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HIGHLIGHTED STUDENT RESEARCH

Biogeographic differences in soil biota promote invasive grass response to nutrient addition relative to co-occurring species despite lack of belowground enemy release

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Abstract

Multiple plant species invasions and increases in nutrient availability are pervasive drivers of global environmental change that often co-occur. Many plant invasion studies, however, focus on single-species or single-mechanism invasions, risking an oversimplification of a multifaceted process. Here, we test how biogeographic differences in soil biota, such as belowground enemy release, interact with increases in nutrient availability to influence invasive plant growth. We conducted a greenhouse experiment using three co-occurring invasive grasses and one native grass. We grew species in live and sterilized soil from the invader's native (United Kingdom) and introduced (New Zealand) ranges with a nutrient addition treatment. We found no evidence for belowground enemy release. However, species' responses to nutrients varied, and this depended on soil origin and sterilization. In live soil from the introduced range, the invasive species *Lolium perenne* L. responded more positively to nutrient addition than co-occurring invasive and native species. In contrast, in live soil from the native range and in sterilized soils, there were no differences in species' responses to nutrients. This suggests that the presence of soil biota from the introduced range allowed *L. perenne* to capture additional nutrients better than co-occurring species. Considering the globally widespread nature of anthropogenic nutrient additions to ecosystems, this effect could be contributing to a global homogenization of flora and the associated losses in native species diversity.

Keywords Belowground · Enemy release · Invasive species · Nutrient availability · Soil biota

Introduction

Plant invasions are a pervasive driver of global environmental change (Vitousek et al. 1997; Sala 2000; Van Kleunen et al. 2015) and are associated with biodiversity loss (Vilà et al. 2011; Seabloom et al. 2015) and economic costs (Pimentel et al. 2005; Pejchar and Mooney 2009). At least 29 hypotheses have been proposed to explain invasive plant species success (Catford et al. 2009) indicating the inherent complexity of plant invasions. Despite a proliferation of biological invasion studies in recent decades (Richardson and Pysek 2008), many studies have focused on single species (Kuebbing et al. 2013) or mechanisms (Gurevitch et al. 2011). This risks oversimplifying a complex process as mechanisms are likely to interact (Blumenthal 2005; Blumenthal et al. 2009; Gurevitch et al. 2011; Maron et al. 2013) and vary for different co-occurring invasive species (Kuebbing et al. 2013). In addition, invasion may be facilitated by other, abiotic, environmental changes, such as increased resource availability via agricultural fertilization,

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In this greenhouse experiment we show that novel soil biota can increase the response of an invasive grass to nutrient additions relative to other species, even in the absence of belowground enemy release. This emphasizes that abiotic and biotic global changes interact to facilitate species invasions.

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disturbance or N-deposition (Davis et al. 2000; Davis and Pelsor 2001; Seabloom et al. 2015). Interactions among such abiotic environmental changes and invasion mechanisms are likely, but rarely studied, resulting in a significant gap in our understanding of the drivers of invasion success (Bradley et al. 2010; Kardol et al. 2012).

A commonly cited mechanism behind invasion success that may interact with resource availability is belowground enemy release (Keane and Crawley 2002; Reinhart and Callaway 2006). Belowground enemy release refers to escape from the inhibitory effects of soil biota, such as root predation, parasitism, disease and competition for resources (Agrawal et al. 2005; Reinhart and Callaway 2006), which are assumed to be greater in a plant's native range due to higher abundances of co-evolved specialized enemies than in the introduced range, where soil biota are evolutionarily naïve of the invader. The benefits of belowground enemy release may also be magnified by increased nutrient availability. According to the growth rate hypothesis, high resource environments, where the cost of replacing tissue is lower than defending it, select for fast-growing species (Coley et al. 1985; Stamp 2003), which are likely to be regulated more heavily by enemies than slower growing, better defended, species (Blumenthal 2006). Since invasive plant species tend to have more exploitative trait values than co-occurring natives, such as higher relative growth rates (RGR) (Leishman et al. 2007, 2014; van Kleunen et al. 2010; Ordonez et al. 2010), they are well positioned to benefit from the interaction of belowground enemy release with increased resource supply (Blumenthal 2006).

Such interactions are likely to be particularly important in grassland ecosystems, where changes in nutrient availability are common due to intensification, and invasion rates are among the highest worldwide (Firn et al. 2011). In addition, grasses are the functional group that generally show the most negative plant–soil feedbacks and are therefore most likely to benefit from belowground enemy release (Kulmatiski et al. 2008). However, the invasive success of different grass species, as measured by their abundance in their native versus their introduced range, can vary (Firn et al. 2011). This suggests that grassland species responses to plant–soil feedbacks and nutrient availability may be species dependent. Here, we use a native New Zealand grassland as a model system. These grasslands are valuable conservation habitats (Mark and McLennan 2005; Rose and Frampton 2007) that experience invasions by a range of non-native species including several grass species, along with parallel declines in native species abundance (Duncan et al. 2001; Rose et al. 2004). As the invasive grasses in this system tend to have more exploitative traits and a higher RGR than the native grass species (Craine and Lee 2003; Gross et al. 2013), and invasion appears to be facilitated by increases in nutrient availability (Williams 1998; Scott 2000; Dickie et al. 2014), it provides an ideal context within which to test how plant–soil feedbacks and nutrient availability interact to influence invasive species growth, and whether these effects are consistent across invasive species. In particular, we hypothesize that:

1. Belowground enemy release interacts with increased nutrient availability to promote growth of three common invasive grass species, *Lolium perenne* L., *Anthoxanthum odoratum* L. and *Agrostis capillaris* L., in grassland soil from their introduced range (New Zealand) compared to their native range (United Kingdom).
2. Invasive grass species differ in the benefit they receive from the interaction of belowground enemy release and nutrient availability.

Materials and methods

Focal species

We used three perennial C3 grass species, *L. perenne*, *A. capillaris* and *A. odoratum*, that are native to the UK and invasive in many parts of the world, including New Zealand (CABI 2017). These species were chosen as they are among the most widespread invasive grasses in New Zealand (CABI 2017), yet they differ in their invasion success rates, in terms of their relative abundances "home" and "away" (Firn et al. 2011) and so may vary in their responses to belowground enemy release and nutrient addition. They were also introduced to New Zealand at a similar time: *A. capillaris* in 1867, *A. odoratum* and *L. perenne* both in 1855 (New Zealand Plant Conservation Network 2016), which controls for differences in the accumulation of belowground enemy pressure due to time since introduction (Diez et al. 2010). We used a common native perennial C3 New Zealand grass, *Poa cita*, that co-occurs with the invaders in their introduced range (Gross et al. 2013). This served as a model native species, which is not invasive anywhere, to which we could compare the responses of the invaders. Seeds of all species were sourced from NZ populations by Speciality Seeds and Home Creek Nursery, except *A. odoratum* which was supplied by B&T World Seeds.

Soil collection

In April 2015, we collected soils from five indigenous montane grassland sites in New Zealand (NZ) and five upland grassland sites in the United Kingdom (UK) (Table 1). British colonizers of New Zealand introduced livestock and pasture grasses from the UK. It is therefore likely that the invasive grass species used in our study originated from UK populations and we therefore chose the UK as the source of

Table 1 List of field sites from where soil was collected in the UK and New Zealand, with elevation (m) and location (WGS 1984/lat. long.)

Site	Country	Elevation (m)	Latitude	Longitude
Edale	UK	507	53.374149	– 1.8304451
Bradfield	UK	306	53.443550	– 1.6111165
Longshaw	UK	334	53.315296	– 1.6070889
Great Dunn Fell	UK	671	54.670539	– 2.4440604
Hartside	UK	551	54.766721	– 2.5596763
Clearwater	NZ	655	– 43.59602024	171.01760960
Lynton	NZ	859	– 43.30431126	171.70230002
Craigieburn	NZ	818	– 43.14667393	171.73990218
Turton	NZ	943	– 43.35302069	171.36680554
Tekapo	NZ	1180	– 43.83077613	170.63581736

our native range soil. Field sites within each country were at least 20 km apart. Sites were suitable habitat for the focal species (*A. capillaris*, *A. odoratum*, *L. perenne* and *P. cita*), not intensively managed and with relatively low fertility. At each site, soil cores (diameter 6 cm, depth 10 cm) were taken from 36 points spaced 10 m apart along six 60 m transects, covering an area of c. 5400 m^2 and amounting to c. 10 L of soil per site. The trowel used to collect soil was sterilized between sites using 30% bleach and rinsed in DI water to avoid any cross contamination of microbes. Abundances of each focal species were also estimated within a 1 m^2 quadrat at each soil core location. Focal species occurred at low mean abundance (< 7%) at each site, representing the early stages of invasion, and there were no significant differences in mean abundance between the UK and NZ ranges. Fresh soil was sieved (4 mm) and homogenized within each site, keeping sites separate to maintain independence (Reinhart and Rinella 2016). Soil was transported on ice to Lancaster University (UK) where experiments were conducted and was stored at 4 °C prior to use in the experiment. A subsample of c. 2 L of soil collected from each site was then sterilized via gamma irradiation at 40 kGy (Synergy Health, UK).

Experimental design

To determine how different species responded to nutrient addition when grown with soil biota from their native and introduced ranges, we conducted a greenhouse experiment using a randomized block design with five replicates. Treatments consisted of a full factorial cross of soil origin (UK or NZ), sterilization (live or sterilized), nutrient addition (control and nutrient addition) and four plant species (*A. capillaris*, *A. odoratum*, *L. perenne* or *P. cita*) grown in monoculture, resulting in 160 pots. Live and sterilized soil was used to assess the effects of soil biota from each range. This holistic approach allows the net effect of both beneficial, such as arbuscular mycorrhizal fungi (AMF), and antagonistic soil biota to be assessed, and thus gives a realistic picture of the impact of soil feedbacks on invasion success (Reinhart and Callaway 2004; Gundale et al. 2014; Maron et al. 2014). Nutrient addition consisted of 30 mL 0.25 strength Hoagland's solution (Hoagland and Arnon 1950) per pot each week, resulting in 22.4 mg N and 3.95 mg P being added over the study period.

Greenhouse conditions

Focal species were germinated in an autoclaved growing medium that consisted of sand and peat (2:1 ratio by volume). This was done in the greenhouse under the same standardized conditions that were used throughout the experiment: lighting regime, L:D 16 h:8 h; temperature 22 °C:16 °C. Seeds were surface sterilized in 95% ethanol (1 min), then 6% sodium hypochlorite (5 min) and then rinsed repeatedly with de-ionized water for 10 min (Bartelt-Ryser et al. 2005) to destroy any microbes that may have been adhering to the surface of seeds prior to sowing. All equipment (e.g. pots) was sterilized in 30% bleach and well rinsed with de-ionized water. Pots (1.5 L, diameter 15 cm) were filled with 1350 mL of the same autoclaved growing medium in which the seeds were germinated (sand:peat mix). This was then inoculated (i.e. gently mixed) with 150 mL (10% of pot volume) of fresh homogenized soil from either a UK or NZ site that was either gamma irradiated (sterilized) or live (unsterilized). This method tested differences in soil biota between similar habitats in the native (UK) and introduced ranges (NZ), whilst minimizing physical and chemical soil differences. The final concentrations of KCl-extractable N concentration (NO_3^--N and NH_4^+-N) and $NaCO_3$-extractable PO_4^--P concentration (Olsen-P) in inoculated pots were determined colorimetrically in a segmented flow stream using an AutoAnalyser (Seal-Analytical). Mean concentrations of soil inorganic N were 3.3 μg N g^{-1} higher in the growing medium inoculated with UK soils (10.6 ± 0.6 μg N g^{-1}) than that inoculated with NZ soils (7.3 ± 0.5 μg N g^{-1}; $F = 44.2$, $p < 0.01$). This difference amounted to 4.4 mg N per pot, which was relatively minor compared to the amount of N added in the nutrient addition treatment (22.4 mg N pot^{-1}) and it was the same across

live and sterilized soils. Soil Olsen-P concentrations and pH (soil:water 1:2.5) did not differ between UK and NZ soil. Mean concentrations of soil inorganic N were 4.1 μg N g^{-1} higher in sterilized soil (11.0 ± 0.5 μg N g^{-1}) compared to live soil (6.9 ± 0.4 μg N g^{-1}; $F = 66.8$, $p < 0.01$), while Olsen-P concentrations were 0.7 μg P g^{-1} higher in sterilized soil (1.4 ± 0.1 μg N g^{-1}) than live soil (0.6 ± 0.1 μg N g^{-1}; $F = 17.9$, $p < 0.01$). These differences were the same across UK and NZ soils. Soil was left in pots for 2 weeks to stabilize (Zuppinger-Dingley et al. 2011); then three seedlings of the same species were transplanted into the pots on 7 May 2015 at the start of the experiment. Any seedlings that died within the first week were replaced. Pots were watered daily with 60 mL of DI water and re-adjusted to 80% water holding capacity of the growing medium twice each week. Blocks were rotated every 2 weeks to minimize the effects of differences in environmental conditions within the greenhouse. Plant biomass was harvested after 17 weeks on 3 September 2015. All soil was washed from roots and the biomass was separated into belowground and aboveground components and dried at 65 °C for 48 h before being weighed to 0.0001 g. Root mass fraction (RMF = belowground biomass/total biomass) was calculated in addition to biomass as it is an important plant trait that indicates the resource investment into roots versus shoots. This provides insight into plant species growth strategies and influences on plant growth due to above- and belowground conditions. Soil inorganic N and P concentrations were also measured at the end of the experiment. Soil inorganic N concentrations were low and slightly higher in live soil (0.11 ± 0.03 μg N g^{-1}) than sterilized soil (0.02 ± 0.003 μg N g^{-1}; $F = 9.56$, $p < 0.01$), whilst they did not differ in relation to nutrient addition treatment ($F = 1.38$, $p = 0.24$). Soil Olsen-P concentrations were also low and slightly higher in NZ soil (0.38 ± 0.03 μg P g^{-1}) than UK soil (0.27 ± 0.02 μg P g^{-1}; $F = 7.89$, $p < 0.01$); they also did not differ in relation to nutrient addition treatment ($F = 1.37$, $p = 0.24$).

We determined the RGRs of each species as they provide a good indication of how exploitative or conservative species are in their traits overall. This may be relevant for interpreting differences in species responses to belowground enemy release and nutrient additions. RGRs were determined by measuring the change in mean above- and belowground seedling biomass (M) between days 14 (t1) and 29 (t2) after germination (Pérez-Harguindeguy et al. 2013). Twenty seedlings were harvested and dried (65 °C for 48 h) at each time point. RGRs were calculated as:

$$\mathrm{RGR} = (\ln M_2 - \ln M_1)/(t_2 - t_1).$$

Statistical analysis

We split our analysis into two elements; one for each hypothesis. To test our first hypothesis, we determined whether belowground enemy release and increases in nutrient availability were interacting to influence individual species biomass responses (mean total biomass (g) and mean root mass fraction). To do this, we conducted a three-way ANOVA with soil origin (NZ or UK), sterilization (live or sterilized), nutrient addition (control and nutrient addition) and all interactions as factors, on the biomass responses of each species independently. To test our second hypothesis, we determined whether species differed to each other in their responses to sterilization and nutrient addition depending on soil origin (NZ or UK). To do this, we conducted a three-way ANOVA with species identity, sterilization, nutrient addition and all interactions as factors, on the biomass responses in NZ and UK soil separately.

ANOVAs used type II sums of squares and therefore conformed to the principle of marginality (Fox and Weisberg 2011). This was necessary, as one replicate each of *A. capillaris*, *A. odoratum* and *L. perenne* were lost due to contamination in seed supply, resulting in a slightly unbalanced design. Tukey HSD post hoc tests were used to assess pairwise significant differences ($p < 0.05$) between the levels of a factor, including any interacting factors. Where significant interactions between factors were found in our three-way ANOVA models, we also decomposed the analysis by separating the data into smaller sections based on the groups of one of the significant factors. This allowed us to gain a greater insight into which mechanisms were influencing biomass responses. Block did not have a significant effect on the biomass responses of any individual species, nor on overall biomass responses in NZ or UK soils and was therefore not included as a random effect. Models that violated assumptions of normality or homoscedasticity received a $\log_{10}(y)$ transformation and all analyses were performed in R version 3.2.4 (R Core Team 2016).

Results

Interaction of belowground enemy release and nutrient addition

When species were analysed independently (to answer hypothesis 1), their total biomasses were all significantly higher when grown with either soil that originated from the UK or soil that had been sterilized (regardless of origin) and when receiving nutrient addition (Table S1 and Figs. 1 and S1–S4). There were no significant interactions between soil origin (UK or NZ) and sterilization treatment (sterilized and live) across any of the species (Table S1). The mean total biomass of *L. perenne* only increased significantly in response to nutrient addition when grown in soil originating from its introduced range (NZ), not its native range (UK), as indicated by a significant interaction between soil origin

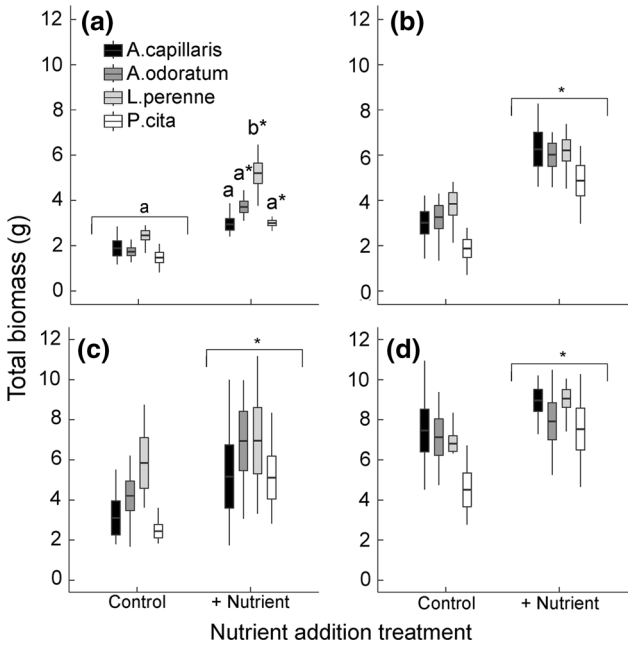

Fig. 1 Total biomass responses of all species when grown in different soil treatments: **a** live New Zealand (NZ), **b** sterilized NZ, **c** live United Kingdom (UK) and **d** sterilized UK. Bar and whisker points indicate mean ± SE ($N = 5$). Means within each nutrient treatment with the same letter are not significantly different (Tukey HSD, $p > 0.05$); asterisk indicates differences in species biomass across nutrient treatments (Tukey HSD; $p < 0.05$). Because species did not respond differently to nutrient additions in panels **b**–**d**, only the overall significant total biomass response (Tukey HSD; $p < 0.05$) to nutrient addition is indicated (see Table 3 for all F and p values)

Table 2 Results of three-way ANOVAs testing effects of species identity (SP), sterilization (ST), nutrient addition (N) and their interactions on total biomass (g) and root mass fraction (RMF) of all species in New Zealand (NZ) and UK soil origin treatments

	df	Total biomass		RMF	
		F	*p*	*F*	*p*
NZ soil					
SP	3	9.5	< 0.01	30.5	< 0.01
ST	1	56.3	< 0.01	77.5	< 0.01
N	1	116.7	< 0.01	1.3	0.26
SP × ST	3	1.5	0.21	3.6	0.02
SP × *N*	3	0.2	0.92	0.9	0.46
ST × *N*	1	5.6	0.02	0.7	0.4
SP × ST × *N*	3	1.6	0.20	0.6	0.64
UK soil					
SP	3	3.5	0.02	14.9	< 0.01
ST	1	23.7	< 0.01	22.9	< 0.01
N	1	15.9	< 0.01	0.4	0.51
SP × ST	3	1.2	0.33	4.0	0.01
SP × *N*	3	0.3	0.81	0.4	0.73
ST × *N*	1	0.1	0.81	0.1	0.73
SP × ST × *N*	3	0.4	0.73	0.4	0.75

All factors are fixed effects

and nutrient addition ($F = 4.6$, $p = 0.04$, Table S1, Fig. S3a). However, when *L. perenne*'s total biomass was analysed in NZ soil only, there was no interaction between sterilization treatment and nutrient addition ($F = 1.3$, $p = 0.28$).

All species showed a higher RMF in sterilized soil than live soil (Table S1; Figs. S1–S4), while *A. capillaris* and *L. perenne* also both showed a higher RMF in NZ soil than UK soil (Table S1; Figs. S1 and S3). There were no interactions between any factors in the ANOVAs on RMF for any species (Table S1).

Interaction of species identity with nutrient addition

When species were analysed collectively (to answer hypothesis 2), differences in how they responded to increased nutrient availability depended on the biogeographic origin of the soil they were grown with (Table 2). In UK soil, all species responded similarly to nutrient addition, as indicated by a lack of interactions between nutrient addition and other factors (Table 2; Fig. 1c, d). In contrast, in NZ soil there was a significant interaction between the effects of sterilization and nutrient addition treatments on total biomass; with species responding more strongly to nutrient addition in sterilized soil than live soil ($F = 5.6$, $p = 0.02$; Table 2). To gain further insight into this result, we decomposed the analysis by sterilization treatment; thereby testing the effects of nutrient addition and species identity in live and sterilized NZ soil separately (Table 3; Fig. 1a, b). In live NZ soil, *L. perenne* responded more strongly to increased nutrient availability than the other species in terms of its total biomass (Fig. 1a), as indicated by an interaction between species identity and nutrient addition ($F = 3.5$, $p = 0.03$; Table 3). Tukey HSD post hoc tests showed that while all species except *A. capillaris* responded positively to nutrient addition in live NZ soil, *L. perenne* responded most strongly (Fig. 1a). It attained a significantly higher mean total biomass than all other species in the nutrient addition treatment but not the control treatment (Fig. 1a). In sterilized NZ soil, however, species total biomass responded similarly to nutrient addition, as indicated by the lack of an interaction between species identity and nutrient addition (Table 3; Fig. 1b).

Differences in RMF between species depended on sterilization treatment in both soil origins, as indicated by a significant interaction between species identity and sterilization treatment ($F = 3.6$, $p = 0.02$ and $F = 4.0$, $p = 0.01$; NZ soil and UK soil, respectively, Table 2, Fig. 2). All species except *L. perenne* showed a significantly lower RMF in live NZ soil than sterilized NZ soil (Table 2, Fig. 2a). Moreover, *L. perenne* maintained a higher RMF

Table 3 Results of two-way ANOVAs testing effects of species identity (SP), nutrient addition (N) and their interaction on total biomass of all species in live and sterilized New Zealand (NZ) and UK soils

	df	Total biomass	
		F	*p*
Live NZ soil			
SP	3	14.1	< 0.01
N	1	91.6	< 0.01
SP × *N*	3	3.5	0.03
Sterilized NZ soil			
SP	3	3.5	0.03
N	1	53.8	< 0.01
SP × *N*	3	0.2	0.87
Live UK soil			
SP	3	2.0	0.13
N	1	6.4	0.02
SP × *N*	3	0.2	0.90
Sterilized UK soil			
SP	3	2.9	0.05
N	1	10.9	< 0.01
SP × *N*	3	0.7	0.56

All factors are fixed effects

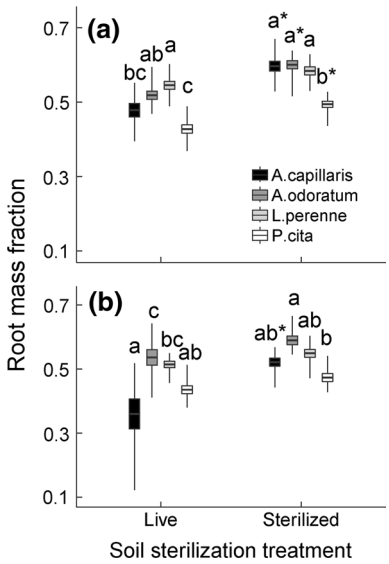

Fig. 2 Root mass fraction (RMF) responses of all species when grown in different soil treatments: **a** New Zealand and **b** UK soil. Bar and whisker points indicate mean ± SE ($N = 10$). Means within each sterilization treatment with the same letter are not significantly different (Tukey HSD, $p > 0.05$); asterisk indicates differences in species' RMF across sterilization treatments (Tukey HSD; $p < 0.05$)

in live NZ soil than both *A. capillaris* and *P. cita* (Fig. 2a). The native grass *P. cita* showed the lowest RMF in NZ soil (Fig. 2a). In UK soil, all species showed similar RMFs except *A. capillaris*, which exhibited a much lower RMF in live UK soil (Fig. 2b).

Discussion

Belowground enemy release did not appear to be a strong factor influencing invasion success in our study. All invasive species showed higher growth in soil from their native range (UK) and the net effect of removing soil biota via sterilization was positive regardless of where soils were from. Nevertheless, biogeographic differences in soil biota affected species responses to nutrients in ways that have implications for their invasion success. In particular, there was strong evidence to suggest that the presence of soil biota in the introduced range (NZ) enabled *L. perenne* to respond more strongly to nutrients than all other species, as its growth response to nutrients was stronger when grown in live NZ soil than other species responses (Fig. 1a). In contrast, all species responded similarly to nutrients when grown with soil biota from the native range (UK) or in sterilized soil (Fig. 1b–d). Unlike many invasive grasses, including *A. capillaris* and *A. odoratum*, *L. perenne* generally shows a greater abundance in its introduced range than its native range (Firn et al. 2011). Our findings suggest that the mechanisms underlying these differences in species relative abundances across their native and introduced ranges may relate to differences in soil biota and nutrient acquisition, even in the absence of belowground enemy release.

There are two likely ways in which the presence of soil biota from the introduced range could enhance *L. perenne*'s acquisition of nutrients relative to other co-occurring species. Firstly, beneficial soil organisms such as AMF could directly increase *L. perenne*'s access to nutrients more than they do other species. While most vascular plant species, including grasses, are capable of forming mutualistic associations with AMF, they vary in the degree of benefit they receive (van Der Heijden et al. 1998; Klironomos 2003). Invasive plant species may be more likely to form mutualistic associations with generalist AM fungi (Reinhart and Callaway 2006; Moora et al. 2011), although research into this is still in its early stages (Dickie et al. 2017). *L. perenne* can benefit substantially from associations with generalist AM fungi, such as *Glomus* spp. (Cliquet et al. 1997; Faure et al. 1998; Torrecillas et al. 2014) and may have developed more positive mycorrhizal associations in introduced soil than other species. Secondly, competition for nutrients from the introduced soil biota may have had a more negative effect on other species than on *L. perenne* (Niu et al. 2016; Zhu et al. 2016, 2017). Our study design did not allow us to separate mutualistic or antagonistic effects of soil biota and therefore the exact mechanism remains uncertain.

In addition to soil biota effects, it is possible that *L. perenne* has some other characteristic that allows it to perform

differently to the other species. For example, *L. perenne* had the highest RGR in our study (0.24), which suggests it may prefer high resource environments compared to the other species. However, the other species also varied in their RGRs; *A. capillaris* (0.21), *A. odoratum* (0.18) and *P. cita* (0.16), yet they showed no consistent differences in their responses to nutrient addition in any soil. Perhaps more significantly, *L. perenne* showed a higher RMF than both *A. capillaris* and *P. cita* in live soil from its introduced range (NZ). Furthermore, it was the only species that did not show a reduced RMF in live soil compared to sterilized soil from its introduced range (Fig. 2a). Maintaining a relatively high RMF could enable it to take up additional nutrients more effectively by pre-empting supply (Craine et al. 2005), thus providing a clear competitive advantage. Interactions between invader root traits and biogeographic variation in soil biota are therefore likely to be important for understanding plant invasions. Belowground traits, such as nutrient acquisition strategy, can influence plant–soil feedbacks (Bennett et al. 2017; Teste et al. 2017) and are increasingly recognized as drivers of ecological processes (Bardgett et al. 2014). Our findings suggest that they may also be important for understanding species invasions, particularly in the context of increasing nutrient availability due to pervasive environmental change.

Whilst biogeographic differences in soil biota were important in controlling species responses to nutrients in our study, we found no evidence for belowground enemy release. The role of belowground enemy release in driving species invasions varies across species and localities (Mitchell and Power 2003; Chun et al. 2010; Sun et al. 2014; Maron et al. 2014). Many of the studies that found strong effects assessed invasive trees or forbs, and used North American and European soils (e.g. Reinhart and Callaway 2004; Gundale et al. 2014; Maron et al. 2014). Fewer studies seem to have found evidence for belowground enemy release driving grass species invasions. This is surprising, as grasses generally show more negative plant–soil feedbacks than other functional groups, and are therefore most likely to realize the benefits of enemy release (Kulmatiski et al. 2008). Some European pasture grasses appear to have more positive associations with soil biota in Californian grasslands than native grasses, although whether this stems from belowground enemy release remains unclear (Bennett and Strauss 2012). In contrast, the native grass species in our study, *P. cita*, responded in a similar way to the invasive grasses, showing higher growth in UK soil and a similarly positive response to sterilization in soils from either origin. Therefore, the growth of native and invasive grasses appears to be constrained to a similar extent by belowground enemies in New Zealand. Only having one co-occurring native species in our study limits the implications of any invasive–native comparisons, although *P. cita* is widespread and therefore ecologically relevant as a comparison. *P. cita* responded as positively to nutrients in live NZ soil as *A. odoratum* and *A. capillaris*, although much less so than *L. perenne*. This suggests that while increases in nutrient additions appear to facilitate invasive grasses in the field in NZ (Scott 2000; King and Wilson 2006; Dickie et al. 2014), this is likely to be species dependent. Other factors, such as disturbance and priority effects, i.e. where the first species to arrive following a disturbance ultimately dominates the community (Seabloom et al. 2003), or superior competitive abilities (Sun et al. 2014; Broadbent et al. 2017), likely underlie the invasions of other grass species, including *A. capillaris* and *A. odoratum*. In combination with findings from previous studies, our results suggest that predicting which invasive plant species are most likely to benefit from belowground enemy release will be difficult, due to large variation within functional groups and across different habitats in the introduced range.

When species responses were analysed individually, all species in our study showed increased growth following nutrient addition. However, for *L. perenne* a positive growth response was only seen in soils from its introduced range (Fig. S3a). This increase did not differ between live and sterilized soil from the introduced range, suggesting that it was not due to differences in soil biota. Instead, differences in nutrient availability between UK and NZ soils may explain this result. This is supported by our analysis of soil chemistry before the experiment started, which indicated that NZ soils had a slightly lower initial inorganic N content than UK soils, even after dilution with 90% of the peat and sand medium was taken into account. This was, however, a snapshot measurement of soil nutrient concentrations, and by the end of the experiment there were no differences between NZ and UK soil inorganic N concentrations. The role of soil biota in driving species responses to nutrients only becomes clear when individual species responses are analysed relative to co-occurring species. This highlights the importance of studying multiple co-occurring invasive species in order to elucidate the species-specific variation in invasion mechanisms.

We used soil that had been conditioned by natural vegetation communities as opposed to experimentally pre-conditioning soil (Kulmatiski et al. 2008). Some studies pre-condition soil prior to starting the experiment by growing artificial plant communities in it, thereby conditioning the soil biota community on those particular plant species. We were interested in how invasive plant species responded to nutrient additions when grown with soil biota that had been conditioned by natural plant communities that are vulnerable to invasion following nutrient increases, compared to similar communities in their native range. Our findings therefore reflect processes occurring at the very early stages of invasion, following colonization by invasive species

(Theoharides and Dukes 2007). Soils conditioned by fast-growing species have been shown to have higher nitrogen availability than soils conditioned by slow-growing species (Baxendale et al. 2014). This subsequently improved the competitive ability of fast-growing species later grown in those soils (Baxendale et al. 2014). This effect could theoretically lead to the facilitative interaction of novel soil biota and nutrient addition on fast-growing invasive species, such as *L. perenne*, becoming prolonged throughout later stages of invasion, even if the original source of nutrient addition ceases. Whether this could account for the higher abundances of fast-growing invasive species, such as *L. perenne*, in their introduced ranges relative to their native ranges, has to the best of our knowledge never been tested, but would make an interesting avenue for further research.

Conclusion

Even when the net effect of an invasive plant's associations with soil biota in its introduced range are negative, the presence of these novel soil biota may still allow it to respond more strongly to nutrient additions than its competitors, compared to soil biota from the native range. This mechanism may contribute to the invasive success of some species and suggests that the range of plant–soil feedbacks associated with successful invasion is far wider than that encompassed in the belowground enemy release hypothesis. We also found evidence that belowground plant traits, such as RMF, may be important in driving responses, although assessing whether this is a general trend or not would require testing across a wider range of species than that tested here. Considering the globally widespread nature of anthropogenic nutrient additions to ecosystems, the effects seen in our study could be contributing to a global homogenization of flora and the associated losses in native species diversity (Firn et al. 2011; Seabloom et al. 2015; Van Kleunen et al. 2015).

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Author contribution statement AB conceived of and conducted the experiments, including fieldwork and analysis of the data; all authors designed experiments and wrote the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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