Received: 10 January 2024 | Accepted: 31 July 2024

DOI: 10.1111/1365-2435.14643

Functional Ecology
BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Contrasting responses of naturalized alien and native plants to native soil biota and drought

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Funding information
Wageningen Graduate Schools, Grant/Award Number: Postdoctoral Talent Grant to Rutger A. Wilschut

Handling Editor: Laura Yahdjian

Abstract

1. Terrestrial plant communities often become invaded by alien species, which may benefit from high growth rates, strong phenotypic plasticity and reduced negative impacts from local soil communities. At the same time, terrestrial communities are increasingly more often exposed to periods of drought. However, how drought affects the competition between alien and native plants directly, and indirectly, through changing impacts of soil communities on plant performance, remains poorly understood.
2. Here, we performed a greenhouse pot experiment in which we examined biomass responses of five native and five naturalized alien species (all occurring in mesic grasslands) to drought and benign soil moisture conditions, while growing in interspecific, intraspecific or absence of competition, in the presence or absence of native soil biota. We expected that alien plant species are less negatively affected by soil biota, but more negatively affected by drought than native species, and that drought indirectly weakens soil-community-driven competitive benefits of alien plant species over native ones.
3. On average, soil-community effects on plant biomass were positive, but native performance was less positively affected by soil communities than alien performance, suggesting reduced impacts of soil-borne enemies on alien plants. Drought more negatively affected alien- than native plant performance. Drought impacts on plant biomass did not depend on soil community presence, but in the presence of soil biota, plants overall invested more in root biomass when exposed to drought. The effects of competition were subtle and species-specific.
4. To better understand the observed positive soil-community effects on plant performance in our study, we examined mycorrhizal root colonization of plants grown in absence of competition. Among-species variation in mycorrhizal colonization explained plant performance differences between soils with and without live soil communities, indicating a key role for arbuscular mycorrhizal fungi as driver of plant performance. However, mycorrhizal colonization did not differ between alien and native plants and was unaffected by drought.

5. Overall, our study suggests that drought may weaken alien plant invasions through stronger direct negative impacts on alien than on native plant performance, but that drought does not affect soil-biota-driven differences in plant performance between alien and native plants.

KEYWORDS
Arbuscular mycorrhizal fungi, biomass allocation, enemy release hypothesis, plant invasions, plant–soil interactions

1 | INTRODUCTION

Many terrestrial ecosystems are invaded by alien plant species, which may outcompete native plant species when they possess traits related to high performance (van Kleunen et al., 2010; Zhang & van Kleunen, 2019) or exhibit high adaptive phenotypic plasticity (Davidson et al., 2011; Richards et al., 2006). Moreover, upon introduction into a new geographic range, alien plant species can become released from specialist enemies occurring in their native range, promoting their performance and likelihood of naturalization (Keane & Crawley, 2002; Liu & Stiling, 2006). As such, alien plant species may negatively affect native biodiversity (Vila et al., 2011; Vilà & Hulme, 2017). At the same time, as a consequence of anthropogenic climate change, terrestrial communities are increasingly more often exposed to extended periods of drought (Spinoni et al., 2014; Trenberth et al., 2014). Droughts can directly reduce productivity of terrestrial plant communities (Breshears et al., 2005), but also affect the composition and functioning of plant-associated soil communities (Lozano et al., 2021; Schimel, 2018; Wilschut & Geisen, 2021). However, it is still poorly understood whether drought may differentially affect the performance of naturalized alien and native plant species, either directly or due to altered plant–soil interactions, and thereby alter competitive interactions between alien and native plant species.

As plant species differ in their tolerance to limited water availability, droughts can modify the composition of plant communities through direct species-specific impacts on plant performance (Hannusch et al., 2020; Tilman & El Haddi, 1992). Plant drought tolerance mechanisms are diverse (Comas et al., 2013; Jaleel et al., 2009) and include increased resource allocation to root growth to optimize water uptake (Eziz et al., 2017). In several experimental studies, naturalized alien plants have been observed to perform better than co-occurring native plant species when exposed to drought (Gao et al., 2018; Li et al., 2023; Wang et al., 2020), possibly due to plastic root growth and decreased water consumption in response to moisture shortages (Li et al., 2023). Two meta-analyses, however, showed that on average, alien plant species appear to be more negatively affected by drought than native plant species, although these overall differences were not significant (Liu et al., 2017; Sorte et al., 2013). Combined, these results suggest that alien drought responses are likely species-specific. However, to draw conclusions on possible differences in alien and native plant performance under drought, it is important to consider potential drought-induced changes in plant interactions with the biotic environment (Zhang et al., 2022).

To understand drought effects on competitive interactions between alien and native plant species, it may especially be critical to assess whether drought differentially affects soil community impacts on native and alien plant performance. Through variation in structural and chemical root traits, plants attract species-specific assemblages of soil biota such as bacteria, fungi and nematodes (van Dam & Bouwmeester, 2016; Wilschut et al., 2019), which jointly affect plant performance. These overall effects of soil communities on plant performance depend on the relative impacts of plant-antagonistic organisms (e.g. microbial pathogens and root-feeding nematodes; Semchenko et al., 2018; Wilschut et al., 2019), and plant-mutualistic organisms (e.g. mycorrhizal fungi and growth-promoting bacteria; Berendsen et al., 2012; Dubey et al., 2019). Soil communities often affect alien plant performance less negatively than native plant performance (Kulmatiski et al., 2008). This enhanced alien plant performance in soils outside of their native range is typically attributed to the absence of belowground specialist herbivores and pathogens that do occur in the original range, as well as reduced negative impacts of generalist belowground enemies occurring in the new range (Inderjit et al., 2021; Jeschke, 2014). At the same time, alien plant species may develop stronger positive interactions with mycorrhizal fungi than native plant species, a phenomenon referred to as the 'enhanced mutualism hypothesis' (Reinhart & Callaway, 2006; Yu et al., 2022). Both the reduced negative impacts of plant-antagonist communities and increased positive impacts of mycorrhizal fungi on alien plant performance have been shown to increase their competitive ability when growing in presence of native plant species (Callaway et al., 2001; Reinhart & Callaway, 2006; Zhang et al., 2017).

Theoretically, interspecific competition between native and alien plants may be altered by drought when differences in positive or negative interactions with soil biota are either exacerbated or reduced. As droughts often negatively affect plant pathogen abundances (Corcobado et al., 2014; de Vries et al., 2023), they may potentially weaken the pathogen-driven competitive benefits of alien over native plants. Furthermore, as belowground plant-antagonists strongly contribute to negative density dependence of native plant species (Stein & Mangan, 2020), drought may weaken pathogen-driven suppression of plants growing in intraspecific competition more strongly for native than for alien plants. Such impacts may especially be relevant in early- and mid-successional grassland plant communities, in which soil community impacts on plant performance are dominated by the effects of plant-antagonists (Hannula et al., 2017; Kardol et al., 2006). On the other hand, as abundances of mycorrhizal fungi typically remain unaffected or even increase under drought (Albracht et al., 2023; de Vries et al., 2018; Lozano et al., 2021), alien plant species may gain a further benefit from associations with mycorrhizal fungi, especially because mycorrhizal fungi can alleviate drought stress (Augé, 2001; Li et al., 2019). Because soil biotic communities can also alter drought-induced increases in plant biomass allocation to roots (Franco et al., 2020), it may be expected that variation in plant–soil interactions between native and alien plant species can also be reflected in differential biomass allocation responses under drought stress; however, this remains untested. Altogether, soil-community-mediated drought effects on plant performance may differ between native and alien plants, but the outcomes of such effects may depend on the dominant soil biotic group driving differences in plant performance between aliens and natives. However, whether such drought impacts are strong enough to alter competition between natives and aliens remains unknown.

Here, we examined how drought affects competition between alien and native plant species, and how this is mediated by the presence of soil biota. To this aim, we set up a greenhouse pot experiment in which we exposed naturalized alien and native grassland plant species growing in interspecific, intraspecific or absence of competition to dry or non-dry soil moisture conditions, in the presence and absence of native soil biota. We hypothesized that (1) alien plant species are less negatively affected by soil biota than native plant species, (2) direct drought effects are more negative for alien plant species than for native plant species and (3) through negative impacts on soil-community activity and pathogen impacts, drought indirectly weakens soil-driven competitive advantages of alien plant species over native plant species. Finally, we expected plant biomass allocation to roots to increase in response to drought and that this may depend on soil community presence and plant origin.

2 | MATERIALS AND METHODS

2.1 | Plant species and germination

To test our hypotheses, we selected five alien plant species (four forbs, one grass) that have become established (i.e. naturalized) in mesic (semi-)natural grasslands in southern Germany (Table 1) and five con-familial native plant species that were selected based on their occurrence in such grasslands in the region of Konstanz, Germany (www.floraweb.de). Seeds were purchased from Rieger Hofmann GmbH (Blaufelden-Raboldshausen, Germany) or provided by one of several European Universities or the botanical garden of the University of Konstanz (Table 1). For each species, we sowed approximately 200 seeds per species in pots filled with standard potting soil (Einheitserde® CL P, Einheitserdewerke Patzer Gebr. Patzer GmbH & Co. KG), which were then placed in a greenhouse compartment (16 h light/8 h dark; 19°C/18°C). Seeds were sown 3 or 2 weeks before the start of the experiment, depending on plant species identity and respective germination time requirements.

2.2 | Soil preparation

Before the start of the experiment, we collected top soil (~0–20 cm) with a shovel excavator from a diverse grassland patch close to the botanical garden of the University of Konstanz (WGS 84: 47.6915195° N, 9.1791881° E). All native plant species used for this experiment occur in this grassland patch or in the direct surrounding (personal observation). In total, we obtained 270 L of mixed, sieved (15 mm mesh) field soil, of which we sterilized half by autoclaving twice at 120°C for 30 min. We then mixed non-sterilized and sterilized soil separately with the same amount of a 1:1 mixture of sand (Quarzsand; Emil Steidle GmbH & Co. KG) and vermiculite (grain size 0.3–0.8 mm; Isola Vermiculite GmbH). We used these soils to fill 1 L square pots that were laid out with chiffon fabric to prevent leakage of substrate. Each pot received 927 g of soil to allow consistent

TABLE 1 List of study species, their plant family, origin (native/alien), life history (annual/biennial/perennial), functional group (forb/grass), Botanical garden seed index number and seed origin (Brno University, Czech Republic (BU); Botanical Garden Konstanz University (KO); Rieger Hofmann GmbH (RH); Krefeld Botanical Garden (KR)).

Plant species	Family	Origin	Life history	Guild	Index no.	Seed origin
Centaurea jacea L.	Asteraceae	Native	Perennial	Forb	–	RH
Erigeron annuus (L.) Desf	Asteraceae	Alien	Annual	Forb	0.1211001Ba	KO
Leucanthemum vulgare Lam.	Asteraceae	Native	Perennial	Forb	–	RH
Solidago canadensis L.	Asteraceae	Alien	Perennial	Forb	0.0216601Rö	KO
Epilobium ciliatum Raf.	Onagraceae	Alien	Perennial	Forb	0.030822	KO
Epilobium hirsutum L.	Onagraceae	Native	Perennial	Forb	0.162305	BU
Sisymbrium officinale (L.) Scop.	Brassicaceae	Native	Annual	Forb	0.1810201He	KO
Lepidium virginicum L.	Brassicaceae	Alien	Annual	Forb	0.053507	KR
Lolium perenne L.	Poaceae	Native	Perennial	Grass	–	RH
Lolium multiflorum Lam.	Poaceae	Alien	Biennial	Grass	0.065405	KO

soil-moisture manipulation (see next section). To this end, we also determined average soil moisture of the soil mixture by drying soil samples for 24 h at 105°C, allowing pot-weight based soil moisture manipulation during the experiment. As soil autoclaving can cause changes in abiotic soil conditions (Anderson & Magdoff, 2005; Berns et al., 2008), we cannot rule out that overall differences in plant responses between sterilized and non-sterilized soils observed in our experiment are partly caused by abiotic rather than biotic differences.

2.3 | Experimental set-up and drought treatment

On 12 April 2021, we transplanted seedlings into pots filled with sterile or non-sterile soil. We established three competition treatments: inter-, intraspecific and absence of competition. For the interspecific competition treatment, we paired each of the five native plant species with each of the five alien plant species, while for intraspecific and without-competition treatments, all native and alien species were grown in the presence of a conspecific neighbour or no neighbour at all, respectively. In total, the experiment thus consisted of 540 pots (25 interspecific native-alien species combinations × 2 soils (sterilized/non-sterilized) × 6 replicates + 10 species × 2 soils (sterilized/non-sterilized) × 2 competition treatments (intraspecific/single) × 6 replicates). Plants in competition were placed in diagonally opposite corners of the pots, whereas plants growing without competition were placed in pot centres. Pots were then transferred to a climatized greenhouse (16 h light/8 h dark; 19°C/18°C), placed on individual saucers to avoid possible contaminations from other pots, and arranged according to a fully-randomized design. To optimize seedling survival in the first weeks following transplantation, top soils were regularly moistened. We replaced dead seedlings until the end of the third week. To obtain an estimate of initial plant size, we determined the leaf number as well as the length and width of the largest leaf of each individual seedling in the first week after seedling transplantation.

After 2 weeks, we started regularly (three–four times per week) standardizing soil moisture in all pots to 20% (w/w). At the end of that week, each pot received 50 mL of 1‰ Everis Scotts Universol® Blue fertilizer solution (18 − 11 − 18 + 2.5 MgO + TE, ICL Deutschland Vertriebs GmbH), in order to avoid nutrient deficiency during the remainder of the experiment. After 4 weeks, we started a drought treatment in half of the replicates ($N = 3$ for all combinations of competition and soil community treatments) by standardizing soil moisture at 10% (w/w), whereas soil moisture in the other half was maintained at 20%. These soil moisture levels were based on drought experiments using comparable substrates in which significant drought effects were observed (e.g. Wilschut & van Kleunen, 2021). During the next 4 weeks, we continued the drought treatment by watering individual pots by weight four to five times per week using demineralized water. On 4 June 2021, after 50 days of plant growth, we harvested shoot biomass of all plants and root biomass of plants grown without competitors. Both shoots and washed root systems were dried in an oven at 70°C until constant weight and weighed afterwards.

2.4 | Mycorrhizal colonization

As a number of plant species appeared to respond positively to the presence of a live soil community, we assessed if colonization by arbuscular mycorrhizal fungi (AMF) partly explained variation in performance of plants grown in the absence of competition, by examining mycorrhizal colonization in each of the three replicates of both the drought-treated and control plants of each species. To this aim, we stained dried roots according to Vierheilig et al. (1998). In short, depending on the size of the roots, we bleached the entire root system for small plants or, for larger plants, randomly selected root pieces from different parts of the root system, for at least 10 min in a 10% KOH solution in a water bath at 95°C. Transparent root systems were subsequently thoroughly rinsed with tap water, after which we stained the roots with a 5% ink-vinegar solution (Parker QUINK Black, France) for 5 min at 95°C. After leaving the roots in the ink solution for 10 min at room temperature, we rinsed them with tap water until run-off water was clear. Stained roots were stored in a 1% vinegar solution until examination. To examine colonization, we randomly selected five root pieces and cut them to ~5 cm length and placed them on a microscope glass. On each root piece, we then randomly made 20 observations under a compound microscope at 40 × 10 magnification, counting the absence or presence of mycorrhizal structures (arbuscules, vesicles and hyphae), resulting in 100 observations per single plant. Our analyses of mycorrhizal colonization showed that a part of the plants growing in previously sterilized soils exhibited (limited) mycorrhizal colonization of their root systems. Most likely the sterilized soil was recolonized by mycorrhizal fungi through air-based spore dispersion (Chaudhary et al., 2020).

2.5 | Replication statement

Our replication statement is outlined in Table 2.

2.6 | Statistical analyses

We performed all statistical analyses in R version 4.1.0 (R Core Team, 2021). Data from pots that contained dead plants ($N = 83/954$ plants, in 76/540 pots) were removed from all main analyses. Yet, we examined effects of treatment combinations on plant survival using a logistic regression model with 'focal species', 'competition', 'soil moisture' and 'soil community' and all their possible interactions as fixed effects, and tested their significance using type-II Wald Chi-squared tests.

To test our hypotheses, we analysed four variables: shoot biomass, which was available for all plants, as well as total biomass, root weight ratio (RWR; calculated as root biomass/total biomass)

TABLE 2 Replication statement for the study, separately described for analyses of shoot biomass (measured for all experimental units) and for analyses of three variables only measured for plants grown in absence of competition (total biomass, root weight ratio (RWR) and mycorrhizal colonization).

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Species	Individuals/pots	*Shoot biomass*: Origin effects: for each level of plant origin (native vs. alien): 25 independent combinations of interspecific competition (five native × five alien plant species) and 5 independent levels of both intraspecific- and no-competition treatments (five native/alien plant species), crossed with two levels of soil moisture (control/drought) and two levels of soil community treatment (present/sterilized), with each treatment combination replicated three times Species effects: for each plant species: Five independent combinations of interspecific competition (five alien/native competitors), and one level of both intraspecific- or no-competition treatments, crossed with two levels of soil moisture (control/drought) and two levels of soil community treatment (present/sterilized), with each treatment combination replicated three times
Species	Individuals/pots	*Root weight ratio, total plant biomass & mycorrhizal colonization rates*: Origin effects: for each level of plant origin five independent levels of both intraspecific- and no-competition treatments (five native/alien plant species), crossed with two levels of soil moisture (control/drought) and two levels of soil community treatment (present/sterilized), with each treatment combination replicated three times Species effects: for each plant species: one level of both intraspecific- or no-competition treatments, crossed with two levels of soil moisture (control/drought) and two levels of soil community treatment (present/sterilized), with each treatment combination replicated three times

Note: In both cases, we describe replication for the main statistical models examining plant origin or plant species effects.

and mycorrhizal colonization, which were only determined for plants grown without competitors. In all analyses, we included natural-log-transformed initial plant size (leaf area × plant height × leaf number) as a covariate. Shoot and RWR data were natural-log-transformed to improve the normality of the residuals. We modelled shoot biomass using a linear mixed-effect model ('lme4 package'; Bates et al., 2014) with 'plant origin', 'competition', 'soil moisture' and 'soil community' as fixed effects with all their possible interactions, and with 'focal species', 'competing species', as well as 'Pot ID' as random intercepts. To also examine biomass response variation among individual focal species, we constructed a similar linear mixed-effect model with 'plant species' instead of 'plant origin' as fixed effect, in which we included 'competing species' and 'Pot ID' as random intercepts. Total biomass and root weight ratio (RWR) data of individually grown plants were modelled using linear mixed effect models with the fixed effect terms 'origin', 'soil moisture' and 'soil community' and all possible interactions, and 'focal species' as random intercepts. Additionally, we constructed species models for both total biomass and RWR (lm-function) with 'focal species' as a fixed factor instead of 'origin'. Due to missing data for *Sisymbrium officinale*, this species was excluded from these species models.

To examine how mycorrhizal colonization was affected by the treatments, we constructed a generalized linear mixed effects model following a binomial distribution with a logit-link function. We modelled proportional mycorrhizal presence data in response to the fixed effects 'origin', 'soil moisture' and 'soil community' and all possible interactions, and 'focal species' as random intercepts. To account for overdispersion of the model, we added 'plant individual' as observation-level random effect (OLRE) to obtain a dispersion parameter below 1 (Harrison, 2014). To analyse whether mycorrhizal colonization differed among plant species, we ran a similar model in which we replaced 'origin' with 'focal species' and from which we excluded the 'soil moisture' term to allow model convergence.

For all models, significances of fixed effects were tested with Wald Chi-squared tests (mixed effects models) or *F*-tests (general linear models) using type-III tests ('Anova' function from 'car package' Fox et al., 2012). We visually examined residual plots to confirm that model assumptions were not violated. We used the 'emmeans' package (Lenth et al., 2018) to further analyse significant interactions, by running post hoc pairwise comparisons of estimated marginal means between treatment levels. To analyse whether plant performance in unsterilized soil was related to mycorrhizal colonization, we used a Pearson correlation test to test the overall correlation between log-response ratios of total biomass (total biomass$_{\text{non-sterilized}}$/total biomass$_{\text{sterilized}}$) and AMF colonization (colonization$_{\text{non-sterilized}}$ (%+1)/colonization$_{\text{sterilized}}$ (%+1)) in non-sterile and sterile soil. To this aim, we combined total biomass and mycorrhizal colonization data for each pair of individual replicates (replicate 1, 2 & 3) grown in sterile and non-sterile soils, so that there were maximally six data points (two moisture levels × three replicates) for each plant species. Finally, to examine whether the correlation strength depended on plant origin and/or soil moisture, we constructed a general linear model to model the log-response ratio of total biomass in response to the log-response ratio of AMF colonization, 'plant origin' and 'soil moisture', as well as all possible interactions, as fixed explanatory variables.

3 | RESULTS

3.1 | Plant survival

Plant survival was plant-species-specifically affected by soil moisture and soil-community presence (Tables S1 and S2). Most notably, both *Epilobium* species—especially under drought—exhibited reduced survival rates in absence of soil biota, while *Sisymbrium officinale* plants growing in presence of a soil community did not survive when exposed to drought (Table S2).

3.2 | Shoot-biomass responses

Soil-community presence positively affected average (transformed) shoot biomass of both naturalized alien and native plant species (Figure 1a), yet negatively affected untransformed shoot biomass (likely caused by strong among-species variation in plant size; see Figure S1). However, this effect was more positive (or less negative) for aliens (untransformed averages: −31.6%; Figure S1A) than for natives (untransformed averages: −50.5%; Figure S1A) (Table S3; Figure 1a). Consequently, alien plant species were on average larger than native plant species in the presence of soil biota, but smaller in the absence of soil biota (Figure 1a; Figure S1A), although these effects were not significant (*emmeans* post hoc tests plant origin effect; absence soil community: $p_{\text{origin}} = 0.79$; soil community presence: $p_{\text{origin}} = 0.53$). Average drought responses also differed between alien and native plants, as alien plant species (untransformed averages: −74.7%) were more negatively affected by drought than natives (untransformed averages: −60.7%) (Table S3; Figure 1b; Figure S1B). Yet, shoot biomass of alien plant species did not significantly differ from native shoot biomass neither under control (*emmeans* post hoc tests: $p_{\text{origin}} = 0.91$) nor drought conditions (*emmeans* post hoc tests: $p_{\text{origin}} = 0.63$). Competition did not have an overall effect on shoot biomass (Table S3; Figure 1c; Figure S1C). However, when species-identity effects were included in the model, instead of the species-origin effect, competition was shown to affect shoot biomass in species-dependent ways, and this effect depended on the presence of soil biota (Figure 2; Table S4). In presence of soil biota, a majority of the plant species accumulated (marginally) significantly more shoot biomass when growing in absence of intraspecific and/or interspecific competitors, while in absence of soil biota only *Erigeron annuus* accumulated more biomass when growing in absence of competitors than in presence of competitors (Table S5; Figure 2). Furthermore, irrespectively of their origin, plant species belonging to the Brassicaceae (*Sisymbrium officinale* and *Lepidium virginicum*) and Poaceae family (*Lolium perenne* and *L. multiflorum*) accumulated more shoot biomass in sterilized soil than plant species of the Asteraceae and Onagraceae families (Figure 2). Plant species also differed in their response to the interactive effect of drought and the presence of soil biota (Figure 2; Table S4). Drought negatively affected shoot biomass in all cases (Table S6), but species that showed a positive biomass response to soil sterilization appeared to be more negatively affected by drought in the absence of soil biota than in the presence of soil biota (Figure 2). Total biomass responses, measured only for plants grown in absence of competition, were partly in line with shoot biomass responses and are presented in Supplementary Data S1.

3.3 | Biomass allocation responses

Soil-community effects on plant biomass allocation to roots (root weight ratio (RWR)) depended on the soil-moisture treatment (Table S7; Figure 3), but this effect was independent of plant origin (Table S7). In the presence of soil biota, plants invested significantly more in root biomass when exposed to drought (untransformed averages: +18.6%), while this was not the case in the absence of soil biota (untransformed averages: +1.8%) (Figure 3). Root weight

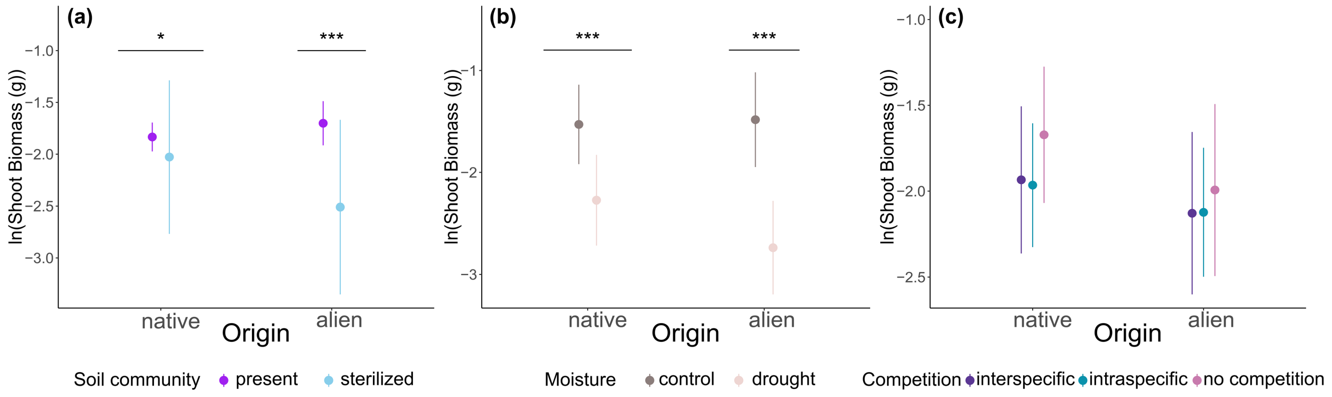

FIGURE 1 Shoot biomass responses (natural-log-transformed) of native and naturalized alien plants to soil community presence (present/sterilized; a), soil moisture (control/drought; b) and competition (interspecific/intraspecific/no competition; c). Dots and bars indicate means ± standard errors, calculated using average species responses ($N = 5$). Asterisks (*) indicate significant post hoc differences between treatment levels, at $p < 0.05$ (*) or $p < 0.001$ (***).

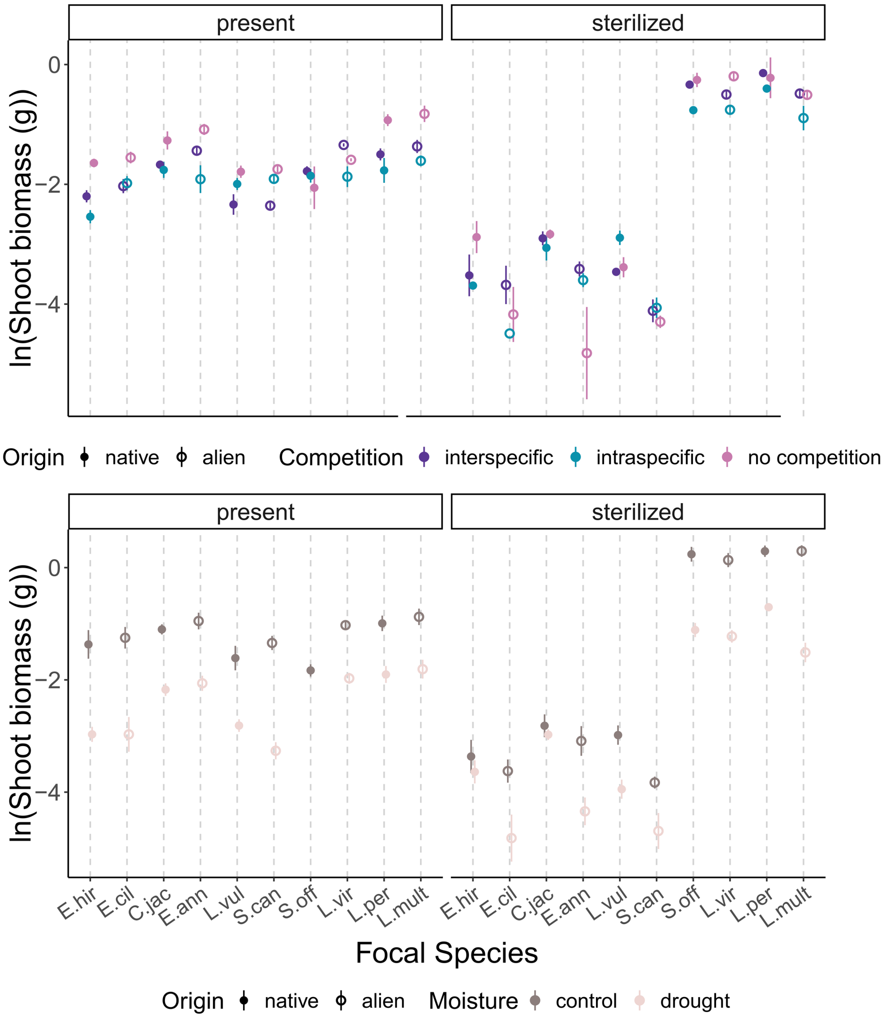

FIGURE 2 Species-level shoot biomass (natural-log-transformed) responses to competition (interspecific competition/intraspecific competition/no competition; top panel) and soil moisture treatments (control/drought; bottom panel) in presence and absence of live soil communities. Dots and whiskers represent means ± standard errors.

ratio responses to the presence of soil biota were species-specific (Figure S2; Table S8). Plants of *Lepidium virginicum* as well as of both *Lolium* species appeared to increase their allocation to roots in the presence of soil biota, whereas all other species appeared to decrease biomass allocation to roots in the presence of soil biota (Figure S2). Drought also affected RWR responses in a species-specific way (Table S8), as some species appeared to invest more in belowground biomass when exposed to drought, whereas other species invested most in belowground biomass under control soil-moisture conditions (Figure S2).

3.4 | Mycorrhizal colonization

Mycorrhizal colonization was significantly higher in plants grown in the presence of soil biota than in sterilized soil (Table S9; Figure 4a), in which mycorrhizal contamination was found for a number of sterilized soil samples ($N = 18$ out of 45 analysed samples; Figure 4a). Our generalized linear mixed effects model indicated that mycorrhizal colonization differed between alien and native plant species, and that this difference depended on soil moisture (Table S9). To analyse whether this effect was robust, or perhaps partly driven by patterns of mycorrhizal colonization in sterilized soils, we also analysed colonization data in only non-sterilized soils. The latter model indicated that colonization rates did not significantly differ between alien and native plant species and did not depend on soil moisture (Table S10), indicating that the aforementioned significant statistical effects were driven by mycorrhizal colonization in previously sterilized soils. Mycorrhizal colonization in non-sterile soils significantly differed among plant species (Table S11; Figure S3), with both Poaceae species and especially both Brassicaceae species exhibiting low levels of colonization. Differences in mycorrhizal colonization between non-sterile and sterile soil correlated to differences in total plant biomass: plants with the highest colonization rates in non-sterile relative to sterile soils also showed the highest performance in non-sterile relative to sterile soil (Figure 4b). The strength of the correlation between mycorrhizal colonization and relative plant performance in non-sterile compared to sterile soils did not differ between alien and native plants or between control and dry soil-moisture conditions (Table S12).

4 | DISCUSSION

Our results indicate that naturalized alien and native plants on average respond differently to the presence of local soil biota and reductions in soil moisture, as we found that alien species benefited more from the presence of local soil biota and suffered more from drought than native species. The observed soil-community effects on plant performance were nevertheless strongly species-specific, as both native and alien species of Brassicaceae and Poaceae exhibited negative biomass responses to soil-community presence. However, alien and native plant responses to drought were not differently modified by the presence of native soil biota. Therefore, our study primarily shows that droughts may negatively affect alien plant performance, but do not reduce or strengthen non-native plant impacts on native plant communities through alterations of plant–soil interactions.

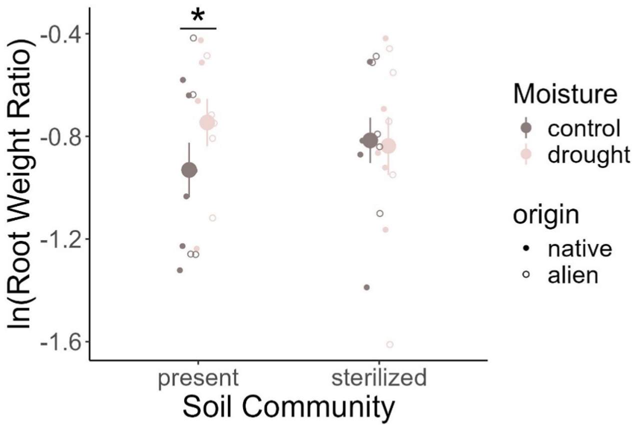

FIGURE 3 Root weight ratio responses to drought treatment (control/drought) in the presence and absence (sterilized) of a live soil community. Dots and whiskers represent means ± standard errors, calculated using average species responses ($N=10$). Asterisk (*) indicates significant post hoc least square means differences between treatment levels, at $p<0.05$.

We expected that alien plants would be less negatively affected by soil biota than native plants (Hypothesis 1). However, overall effects of soil biota on plant performance were positive rather than negative (Figure 1a, but see Figure S1A), yet more positive for alien than for native plants. These results indicate that plant-beneficial soil biota played an important role in our study. Indeed, colonization rates of arbuscular mycorrhizal fungi positively correlated to differences in plant performance between non-sterilized and sterilized soils, suggesting a key role for AMF as drivers of plant performance. Plant species of families that typically develop no or weak associations with arbuscular mycorrhizal fungi, that is, Brassicaceae and Poaceae species (Cosme et al., 2018; Grime et al., 1987; Romero et al., 2023), indeed showed limited mycorrhizal colonization rates and exhibited negative responses to soil-community presence. However, mycorrhizal colonization rates did not differ between native and alien plant species, and the correlation between mycorrhizal colonization rates and relative plant performance was similar for alien than for native plants. As such, we did not find support for more successful plant-AMF associations of alien compared to native plant species

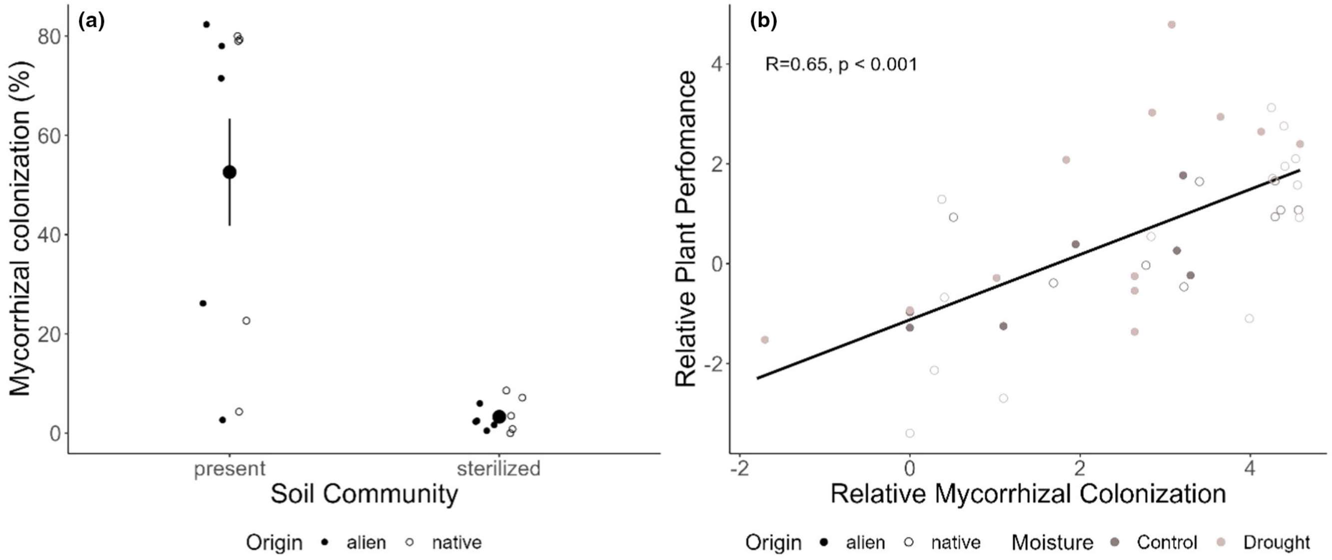

FIGURE 4 (a) Mycorrhizal colonization in the roots of plants grown without competition in the presence and absence (sterilized) of a native soil community. Dots and bars indicate means ± standard errors, calculated using average species responses ($N=10$). Points (jittered horizontally to increase visibility) show average colonization rates of native (open circles) and alien plants (closed circles). (b) Correlation between relative mycorrhizal colonization ($\ln(\text{colonization}_{\text{non-sterilized}}/\text{colonization}_{\text{sterilized}})$) and relative performance ($\ln(\text{total biomass}_{\text{non-sterilized}}/\text{total biomass}_{\text{sterilized}})$) in non-sterile compared to sterile soils, calculated for pairs of individual replicates, for both control (dark circles) and drought (light circles) conditions. Results of the Pearson correlation test, and the associated slope of the simple regression are also indicated.

('enhanced mutualist hypothesis'; Reinhart & Callaway, 2006; Yu et al., 2022), nor for weaker positive effects of AMF on alien plant growth (Bunn et al., 2015). A previous study suggested that plant-size-related differences in chemical stimulation of mycorrhizal colonization may have explained the more positive effects of AMF on alien plant performance (Yu et al., 2022). Since alien and native plant species overall did not differ in performance in our study, this may explain the lack of observed differences in mycorrhizal colonization. Instead, reduced negative impacts of plant-antagonistic soil biota ('Enemy release hypothesis'; Callaway et al., 2004; Engelkes et al., 2008; Keane & Crawley, 2002) may explain the on-average more strongly positive responses of alien plants to the presence of native soil biota.

In line with our second hypothesis, drought affected alien plants more negatively than native plants. This result is in line with the meta-analyses of Liu et al. (2017) and Sorte et al. (2013) that on average show trends of more negative drought impacts on alien compared to native plant species, but contrasts various experimental studies (Gao et al., 2018; Li et al., 2023; Wang et al., 2020). The ability to exhibit strong phenotypic plasticity in response to changing environments has been proposed as a key mechanism contributing to the success of invasive alien plant species (Richards et al., 2006). Indeed, also in response to drought, some alien plant species have been shown to exhibit stronger plastic root growth responses than related native plant species, thereby maintaining a higher performance under limited soil-moisture availability (Li et al., 2023). Possibly, the limited pot depth in this experiment may have partly inhibited plastic responses, for example, in rooting depth (Poorter et al., 2012; Turner, 2019). However, we observed that plants on average did allocate more biomass to roots in response to drought—although only in non-sterilized soil—indicating that plants to some extent exhibited plastic responses, despite the limited pot size. These biomass-allocation responses nevertheless did not differ between native and alien plants. A previous meta-analysis indicated that alien plant species exhibit a greater stomatal conductance than related native species (Cavaleri & Sack, 2010), likely due to higher metabolic rates and photosynthetic activity (Leishman et al., 2007). Additionally, as the set of native plant species included more perennial species than the set of alien plant species (Table 1), this may have further contributed to their on-average stronger resistance to drought (Ruppert et al., 2015). While our study thus is in line with previous meta-analyses, it is likely that outcomes of comparisons of drought responses between alien and native plants for an important part depend on the identity of the examined species, but field studies that also allow plastic root responses are needed to confirm this.

We expected that drought would modify impacts of soil biota on plant performance, and that these modifications would differ between alien and native plants, for example due to drought-induced reductions of plant-pathogen pressure (Corcobado et al., 2014), which would especially benefit native plants (Hypothesis 3). While native plants indeed experienced less positive impacts from soil communities than alien plants, drought did not differently modify this pattern. Instead, drought modifications of soil community impacts were plant species-specific. Most notably, drought appeared to weaken negative impacts of soil biota on plant performance most strongly in the case of the alien grass species *Lolium multiflorum*, and dampened positive soil-community impacts most strongly in the case of the forbs *Epilobium hirsutum* and *Centaurea jacea*. In other plant species, drought did not appear to modify soil community impacts on plant performance. Interestingly, however, patterns of plant survival (Table S2) suggested that soil-community presence either strengthened (*Sisymbrium officinale*) or weakened (*Epilobium* species) negative drought impacts on plant survival, but this was not supported by our statistical analyses (Table S1). Altogether, these results are in line with previous studies showing that drought modifications of plant–soil interactions are often subtle and species-specific (Buchenau et al., 2022; Wilschut & van Kleunen, 2021). In line, the positive correlation between mycorrhizal colonization and plant performance in non-sterilized soils was not stronger for drought-exposed plants, and drought did not increase mycorrhizal colonization rates. While our study indicates a clearly positive effect of AMF on plant performance, our results therefore do not support earlier experiments showing that AMF benefit their hosts more under drought stress (Augé, 2001; Chareesri et al., 2020; Li et al., 2019). Interestingly, however, we did observe a positive effect of live soil communities on plant biomass allocation to roots in response to drought, which did not depend on species identity (Table S8). Positive impacts of AMF may partially explain this effect, but not for species of Poaceae and Brassicaceae, in which AMF colonization was limited. For these species, plant growth-promoting bacteria (Rubin et al., 2017), on which non-mycorrhizal plant species typically more strongly depend (Williams & de Vries, 2020), may have driven the positive effect of soil communities on plant biomass allocation to roots. Possibly, this enhanced biomass allocation to root growth, induced by soil-community presence, may be beneficial under continued or recurrent drought (Markesteijn & Poorter, 2009), but we did not test this. Overall, we thus conclude that drought-driven modifications of soil-community impacts on plant performance were subtle and did not consistently differ between alien and native plants.

We examined effects of soil-community presence and drought on native and alien plants grown in interspecific-, intraspecific- and the absence of competition, but—surprisingly—did not detect overall competition effects on shoot biomass (Table 1). Moreover, our results indicated that alien plant species did not have a competitive benefit over native plants when growing together, even not in the presence of a soil community. Possibly, by selecting con-familial alien and native plant species, we examined plant species that all possessed traits associated with high plant performance and abundance (van Kleunen et al., 2015, 2020), leading to overall similar responses to intraspecific competition, and reducing differences in competitive ability (Zhang & van Kleunen, 2019). Nevertheless, competition treatments did affect shoot biomass in species-specific ways, and these effects depended on soil-community presence (Table S2). In the presence of soil biota, most species exhibited the highest shoot biomass in the absence of competition, while competition effects on shoot biomass were subtle and strongly species-specific in the absence of soil biota. Possibly, negative effects of competition may have been less strong in the absence of soil biota due to reduced nutrient and soil-moisture limitation following the often lower plant biomass in the absence of plant-beneficial soil biota, or the expectedly higher nutrient availability caused by soil sterilization. However, as we did not examine root biomass of plants growing in competition, we cannot exclude that plants growing in competition allocated more resources to root growth to improve their competitive ability (Tang et al., 2022; Tilman, 1990), while maintaining similar shoot biomass levels. Should plants growing in competition indeed have allocated more resources to belowground biomass, total biomass measurements might have revealed more distinct effects of soil-community presence and soil moisture on interspecific competition between alien and native species.

To conclude, our study shows that naturalized alien plant species are more positively affected by soil communities than native plant species, but more negatively affected by the direct effects of drought. As such, our study does suggest that climate change-associated droughts weaken the competitive advantage that alien plants may have over native plants, for example due to reduced negative impacts by aboveground or belowground biota. However, alien and native plants did not differ in their responses to interactive effects of soil communities and drought, suggesting that soil biota will not mediate drought effects on native and alien plant performance. Yet, fully understanding the consequences of droughts for plant invasion dynamics also involves examining whether native and alien plant species differ in their responses to soil rewetting (Zhang et al., 2022) and examining whether droughts differently alter plant–soil feedback effects of native and alien plant species on succeeding conspecific individuals (Thakur et al., 2023). Our study furthermore indicates a key role for AMF as positive drivers of plant performance, but does not provide evidence that AMF alleviate plant drought stress or differently affect native and alien plant performance. Nevertheless, our results do show that soil-community presence supports plant resource allocation to root growth in response to drought, to some extent supporting previous research showing the importance of soil communities as mediators of plant responses to drought (de Vries et al., 2020). Overall, our study therefore underlines the need to incorporate plant–soil interactions in studies examining impacts of alien plants and climate change on terrestrial communities.

AUTHOR CONTRIBUTIONS

R.A.W. conceived the initial idea for the study. All authors contributed to study design. H.K.R. performed the greenhouse experiment and mycorrhizal analysis. Data analysis was performed by H.K.R. and R.A.W., with inputs from M.v.K. The manuscript was written by H.K.R. and R.A.W., with inputs from M.v.K.

ACKNOWLEDGEMENTS

We thank Werner Öri, Claudia Martin, Heinz Vahlenkamp and Otmar Ficht for technical assistance and Zhijie Zhang and Marc Stift for their advice on statistical analyses. Rutger A. Wilschut acknowledges funding from the Postdoc Talent Programme of the Wageningen Graduate Schools (WGS).

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

Biomass and mycorrhizal colonization data are publicly available from Figshare https://doi.org/10.6084/m9.figshare.26501671.v2 (Wilschut et al., 2024).

STATEMENT ON INCLUSION

The authors of this study all were affiliated to the same university at which the study was also performed. All authors were involved in the design of the study as well as in discussions on all subsequent phases of the research project, ensuring that their specific research interests and visions on project progress were fully considered.

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SUPPORTING INFORMATION

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

Supplementary information.

How to cite this article: Ruppert, H. K., van Kleunen, M., & Wilschut, R. A. (2024). Contrasting responses of naturalized alien and native plants to native soil biota and drought. *Functional Ecology*, *38*, 2421–2432. https://doi.org/10.1111/1365-2435.14643