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Soil biotic effects and competition; what are the mechanisms behind being a successful invader?

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Abstract

The global threat of plant invasions to native ecosystems mandates an understanding of the mechanisms that determine invasion success. While some exotic species establish, spread and impact native ecosystems, others establish with little or no measurable impact. Competitive ability has been highlighted as a key mechanism influencing invasion success and impact, but there is growing evidence that interactions between plants and soil biota may also be important. In particular, escape from natural enemies during the early stages of establishment may give exotic species an advantage over native species subject to their own natural enemies in the soil. Here, we evaluated whether the invasion success and impact of exotic grass species could be explained by competitive superiority over resident native species, advantages gained from the positive effects of native soil communities, or both. We assessed the competitive abilities of six grass species that vary in their invasion success relative to three widespread native grasses, quantified the effects of native soil microbial communities on the performance of both native and exotic grass species, and determined whether there was an interaction between competitive and soil effects. Overall, we found that exotic species were stronger competitors than natives and that native soil effects were weak and did not predict invasiveness. Differences in species relative competitive abilities also did not correlate with invasiveness but demonstrate how some exotic species could outcompete natives and suppress their growth during the invasion process.

Introduction

Invasion by exotic plant species poses a major threat to many native ecosystems (Grice, 2006) but not all exotic species are equally successful invaders. While some exotic plant species can establish, spread, become locally abundant and have significant negative impacts (Richardson et al., 2000), other exotic species establish in native ecosystems with little or no measurable impact (Hulme et al., 2013; van Klinken & Friedel, 2017). Understanding the reasons why some exotic species but not others are highly invasive and significantly impact the ecosystems they invade should allow us to identify potentially problematic invaders before they are introduced or become established in a region (Rejmanek & Richardson, 1996), and contribute to identifying and implementing effective management interventions for current invasive exotics. Consequently, much research has focused on understanding the mechanisms that contribute to both the invasion (the processes of establishment and spread) and subsequent impact of exotic species on native ecosystems (Hulme et al., 2013).

Competitive ability has long been held as a key factor underlying the differential impact of invasive plant species (Gioria & Osborne, 2014). In Australia, for example, most invasive exotic grass species were originally introduced to increase pasture productivity and hence were chosen to have characteristics such as rapid growth rate and high biomass production (van Klinken & Friedel, 2017). These traits are often associated with greater ability to capture resources above and below ground (Goldberg & Landa, 1991), which may give exotic species a competitive advantage relative to native species that are often slower growing (van Klinken & Friedel, 2017). This appears especially true for exotic species that occupy similar niches or are in similar functional groups as natives (Chesson, 2000). Many studies have documented competitively superior exotic species displacing native species (Callaway & Aschehoug, 2000; Groves et al., 2003; van Kleunen et al., 2010). In contrast, exotic species that are poor competitors, while sometimes common and widespread, are often found at lower abundance and appear to have less impact on native communities (Grice, 2006; O'Reilly-Nugent et al., 2019). Hence, differences in the relative competitive ability of invasive species may help explain differences in the extent to which they can invade and impact native ecosystems.

More recently, interactions between plants and soil microbes have been shown to influence plant invasion (Bever, 2003; Inderjit & van Der Putten, 2010). Exotic species performance, including growth, seedling establishment and competitive ability (van der Heijden, Bardgett and van Straalen, 2008), can be enhanced by the loss of natural enemies and thus reduced pathogen load (the enemy-release hypothesis) (Reinhart et al., 2010; Reinhart & Callaway, 2004; van der Putten et al., 2005), or by association with local mutualistic biota (Callaway et al., 2004; Niu et al., 2007). Exotic species that are generalist, or those that have reduced responsiveness to soil biota (Bennett & Strauss, 2013; Reinhart & Callaway, 2006), can also gain a relative advantage over natives as they are less reliant on mutualists to occupy new areas (Simonsen et al., 2017). Meta-analyses have shown that, relative to native plant species, invasive species tend to experience more positive or at least less negative interactions with resident native soil biota (Kulmatiski et al., 2008), which may give some exotic plant species a substantial performance advantage relative to native species, leading to greater invasion success (Kulmatiski et al., 2008).

Plant-soil interactions, however, can change over the time course of an invasion (Lau & Suwa, 2016). While exotic species are likely to encounter a soil biota that is new to them when initially colonising an area, they will begin to modify the original soil community as they spread and increase in abundance by cultivating a different suite of soil organisms which then affect plant responses (Diez et al., 2010; Dudenhöffer et al., 2017; Flory & Clay, 2013). Consequently, the response of exotic species to soil biota at the start of an invasion or at an invasion front may differ from their response during later stages of that invasion (Wandrag et al., 2013). Studies of plant-soil interactions have mostly focused on these later invasion stages, examining how native and exotic species respond to soil biota cultivated by each other (Lekberg et al., 2018; Shannon et al., 2012; van Grunsven et al., 2007). However, the responses of exotic species to native soil biota when they first colonise an area may be critical to their subsequent invasion success. For example, we could hypothesise that exotic species with more positive early responses to native soil biota will more readily invade new areas and thus spread and increase in initial abundance. Moreover, positive responses to native soil biota could add to or interact with competitive ability to further alter invasion dynamics.

The above arguments suggest three ways in which an exotic species could gain an advantage over native species when invading a native community: 1) by having an inherent advantage as a superior competitor; 2) by gaining an advantage through interactions with the native soil biota either through low responsiveness, as a generalist, or due to more positive interactions with native soil biota, relative to both native species and exotic species that are less successful invaders; or 3) because soil biotic effects enhance competitive ability (a positive interaction). We might expect widespread invasive species that have large impacts on the ecosystems they invade to benefit in one or more of these ways.

Here we aim to simultaneously examine the importance of interactions with native soil biota and plant competitive ability in explaining the relative performance of species classed as either high-impact invasive, low-impact invasive or native species. We ask: 1) Are high-impact invasive species better competitors than low-impact invasive and native species? 2) Do interactions with native soil biota advantage high-impact invasive species relative to low-impact invasive and native species? and 3) Are the potential effects of soil biota and competition on plant performance additive or interactive?

Methods

Plant species

We selected three native and six exotic grass species that commonly co-occur in Australian temperate grassy ecosystems. The three native grass species were *Themeda triandra* Forssk., *Poa sieberiana,* Spreng., and *Austrostipa scabra,* Lindl. These three species were selected because they are dominant native grasses often characteristic of distinct grassland types (Prober et al., 2005). The six exotic grass species were *Lolium perenne* L., *Festuca arundinacea* Schreb., *Dactylis glomerata* L., *Phalaris aquatica* L., *Eragrostis curvula* Schrad., and *Nassella neesiana* Trin. & Rupr. Three of these species, *Phalaris aquatica, Eragrostis curvula* and *Nassella neesiana*, are listed as problem weeds throughout Australian temperate grasslands, are frequently recorded as dominant and present in high abundance and have been shown to replace native species (VIC EVC - Department of Sustainability Environment, 2004; Department of Sustainability Environment Water Population and Community, 2011; NSW Weed Risk assessment - Department of Planning, Industry and Environment, ACT and NSW Department of Planning, Industry and Environment; Groves, Austin and Kaye, 2003; Faithfull, 2012). We classified these species as high-impact invaders. The other three species, *Lolium perenne*, *Festuca arundinacea, Dactylis glomerata,* are widespread in Australian temperate grasslands and usually locally present but not dominant or seen as causing high impacts (VIC EVC - Department of Sustainability Environment; Department of Sustainability Environment Water Population and Community, 2011; NSW Weed Risk assessment - Department of Planning, Industry and Environment, ACT and NSW Department of Planning, Industry and Environment; Bourdôt and Hurrell, 1989; Morgan, 1998). We classified these species as low-impact invaders. We focused on perennial grasses to enable comparison of soil responses and competitive interactions for exotic and native grasses within the same functional group (Gioria & Osborne, 2014).

Glasshouse experiment

Field soil collection and soil treatment

In May 2018 we collected field soils from three sites in the Australian Capital Territory (ACT) for use as inoculum in our glasshouse experiment (Site A; 35°11'54"S 149°08'05"E, site B; 35°11'18"S 149°02'59"E, site C; 35°23'43"S 149°01'35"E, Canberra, Australia). We chose sites at least 10 km apart that were as similar as possible in terms of: a) having low cover of exotic plant species, and hence representing relatively uninvaded native grassland; b) having similar land-use history (no ploughing and reduced human modification, such as mowing or herbicide use); and c) being dominated by the native grass *Themeda triandra*, the most common dominant of temperate grasslands in the study region, and having both *Austrostipa scabra* and *Poa sieberiana* present as subordinates or dominant in patches. At each site, we removed any litter and collected the top 0-10 cm of soil from at least 30 locations where *Themeda triandra* had a minimum cover of 60% and any exotic species were at least 2 metres away. The soil from each site was bulked and homogenised to provide one overall soil sample per site. We considered the soil microbial community derived from these soil samples as representative of the soil community associated with the dominant grass *Themeda triandra* and its associated native plant community. We chose three sites to capture variation in soil biotic communities between sites to ensure our results were representative of the general area and not site-specific. The bulked soil from each location was air-dried, sieved (4mm) and homogenised. To maintain the ability to test for any site differences we kept the soil from each site separate. To measure the response of plant species to the native soil biota, we set up four treatments in which pots of sterile soil were inoculated either with live soils from one of the three field sites or with gamma irradiated field soil (>30 kGy, Steritech Pty. Ltd., Sydney, Australia). We used gamma irradiation to create a sterile treatment because it is known to sterilise soil biota effectively and evenly (McNamara et al., 2003). To inoculate pots (4 litres) with soil biota while minimising the effect of different abiotic properties of the soils from each site, we added a small amount of field soil (6% of the total soil volume of our pots) to a steam sterilised (65 ^{o}C for 1.5h) potting medium of 1:1:1 peat moss: river sand: potting mix that filled 90% of the pot (4.7% nitrogen w/w and 2.1% phosphorous w/w). We then topped up each pot with the remaining 4% sterile potting mix and sterile expanded clay pebbles to reduce the potential for cross-contamination of live soil between pots. Sterile pots differed in having 6% of the irradiated soil added to pots rather than live field soils.

Seeds

Seeds were commercially sourced (Smyths Seed, Victoria, Australia; AUSTRALIAN GRASSES, NSW, Australia). To maximise germination and break dormancy where required, seeds of each of the three native (*Themeda triandra, Poa sieberiana* and *Austrostipa scabra*) and one of the six exotic (*Nassella neesiana*) grass species were treated prior to germination. These treatments included removal of awns (*Themeda triandra, Austrostipa scabra* and *Nassella neesiana*), removal of the seed coat (*Themeda triandra*), soaking in deionised water (*Poa sieberiana*) or 100 ppm gibberellic acid (*Themeda triandra*, *Austrostipa scabra* and *Nassella neesiana*). These treatments were identified as effective in ensuring germination in a series of trials prior to the experiment. Following treatment for germination, all seeds were sterilised (1 min in 70% ethanol, 5 minutes in 6% bleach and then rinsed 3 times with deionised water) and germinated on sterile sand vermiculite mix (1:1) in growth cabinets set to a 12/12h light-dark regime with two different temperature regimes (either 15/25 °C or 20/30 °C) to optimise germination for the different species. After germination, seedlings were kept in growth cabinets until their first true leaf appeared, when they were transplanted into pots in the glasshouse (19/06/2018-22/06/2018). Glasshouse temperatures were set to 18-24 °C with ambient light conditions.

Experimental design

To quantify the influence of soil biota on the performance of each species, and to quantify the competitive ability of each of the six exotic species relative to each of the three native species, we planted two seedlings in each pot. We used a split plot design to minimise cross contamination of soil microbiota between each of the four soil treatments (three field sites and one sterile control). Each soil treatment was randomly assigned to a bench within the glasshouse, with five replicate benches per soil treatment. Each bench had one replicate of each of 27 species x competition treatments: either two conspecific seedlings of each of the three native and six exotic species (nine pots), or one seedling of each native species paired with one seedling of each exotic species (18 combinations: six exotic species x three native species). This design resulted in a total of 540 pots: each of the 27 species x competition treatments planted in each of the four soil treatments, each with five replicates. Pots were randomly assigned to a location on each bench, and pot locations were randomly reshuffled on each bench at week 8 to reduce location bias. Plants were watered as required and pots weeded of all non-target plants weekly. Plant height was measured 2-3 days after seedlings were transplanted into treatments, with these measurements used to determine the mean and standard deviation of initial height for each species. Seedlings were replaced if they were 2 standard deviations shorter or taller than the mean height for each species (five seedlings in total) to minimise initial size differences. Seedlings that did not survive the first 3 weeks were replaced (eight seedlings in total) and seedlings that died after that were considered a treatment effect.

To determine when to harvest plants, we constructed growth curves for each species, aiming to harvest once the growth of all nine species had reached an asymptote. To do this, we counted the number of leaves per plant for a subset of plants each week. Growth, in terms of number of leaves produced, reached an asymptote for all species at around 18 weeks, which is when we harvested above and below ground biomass. Below ground biomass was collected by rinsing soil from root material and submerging root material in water to facilitate disentangling roots by hand. Above ground biomass was collected by removing leaf, stem and flowering material. Below and above ground tissue was oven-dried at 50 ^{o}C for a minimum of 72 hrs and weighed. Above and below ground biomass was summed to get total biomass.

Analysis

Data analyses were performed with the software R version 3.6.1 (R development Core Team 2019). Total biomass (dry weight in grams) for each plant and biomass was $\log_e$ transformed before analysis to normalise the data and homogenise variance.

To test whether soil biotic and competitive effects were additive or interactive, we compared the fit of seven linear mixed effects models to the biomass data for each species using the R package '*lme4*' (Bates *et al.*, 2014) assuming normally distributed errors. We fitted a separate model for each species due to substantial differences in both the mean and variance of biomass between species. Fitting separate models allowed for the different biomass variances between species. Each model was fitted using $\log_e$ transformed total biomass as the response, with variables coding for the soil and competition treatments as fixed effects. We included glasshouse bench as a random effect in all the models to allow for possible differences in mean growth rate among benches due to location in the glasshouse. We included soil effects in one of two ways. In Model 1, soil was set as a two-level factor, either live (regardless of collection site) or sterile (sterile controls). In Model 2, we allowed for differences in plant responses to the soil biota from the three different collection sites by including soil as a four-level factor, coded for each field site and the sterile control. We fitted Models 1 and 2 specifying additive effects of soil biota and competition by including main effects only, and then fitted the same models but included a two–way interaction between soil biota and competition (Models 3 and

4). We also fitted three models with a single fixed effect of either competition (Model 6), soil (live or sterile) (Model 5) or soil treatment (each three field sites or sterile) (Model 7).

We used Akaike's Information Criterion (AIC) to compare the fit of the seven models to the data for each species and used the best-fitting model to infer soil biotic and competitive effects. Differences in AIC between models measures the relative fit of models to the data. Generally, a difference in AIC ≤4 indicates only weak support for one model relative to another, while a difference in AIC >10 would indicate clear support for the model with the lowest AIC providing the best fit to the data (Burnham & Anderson, 2004). For each species, we specified growth in competition with a conspecific on sterile soil as the reference class. This meant that the model parameters estimated the effect of a competitor species on a target species relative to the effect of the target species on itself (i.e., the effect of interspecific competition on plant growth was estimated relative to the strength of intraspecific competition), and the effect of soil biota on plant growth was estimated relative to performance on sterile soil. Since we were interested in comparing species groups (native, low-impact and high-impact exotics), we also fitted Model 1 with the biomass data for each group (native, low-impact and high-impact exotics) as the response to estimate of how group-level biomass varied in response to competition and soil biota treatment.

Results

Model 6, which included competitive effects but excluded soil biotic effects, fitted the data best for 5 out of the 9 species (Table 1). AIC values differed little between the best-fitting (Model 6) and second best-fitting model (Model 1) for each species (all differences were ≤ 4). For one species (*Austrostipa scabra*), Model 2 was the best-fitting, although the difference in performance between Models 1 and 2 (AIC difference = 4) indicated the models had similar fits for this species. Similarly, for *Dactylis glomerata*, Model 4, which distinguished field collected soils and specified an interaction between soil biota and competition, was the best-fitting but this was only marginally better than Model 2 (AIC difference = 1.3), implying only weak evidence for an interaction.

Overall, due to the small difference between the AIC values, there was little evidence that soil biota and interspecific competition interacted to affect plant performance, or that the soil biota, either defined as live or as associated with the three field collection sites, differentially affected plant growth for most species. Nevertheless, we report the results for Model 1 in the main text below because we wanted to examine the response of all nine species to both soil biotic and competitive effects. Results relevant to the other models are included in the Appendix.

Table 1: Comparison of the performance of seven mixed linear effect models fitted to the biomass data for each of the nine species in each of the three species classes (high impact invasive, low impact invasive, native). For each species, Δ_i is the difference between the model's AIC (Akaike's Information Criterion) value and the minimum AIC value. Values of zero indicate the best fitting model, with the model that fitted best for each species shown in bold and Model 6, which fitted best for five of nine species, highlighted in grey. K is the number of parameters and n is the sample size. Each model was fitted with natural log transformed total dry weight biomass as the response variable, competition (intraspecific or interspecific) as a fixed effect, and bench (location in the glasshouse) as a random effect. Soil was a fixed effect in one of two ways. *Live* indicates where soil was defined as either live (including soils from all three sites) or sterile (sterile controls), whereas *Soil treatment* is when soil is defined as originating from either one of each of three field sites or sterile controls (4 groups).

Model	Model details	Species class	Species	K	AIC	Δ_i	n
Model 1	~Live + Competition	High impact invasive	*Eragrostis*	7	262.20	2.6	93
			Nassella	7	206.69	1.7	87
			Phalaris	7	245.07	1.3	91
		Low impact invasive	*Dactylis*	7	206.48	7.6	79
			Festuca	7	239.51	1.9	88
			Lolium	7	189.77	2	74
		Native	***Poa***	**10**	355.81	**0**	**143**
			Austrostipa	10	372.14	4	131
			Themeda	10	372.89	1.8	120
Model 2	~Soil treatment + Competition	High impact invasive	*Eragrostis*	9	264.92	5.4	93
			Nassella	9	209.02	4	87
			Phalaris	9	248.82	5	91
		Low impact invasive	*Dactylis*	9	200.22	1.3	79
			Festuca	9	242.14	4.5	88
			Lolium	9	191.19	3.4	74
		Native	*Poa*	12	359.57	3.8	143
			Austrostipa	**12**	**368.13**	**0**	**131**
			Themeda	12	375.34	4.3	120
Model 3	~Live x Competition	High impact invasive	*Eragrostis*	10	264.52	5	93
			Nassella	10	211.33	6.3	87
			Phalaris	10	250.13	6.3	91
		Low impact invasive	*Dactylis*	10	206.00	7.1	79
			Festuca	10	245.28	7.2	88

			Lolium	10	193.92	6.1	74
		Native	*Poa*	16	365.96	10.2	143
			Austrostipa	16	374.30	6.2	131
			Themeda	16	377.32	6.2	120
Model 4	~Soil treatment x Competition	High impact invasive	*Eragrostis*	18	275.49	15.9	93
			Nassella	18	219.15	14.1	87
			Phalaris	18	262.55	18.8	91
		Low impact invasive	***Dactylis***	**18**	**198.89**	**0**	**79**
			Festuca	18	252.77	14.7	88
			Lolium	18	198.43	10.6	74
		Native	*Poa*	30	381.45	25.6	143
			Austrostipa	30	377.87	9.7	131
			Themeda	30	395.21	24.1	120
Model 5	~live	High impact invasive	***Eragrostis***	**4**	**259.56**	**0**	**93**
			Nassella	4	209.19	4.2	87
			Phalaris	4	251.42	7.6	91
		Low impact invasive	*Dactylis*	4	206.58	7.7	79
			Festuca	4	239.45	2.3	88
			Lolium	4	199.62	11.8	74
		Native	*Poa*	4	364.81	9	143
			Austrostipa	4	373.63	5.5	131
			Themeda	4	384.66	13.6	120
Model 6	~Competition	High impact invasive	*Eragrostis*	6	260.35	0.8	93
			Nassella	**6**	**205.03**	**0**	**87**
			Phalaris	**6**	**243.78**	**0**	**91**
		Low impact invasive	*Dactylis*	6	204.49	5.6	79
			Festuca	**6**	**237.87**	**0**	**88**
			Lolium	**6**	**187.81**	**0**	**74**
		Native	*Poa*	9	356.96	1.2	143
			Austrostipa	9	370.51	2.4	131
			Themeda	**9**	**371.09**	**0**	**120**
Model 7	~Soil treatment	High impact invasive	*Eragrostis*	6	262.43	2.9	93
			Nassella	6	211.08	6	87
			Phalaris	6	255.38	11.6	91
		Low impact invasive	*Dactylis*	6	201.46	2.6	79
			Festuca	6	242.11	4.9	88
			Lolium	6	200.44	12.6	74
		Native	*Poa*	6	368.54	12.7	143
			Austrostipa	6	371.51	3.4	131
			Themeda	6	386.94	15.9	120

Competitive effects

The effects of interspecific competition (measured relative to intraspecific) on plant growth were larger and more apparent than the effects of soil biota on plant performance (Figure 1). Overall, exotics were stronger interspecific competitors relative to native species. For the native species, biomass tended to decrease in competition with exotic species relative to

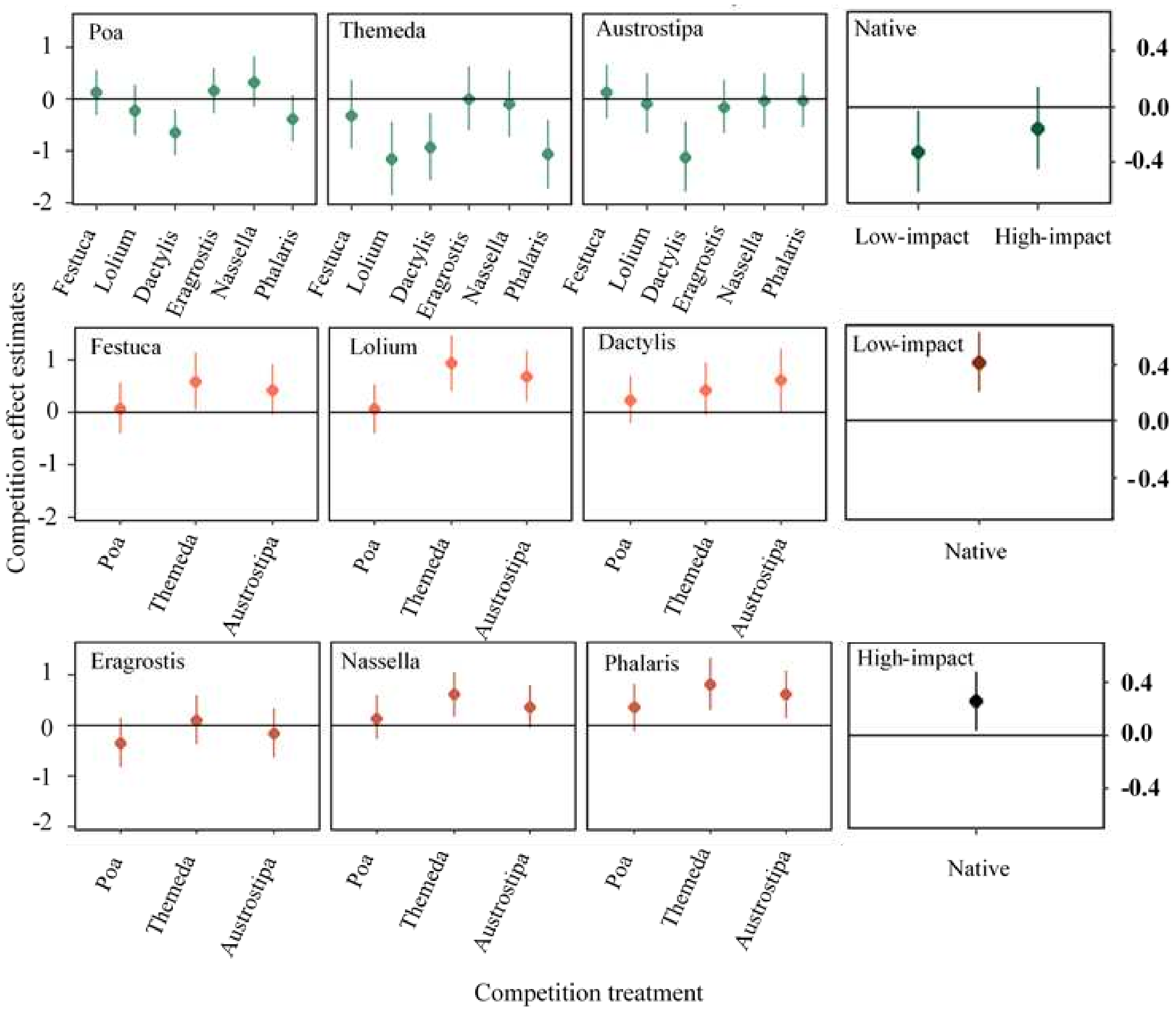

Figure 1: Estimates of competitive effects of species groups (right hand column) and individual species (first three columns) for three native species (green), three low impact (orange) and three high impact invaders (red). Competitive effect was estimated as the log (intraspecific biomass) – log (interspecific biomass) – 1 for each native-exotic pair. Values greater than zero indicate that plant performance was greater in interspecific competition than in intraspecific competition. X-axis indicates which species or group was the competitor and panel heading indicates target species or group. Error bars are 95% confidence intervals calculated by fitting a mixed effect model with log-transformed plant biomass as the response variable and soil treatment and competition as a categorical explanatory variable.

intraspecific competition (Figure 1). The outcomes varied, however: *Eragrotis curvula*, *Festuca arundinacea* and *Nassella neesiana* had relatively little impact on native biomass relative to the effect of natives on themselves, while the remaining three species all had clear impacts on one or more native species.

For the exotic species, all except *Eragrostis curvula* had greater biomass when in competition with *Themeda triandra* and *Austrostipa scabra* than when in competition with themselves. In contrast, all exotics except *Phalaris aquatica* grew to a similar size when in competition with *Poa sieberiana* as when in competition with themselves. Overall, both low-impact and high-impact invasive species had greater biomass when in competition with natives relative to competition with themselves, while natives had lower biomass in interspecific competition, with low-impact invaders causing, on average, a greater decline in biomass.

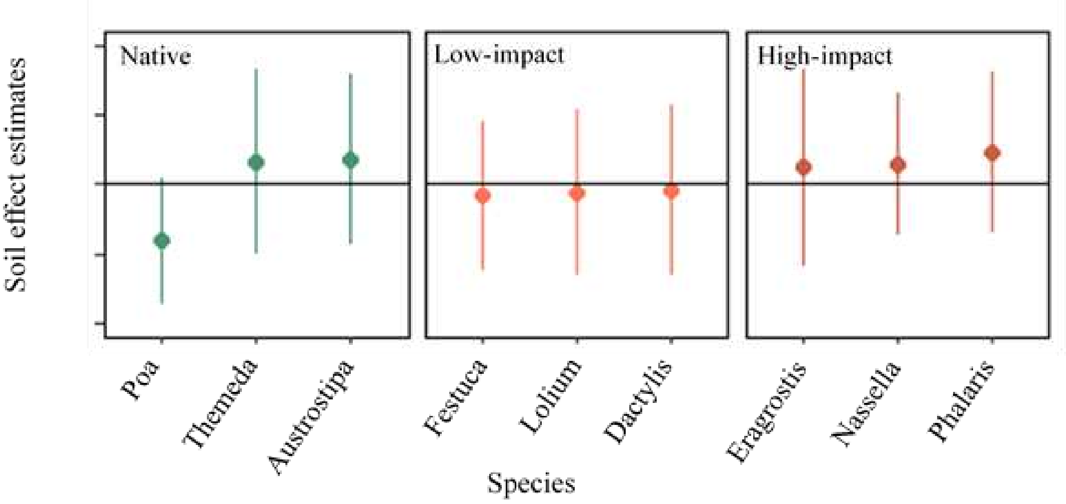

Figure 2: Effect of soil treatment on total biomass of nine grass species. Three native (green), three low impact (orange) and three high impact (red) invasive species. Soil biotic effect is estimated as the natural log (live biomass) – natural log (sterile biomass) – 1 for each species. Values greater than zero indicate that plant performance was greater on live soil than sterile. Error bars are 95% confidence intervals calculated by fitting a mixed effect model with log-transformed plant biomass as the response variable and soil treatment and competition as a categorical explanatory variable.

Soil biotic effects

The estimates of soil biotic effects obtained from Model 1 revealed substantial uncertainty around the effects of live soil biota on species performance relative to sterile soil: for all species except *Poa sieberiana*, the 95% confidence intervals substantially overlapped zero revealing little evidence for either strong positive or negative effects of soil biota on plant biomass (Figure 2). Although all three high–impact exotic species grew better on live soil and all low-impact invaders grew slightly worse, these differences were not large. Only the native *Poa sieberiana* showed evidence of a clear response to soil biota, on average growing slower in live relative to sterile soil.

Discussion

This study aimed to understand whether invasive species success could be explained by differences in their response to soil biotic effects, competitive effects or both. While no clear soil biotic effects were found, high-impact invasive species did experience slight positive soil biotic effects when exposed to the native soil community, effects that were greater than observed for both low-impact invasive and native species. Nevertheless, competitive effects were much larger than soil biotic effects.

Do soil biotic effects and competitive fitness have an additive or interactive effect?

Previous work has shown that soil biotic and competitive effects can interact, although overall the outcomes have been mixed. Some studies have found no evidence for an interaction, even in cases with significant soil biotic and competitive effects (Maron et al., 2016; Perkins & Nowak, 2012), or significant soil effects only (Casper & Castelli, 2007). Other studies have found evidence of an interaction, with examples of soil biotic effects being greater under intraspecific competition (Pendergast et al., 2013) and examples of increased competitive ability for invasive species (Marler et al., 1999; Perkins & Nowak, 2012). This suggests that either soil biotic effects, competition or both are context dependent and highlights the importance of including competition when studying soil biotic effects to ensure ecologically relevant findings. Here we did not find an interaction between soil biotic and competitive effects (Table 1), most likely because competitive effects were much greater than soil biotic effects for the nine grass species tested.

Are high-impact invasive species better competitors than native and low-impact invasive species?

Competitive advantage was greater for exotic species than natives. While competitive advantage between species pairs was generally species-specific, exotics tended to have larger biomass when grown with natives compared to when grown with themselves, while natives were smaller in biomass when grown with exotics (Figure 1). Competitive ability did not correlate with the invasion categories of high- and low-impact invaders. One reason for this may be that low-impact species on average had significantly larger biomass (with mean biomass and standard deviation of 12.8 ± 8.56 g for *Lolium perenne*, 18.9 ±15g for *Dactylis glomerata* and 19 ±24.5 g for *Festuca arundinacea*) than two of the three native species (with mean biomass and standard deviation of 2.91 ±2.61 g from *Themeda triandra* and 1.23 ±0.633 g for *Austrostipa scabra*). Larger biomass may give species an advantage at establishing due to superior competitive ability over natives, but could also mean greater susceptibility to the effects of intraspecific competition (Adler *et al.*, 2018). Advantages gained from growing with native species at establishment would reduce over time if natives were replaced by conspecific neighbours and density dependent intraspecific competition reduced individual biomass limiting further population growth (Chesson, 2000). This could at least partly explain the difference between low-impact invasive and high-impact invasive species, with low-impact invaders being more strongly self-limited by intraspecific competition.

In our study, while there were no general relationships between competitive ability and classification as high-impact or low-impact species, there were patterns that give some insight into how invasion processes may play out for these species. First, our results indicate that the success of the high-impact invader *Eragrostis curvula* is not due to superior competitive ability (Figure 1). Rather, its invasion success and high-impact status is likely due to other traits, notably its high fecundity and ability to take advantage of open patches in the landscape (Firn, 2009). Second, the high-impact invader *Phalaris aquatica* and the low-impact *Dactylis glomerata* most strongly reduced the biomass of native neighbours (Figure 1). For *Phalaris aquatica*, this could explain its large impact on native ecosystems (Godfree et al., 2017) particularly under high resource conditions, as both *Phalaris aquatica* and more so *Dactylis glomerata,* are limited by their tolerance of low nutrient and drought conditions (Wandrag et al., 2019), which is a common situation in Australian temperate grasslands (Bolger et al., 2005). The native species *Poa sieberiana* was less impacted by competition (Figure 1), suggesting grassy ecosystems dominated by *Poa sieberiana* may prove more resilient to resisting establishment by exotics, and that *Poa sieberiana* could be a useful revegetation species in appropriate grassy ecosystems under invasion threat.

Do high-impact invasive species gain advantage from soil biotic communities compared to native and low-impact invasive species?

Identifying the role of plant-soil interactions in determining invasion outcomes requires demonstrating a relationship between invasion status and the relative advantage exotics gain from soil biota. Our experimental design allowed us to directly compare the soil biotic response of native, low-impact and high-impact invasive species. Overall, exotic grass species biomass was not significantly altered by the soil biotic community of native grasslands compared to sterile soil (See Appendix A1). While high-impact invasive species did exhibit greater positive soil biotic effects than low-impact invaders (Figure 2), the differences were not strong and likely insufficient to explain invasion outcomes. This is a similar finding to another study that directly compared soil biotic effects for exotics of differing invasion abilities and found that soil biotic effects predicted invasion status for seedling establishment, but not biomass production (Aldorfová, Knobová and Münzbergová, 2020). Other studies of soil biotic effects on invasion have produced mixed outcomes (Kulmatiski et al., 2008; Lekberg et al., 2018; Suding et al., 2013), noting that a substantial body of research has found strong soil biotic effects for highly invasive species (Callaway *et al.*, 2003; Reinhart *et al.*, 2003; Nijjer, Rogers and Siemann, 2007; Gundale *et al.*, 2014; Perkins, Hatfield and Espeland, 2016, but see Birnbaum and Leishman, 2013). These mixed results could arise due to the context dependence of plant-soil interactions (Suding et al., 2013) or because study designs strongly affect outcomes (Brinkman et al., 2010; Kulmatiski, 2016). This suggests that while soil biotic interactions may increase invasion advantage in some systems, they are unlikely to be the only mechanism driving successful invasion.

There could be several reasons for the lack of strong soil biotic effects in this study. Soil biotic response can be context dependent (Suding et al., 2013) and environmental factors such as drought and nutrient stress can alter interactions (Thrall *et al.*, 2005; Kaisermann *et al.*, 2017), with mutualistic associations becoming more rewarding for plants as bioavailable forms of nutrients and water become limited. Because we tested plant responses to native soil biotic communities without drought or nutrient stress, plants may not have needed to form such associations to obtain required nutrients and water. Furthermore, we focused on the establishment stage of invasion where exotics encounter the native soil biotic community. The effects of soil biota could accumulate over time such that exotics select for increasingly positive feedbacks relative to natives, which could contribute to invasion success (plant-soil feedbacks) (Bever et al., 1997; Kulmatiski et al., 2008; Levine et al., 2006; van Grunsven et al., 2007). It is possible that the invasion success of the exotic species in this study is linked to long-term, but not short-term, outcomes of plant-soil feedbacks.

It is also possible that the species included in this study are generally unresponsive to the soil microbes. Exotic species that rely on symbiotic soil mutualists are limited in their ability to establish in new areas when they have specialised symbionts (Simonsen et al., 2017), meaning that species that are less responsive to soil biotic communities may be more likely to successfully invade (Bennett & Strauss, 2013; Owen et al., 2013). Most species in this study have not been previously tested for their response to soil biotic communities. Of those that have, *Dactylis glomerata* has shown greater performance in live soil communities compared to sterile soil (Heinze et al., 2015), while *Lolium perenne* has shown both a positive (Heinze et al., 2015) and no strong response to soil biotic conditions (Jing, Bezemer and van der Putten, 2015), again highlighting the potential for context-dependent responses to soil biota. We also found that soil biotic effects were consistent across the three live soil inocula collected from the three field sites (see Appendix A2), suggesting either that the soil microbial community was similar at the three sites, or that the nine species responded similarly despite any local soil biotic differences influences by abiotic differences.

A final explanation may lie in our experimental and analytical approach. It is important to highlight that since plant-soil interactions are context-dependant, differences in experimental approach, such as methods of sterilisation and soil handling could influence outcomes (Brinkman et al., 2010). We used gamma irradiation to sterilise live field soils for inoculation of the sterile soil treatment but, due to the large volume of soil we had to process, used steam sterilisation to sterilise the background potting mix. It is possible that steam sterilisation did not kill all of the soil biota and this, coupled with a lack of nutrient and water stress, may have muted differences between the live and sterile treatments. Nevertheless, steam sterilisation is commonly used in plant-soil feedback studies that have produced clear soil biota effects (Cardinaux et al., 2018; Larios & Suding, 2015; Owen et al., 2013). The large uncertainties around our estimates of soil biotic effects (Figure 2) could also arise because the modelling approach we used correctly accounted for the uncertainties in our data. Many approaches do not propagate all relevant uncertainties in the data through their models, potential leading to underestimates of the associated uncertainties and overestimation of soil biotic effects (Bates et al., 2019). There is a clear need to use more consistent approaches to testing and measuring soil biotic effects if we are to develop a general understanding of their role in plant invasions.

In summary, differences among exotic species in invasiveness could not be explained by soil biotic effects in this study. Exotics were overall stronger competitors than natives although high impact invaders were not always strong competitors, suggesting there are other ways in which some invaders enter into and impact native communities.

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Appendix figures

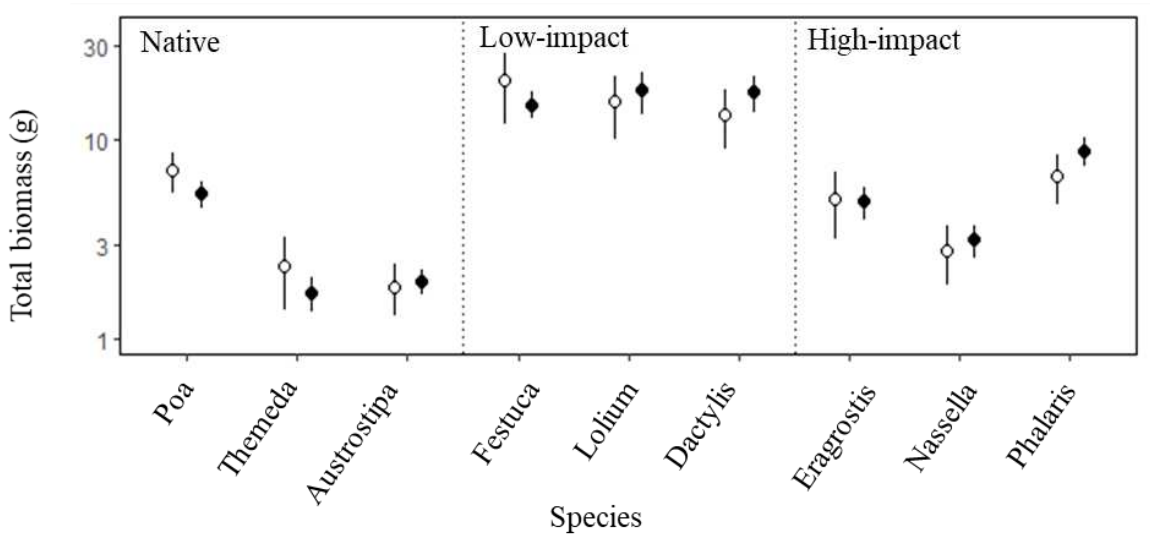

Figure A1: Total biomass (dry weight in grams) of nine grass species, grown on sterile (clear circles) or live soils (solid circles). Error bars are 95% confidence intervals (2 x standard error) (y-axis is displayed on the natural log scale).

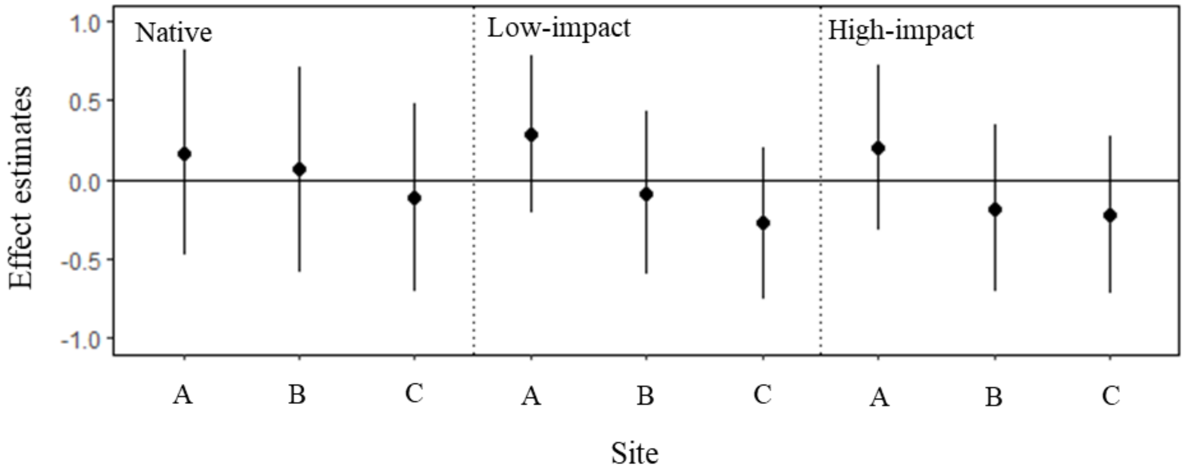

Figure A2: Biotic effect of three live soils (sites A -C) on plant growth compared to sterile soil. Biotic effect was estimated as the log (live biomass) – log (sterile biomass)-1 for each site for exotic and native species separated by the dotted line. Exotics are grouped into high impact and low impact invasive species. Each specie category is a group of three species. Error bars 95% confidence intervals calculated by fitting a regression model with log-transformed plant biomass as the response variable and soil treatment as a categorical explanatory variable.