whereas exotic-dominated communities have higher than random sharing.

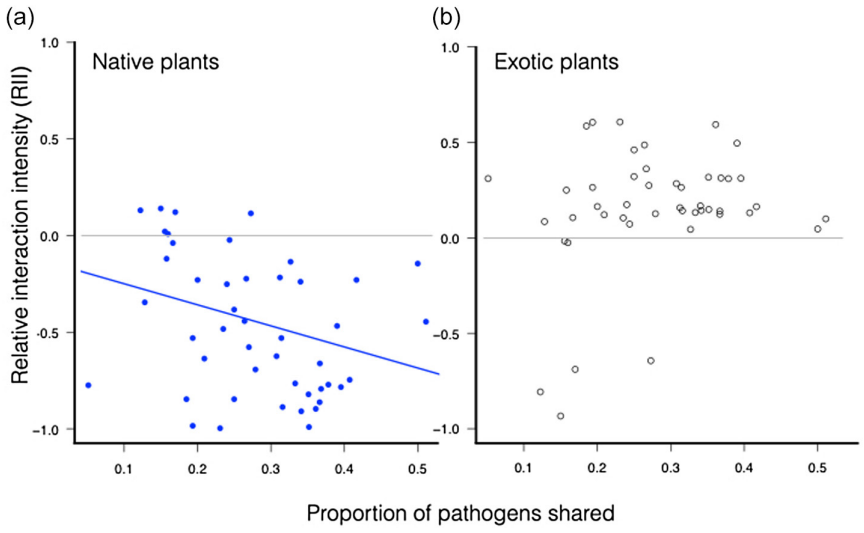

FIGURE 4 Relationship between the proportion of pathogens shared between native and exotic plants and the impact on realised biomass of (a) native and (b) exotic plants in mixed communities. Impact on biomass was quantified using the relative interaction intensity index (RII), which measures the relative change in biomass from the beginning to the end of the experiment. Values above the horizontal grey line indicate plant growth that was greater than expected and below the line, lower than expected. Native plants performed more poorly than expected in mixed communities and exotic plant impact on native plants increased as the proportion of pathogens shared between native and exotic plants increased (RII ~ proportion of pathogens shared, $\chi^2=3.74$, $p<0.05$, represented by the black line in panel a).

(as reported in Waller et al., 2020). Exotic plants commonly change the biotic and abiotic soil environment (Ehrenfeld, 2010; Waller et al., 2020), including suppression of mycorrhizas (Wilson et al., 2012; Wolfe et al., 2008), which can influence fungal pathogen abundance and distribution. Notably, reductions in AM fungal biomass in exotic-dominated communities also likely contributed to reduced native

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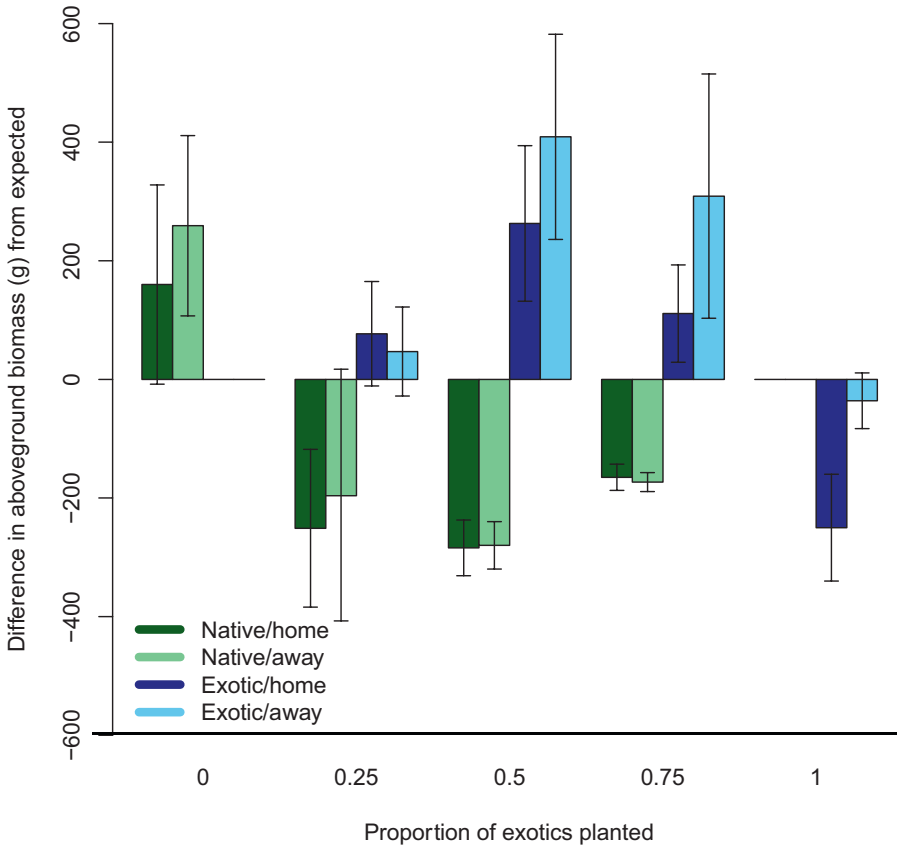

FIGURE 5 Mean (±S.E.) of the difference in realised aboveground biomass of native and exotic plants from what was expected. Expected biomass of purely native and purely exotic communities was calculated by taking the mean plant biomass from all communities, and expected biomass in mixed communities was calculated by taking 25%, 50% and 75% of the mean biomass. Green bars represent native plant growth (dark green for plants grown in home soil, light green for plants grown in away soil) and blue bars represent exotic plant growth (dark blue for plants grown in home soil, light blue for plants grown in away soil).

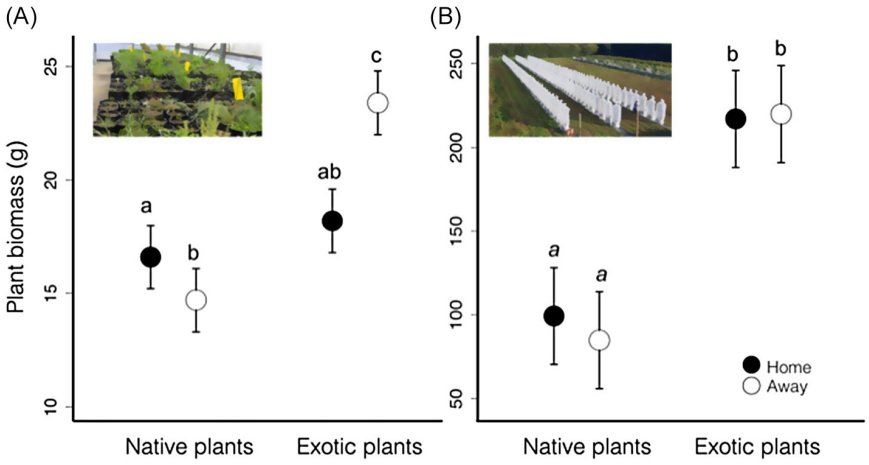

FIGURE 6 Estimated marginal means (±S.E.) of aboveground native and exotic plant dry biomass when grown in home or away soil in the (A) monoculture plant–soil feedback experiment (provenance × soil interaction: $\chi^2 = 48.81$, $p < 0.001$) and (B) community plant–soil feedback experiment (provenance: $\chi^2 = 20.07$, $p < 0.001$). Different lowercase letters indicate significant differences ($p < 0.05$) between means. Inset photos show the monoculture and community plant–soil feedback experiment.

performance, particularly in light of the high AM fungal biomass in native-dominated communities which also over-performed, compared with mixed communities, where native plants under-performed. Increases in pathogen relative abundance in exotic-dominated communities may have occurred because declines in AM fungi reduced plants' ability to suppress pathogens in their roots (Sikes et al., 2009). Further, declining biomass of mycorrhizal fungi may have indirect negative effects on native plants; lower AM fungal biomass may lead to reduced competition against pathogens in the root-soil environment or reduce the performance of native plants that rely on mutualists for protection, making them more susceptible to pathogens.

The often "quick-return" traits of exotic invaders may influence the extent of pathogen accumulation (Allen et al., 2021; Cappelli et al., 2020; Cronin et al., 2010; Fahey et al., 2022; Strauss & Agrawal, 1999). The exotic plants used in this study were representative of the quick-return end of the nutrient use spectrum compared with the native plants; both exotic woody plants and grasses had higher specific leaf area and faster growth compared with native woody plants and grasses (reported in Waller et al., 2020). Moreover, trait differences of exotic plants, and not biomass, explained how biotic interactions differed with exotic plants compared with natives in that experiment (Waller et al., 2020). These qualitative differences are also likely to explain differences in the way exotic plants interacted with the fungi identified to have pathogenic function in the current study.

Exotic plant invasions threaten biodiversity and ecosystem functions worldwide (Mack et al., 2000). Understanding how some

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invaders come to dominate native systems is therefore crucial to mitigating their impacts. Our results highlight another threat posed by exotic plant invasion and indicate that exotic plants have the potential to benefit from fungal pathogens via disproportionate pathogen sharing with native plants. Future work should focus on how exotic reservoir potential and spillover is affected by increasingly high global invasion rates and other global change factors.

AUTHOR CONTRIBUTIONS

Ian A. Dickie, Leo Condron and Jason M. Tylianakis obtained funding for the main experiment. Amanda Black obtained funding for writing of the manuscript. Warwick J. Allen, Ian A. Dickie, Leo Condron and Lauren Waller designed the experiment. Lauren Waller and Warwick J. Allen conducted the experiment and collected data, assisted by Angela Wakelin. Lauren Waller led analyses, with assistance from Warwick J. Allen, Ian A. Dickie, Jonathan D. Tonkin and Jason M. Tylianakis, and wrote the first draft of the manuscript. All authors contributed to revisions.

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CONFLICT OF INTEREST STATEMENT

None of the authors have a conflict of interest to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data reported in this paper are deposited in the Dryad Depository: https://doi.org/10.5061/dryad.wwpzgmsgb (Waller et al., 2020a) and https://doi.org/10.5061/dryad.c866t1gfz (Waller, 2024).

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SUPPORTING INFORMATION

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

Table S1. Plant species name, family, provenance and functional group of each plant used in the single-species and community-level plant-soil feedback experiments.

Table S2. Structures and results of generalized linear mixed-effects models.

Table S3. Structures and results of generalized linear mixed-effects models for plant-soil feedback.

Figure S1. Mean (±S.E.) of the realised aboveground biomass of native and exotic plants grown in home and away soil.

Data S1. Pathogen taxa.

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