Biol Invasions
https://doi.org/10.1007/s10530-022-02919-y

ORIGINAL PAPER

Invaders responded more positively to soil biota than native or noninvasive introduced species, consistent with enemy escape

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Received: 10 November 2021 / Accepted: 19 September 2022

Abstract Understanding the mechanisms governing biological invasions has implications for population dynamics, biodiversity, and community assembly. The enemy escape hypothesis posits that escape from enemies such as herbivores and predators that were limiting in the native range helps explain rapid spread in the introduced range. While the enemy escape hypothesis has been widely tested aboveground, data limitations have prevented comparisons of belowground mechanisms for invasive and noninvasive introduced species, which limits our understanding of why only some introduced species become invasive. We assessed the role of soil biota in driving plant invasions in a phylogenetic meta−analysis, incorporating phylogeny in the error structure of the models, and comparing live and sterilized conditioned soils. We found 29 studies and 396 effect size estimates across 103 species that compared live and sterilized soils. We found general positive effects of soil biota for plants (0.099, 95% CI = 0.0266, 0.1714), consistent with a role of soil mutualists. The effect size of soil biota among invaders was 3.2× higher than for natives, the strength of effects was weaker for older conditioning species with a longer introduced history, and enemy escape was stronger for distant relatives. In addition, invasive species had a weaker allocation tradeoff than natives. By demonstrating that the net effect of soil biota is more positive for invasive than native and noninvasive introduced species, weakens over time since introduction, and strengthens as phylogenetic distance increasing, we provide mechanistic insights into the considerable role of soil biota in biological invasions, consistent with the predictions of the enemy escape hypothesis.

Keywords Biotic resistance · Darwin's naturalization hypothesis · Enemy escape · Functional traits · Plant invasion · Soil biota

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10530-022-02919-y.

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Introduction

Studying the mechanisms leading to biological invasions contributes to our understanding of biodiversity and community assembly. Invasive species spread rapidly in the introduced range, while noninvasive

Published online: 27 September 2022

introduced species (sensu Burns 2004) might naturalize, but do not spread rapidly (Richardson et al. 2000). Mechanisms explaining plant invasiveness include many aboveground interactions, such as competition and herbivory (reviewed in Richardson and Pyšek 2006; Zou et al. 2008; Suwa and Louda 2012; Schultheis and MacGuigan 2018). Belowground interactions with soil microbes (i.e. "soil biota") are gaining increasing attention as possible drivers of invasiveness (Reinhart and Callaway 2006; Dawson and Schrama 2016; Bickford 2020). Until recently, few plant−soils studies were available to compare invasive with noninvasive introduced species or compare across times since introduction (reviewed in Crawford et al. 2019). Incorporating noninvasive introduced species answers the question: "why do some species succeed upon introduction while others do not?", generating mechanistic insight into the invasion process (e.g. Grotkopp et al. 2002; Burns 2004). Thus, it remains unknown whether soil biota effects differ for invasive, noninvasive, and native species or across time since introduction.

The soil biota, including soil pathogens and mutualists, are critical factors determining plant coexistence (Bever et al. 2015) and influencing plant invasions (Callaway et al. 2013). Plant−soil interaction studies generally use either a comparison of live soils to one another, as for pairwise plant−soil feedbacks, where each of two species is grown in conspecific and heterospecific soils (Bever et al. 1997) or compare live and sterilized soils (reviewed in Bardgett and Van Der Putten 2014). Pairwise plant−soil feedback metrics have the advantage of making a coexistence prediction (e.g. Anacker et al. 2014; Münzbergová and Šurinová 2015), and have been extensively reviewed (e.g. Kulmatiski et al. 2008; Crawford et al. 2019). Such live−live soil comparisons do not identify mechanisms in the soil instead treating the soil biota as a "black−box", where mechanisms are unidentified (Brinkman et al. 2010). Comparisons of live versus sterilized soils (e.g. Maron et al. 2014; Crawford and Knight 2017; Liu et al. 2020) have the potential disadvantage of artifacts of sterilization, but measure the net effects of soil biota and have the advantage of directly addressing mechanism by quantifying the relative importance of soil biota in isolation. To address the enemy escape hypothesis, a comparison of the net effects of soil biota using sterilization controls will address whether soil biota are more beneficial (or less costly) for invasive species. Thus, here we focus on the net effects of soil biota, rather than plant−soil feedbacks, *per se*, adding to a growth body of literature on the role of belowground mechanisms in biological invasions (e.g. Bever et al. 1997; Kulmatiski and Kardol 2008; Mehrabi and Tuck 2015; Crawford et al. 2019).

Net effects of soil biota are likely influenced by both enemy escape and mutualists simultaneously. The enemy escape hypothesis suggests that introduced species might grow faster without the limitations of their natural enemies (Keane and Crawley 2002). Tests for enemy escape have generally focused on herbivores (Hawkes 2007; Meijer et al. 2016; Mlynarek et al. 2017), rather than the effects of soil pathogens (Flory and Clay 2013; but see e.g. Dawson 2015; Dawson and Schrama 2016). Over time, the strength of enemy escape might weaken, as the introduced plant species spreads and encounters herbivores and pathogens, as new enemies become introduced (Hawkes 2007; Gruntman et al. 2017), or as the native soil organisms evolve to consume the invaders (Carlsson et al. 2009). Closely related plant species sharing pathogens might lead to more negative effects of soil biota for close relatives, or a "phylogenetic Janzen−Connell effect" (Liu et al. 2012; Sweet and Burns 2017), though whether escape from soil enemies is greater in soils conditioned by distant relatives in general is unknown (Crawford et al. 2019).

Not all introduced species might be equally predisposed to benefit from enemy escape, and functional traits might predict the performance of invasive species (Drenovsky et al. 2012; Murphy et al. 2016; Winkler et al. 2018), either because of preexisting function trait differences (Matzek 2012; Van Kleunen et al. 2010), plasticity (Davidson et al. 2011), or evolved differences in the introduced range (i.e. "evolution of increased competitive ability" EICA) (Callaway and Ridenour 2004, but see Felker−Quinn et al. 2013). Functional traits such as specific root length (SRL) and specific leaf area (SLA) indicate whether plants have a more resource acquisitive (i.e. higher SRL; higher SLA) or resource conservative (lower SRL; lower SLA) strategy (Reich 2014; Medeiros et al. 2017). If functional traits correlated with faster growth rate trade off with defense (Lemmermeyer et al. 2015), we predict traits associated with faster growth might correlate with enemy escape (Drenovsky et al. 2012; Winemiller et al. 2015).

In our phylogenetic meta−analysis, we calculated a log−response ratio (lnR) as contrasting performance in live and sterilized soils [ln(live)−ln(sterilized)] and explore how soil microbes might relate to plant invasiveness. We addressed the following questions. (1) Do invasive species differ from noninvasive introduced and native species in soil biota effects? If invasive species have more positive soil biota effects than noninvasive introduced species, this implicates escape from soil biota as a mechanism governing variation in invasion success. We further predicted that more recently introduced species might cultivate fewer pathogens overall (Hawkes 2007), leading to more positive lnR in the soils of more recent introductions. (2) Do functional traits correspond to soil biota effects? We predicted that a reduction in pathogens in invasive species would lead to a weaker tradeoff between growth and defense. In contrast, native species with a higher SLA or SRL might have a more negative response to soil biota, because those species that allocate more to growth might do so at a cost to allocation to defense (Lemmermeyer et al. 2015). (3) Do focal and conditioning status interact to influence soil biota effects? If soil biota contributes to biotic resistance, we predict invaders will have a more negative response to soils conditioned by natives than invasive species (Callaway et al. 2013). If conserved pathogens increase biotic resistance, we also predict a more negative effect size in the soils of congeners than more distant relatives (Darwin 1859; Daehler 2001; Diez et al. 2010).

Materials and methods

Literature search and data collection

We used a literature search of published ISI indexed journals (web of science) using search terms "plant−soil and feedback", "soil, feedback and experiment" or "plant, soil and transplant" (Kulmatiski et al. 2008), through 12 May 2020, and including all published papers referenced in previous meta−analyses (Kulmatiski et al. 2008; Suding et al. 2013) that met our criteria. A significant number of studies in this literature search use an experimental design that compares live and sterilized soils, a technique that many authors have called a "plant−soil feedback" experiment (sensu Brinkman et al. 2010). Note, however, that we are not quantifying plant−soil feedbacks here (sensu Bever et al. 1997; Crawford et al. 2019). In addition, we included data from our experiment (Liu et al. 2020). To be included in our meta−analysis, studies had to include (1) at least one focal plant species grown in at least one live soil, conditioned by a single species, so we aimed at the circumstance where a focal species grew in the live soil containing the soil biota associated with a single conditioning species. The soil could be under either manipulated (e.g. conditioned in the greenhouse or grown experimentally) or natural conditions. (2) There was a sterile soil treatment (e.g. autoclaved, gamma−irradiated or microwaved conditioned soils). If a study included other experimental manipulations that might alter soil microbial communities (e.g. fertilizer treatments or fungicide treatments), we only extracted the data under the non−manipulated treatment, excluding additional manipulations. For a study where there was no unmanipulated treatment, we collected the data from multiple treatment levels, keeping track of treatment levels in the database. If a study was conducted across different environments, we distinguished them by reporting their replicate sites. To prevent pseudoreplication, we then aggregated multiple measures per species following (Borenstein et al. 2009) (see "data aggregation" section below).

Soil biota effect size

To measure the effect of soil biota, we compared live and sterilized soil treatments. We recorded plant performance (e.g. total biomass) in live and sterile soils, and their respective sample sizes and standard errors, and used that data to calculate the log−response ratio (lnR) and its variance. For papers where the means and standard errors were available in graph form, we extracted this data using WebPlotDigitizer (Version 4.4) (Rohatgi 2020). In other cases, data was available directly in tables or from the authors. The lnR was calculated according to (Rosenberg et al. 2013: Chap. 6, Page 64) as natural log of mean performance in live soil (Y_{Live_soil}) minus the natural log of mean performance in sterile soil ($Y_{Sterile\_soil}$). A higher value of lnR suggests a better plant performance in the presence of soil biota.

$$\ln R = \ln(Y_{Live\_soil}) - \ln(Y_{Sterile\_soil}).$$

For some studies that reported inoculation effects, we did a mathematical transformation to get the corresponding lnR (e.g. Te Beest et al. 2009).

$$\ln R = \ln(1 + inoculation\_effect)$$

Plant invasiveness

We collected data on the native or invasive status of the focal and conditioning species and year when those introduced species were first introduced, either from the original publication, or from a search of the USDA Plants database (USDA 2021) and Global Compendium of Weeds (Randall 2017). We followed Richardson et al., (Richardson et al. 2000) in defining invasive taxa as those that had spread rapidly in their introduced range where the experiments were conducted. We made estimations for introduced year if the descriptions from published sources were vague. If a range of introduced year was offered, we took the median year as the introduced year for that species. In addition, if a very rough estimation was given, for example, 19th century or early 20th century, we recorded as 1850 or 1900 respectively. To keep consistency with published literature (e.g. Hawkes 2007; Diez et al. 2010; Gruntman et al. 2017), we report "years since introduction" from 2020. We report years since introduction for all introduced conditioning species; note that native species can respond to these conditioning species, but do not themselves have a year of introduction.

Soil handling approach

We recorded soil manipulation approaches such as soil inoculum type (e.g. soil or watery inoculum) and soil pooling strategy (pooled or unpooled). Soil pooling might dramatically influence both the direction and the magnitude when evaluating the soil microbial effects on plant performance (Peacher and Meiners 2020). Soil pooling is likely to overestimate local microbial mutualistic or antagonistic interactions when studying plant−microbial interactions (Peacher and Meiners 2020), and has been considered a form of psuedoreplication (e.g. Rinella and Reinhart 2018), though it is considered appropriate and necessary in some cases (Dukes et al. 2019; Peacher and Meiners 2020). We recorded the soil pooling information to determine whether it influenced our conclusions.

Plant functional traits

We requested plant functional traits including specific leaf area (SLA) (Trait ID: 3115, 3116 and 3117) and specific root length (SRL) (Trait ID: 1080) from TRY Plant Trait Database (Kattge et al. 2011). We requested trait data of our species from both public and restricted databases. We combined SLA data from three aforementioned databases and took the mean of SLA values for each species. Similarly, we calculated the mean of SRL.

Data aggregation

We aggregated some data rows to prevent psuedoreplication, when lnR was reported from both root and shoot biomass within the same study. We aggregated these multiple measures per species combination following (Borenstein et al. 2009). We took the mean for each pair of lnR as an aggregated lnR.

$$Y = \left(\overline{Y}_1 + \overline{Y}_2\right)/2$$

We then calculated an aggregated variance assuming a correlation ratio between root and shoot as 1 (r = 1) so that we maximized the possible variance during aggregation.

$$V_Y = (V_{Y1} + V_{Y2} + 2r\sqrt{V_{Y1}}\sqrt{V_{Y2}})/4$$

All data analyses presented were on this aggregated lnR and its variance.

Phylogeny construction and phylogenetic analysis

We constructed the phylogenetic tree through an established phylogeny super tree (Zanne et al. 2014). Specifically, we merged our full species list with the super tree in R (see "data analysis" below), so that we extracted the tips and branches of our included

species and saved the merged tree as our phylogeny. Only three species could not be found in the super tree: *Cardamine laciniata*, *Cardamine maxima*, and *Heliopsis helianthoides*. We added these three species into the phylogeny using both taxonomic and phylogenetic information (Urbatsch and Jansen 1995). Phylogenetic pairwise distances across all species were calculated with function cophenetic.phylo from the "ape" package (Paradis and Schliep 2019).

Model estimation and analysis

We estimated heterogeneity for our dataset following recommendations in (Nakagawa and Santos 2012; Senior et al. 2016). For all of the analyses, we used mixed−effect phylogenetic meta−analyses to analyze the effect size of soil biota. As in standard meta−analysis, responses were weighted by inverse of the variance, such that estimates with greater precision are more heavily weighted (Koricheva et al. 2013). The models were coded with rma.mv function from package metafor R (Viechtbauer 2010a, b). Compared with traditional generalized linear models, ours additionally included the phylogeny as an error structure and a random effect of focal plant species, because the data contained multiple effect sizes per species. Thus, our meta−analyses are all "phylogenetic", with phylogeny included in the error structure (Viechtbauer 2010a, b). We used ANOVA to test the statistical significance of focal interactions. If the interactions were significant, we then conducted post-hoc comparisons among means with a Holm adjustment for multiple comparisons. If the interactions included continuous variables (e.g. SLA or SRL), we subset and separately tested each correlation within each category of focal plant invasiveness (i.e. native, invasive or noninvasive).

In addition to phylogenetic analyses, the averaged estimates of lnR and their 95% Confidence Interval (95% CI) were calculated to test whether lnR was significantly different from 0 (either higher or lower than 0) by checking whether 95% CI overlapped with 0. We calculated 95% CI for appropriate subsets of focal categories to test the hypotheses of enemy escape, biotic resistance and Darwin's naturalization.

To address the question: (1) Do invader species differ from noninvasive introduced and native species in soil biota effects? We analyzed the correlation between the soil biota effect (lnR) and each of these including interactions: focal invasiveness status, years since introduction, phylogenetic distance, or taxonomic distance (i.e. conspecific, congeneric, confamilial, and distant). Taxonomic distance was defined as the distance between the focal (responding) species and the species that conditioned the soil. For example, a species might be responding to conspecific soils or heterospecific soils. Also, we explored the potential effect of methodological covariates on enemy escape. The 95% CI analysis quantified the soil biota effect (lnR) of invasive, native and noninvasive species, and detected whether the soil biota effect was significantly positive or negative. In addition, 95% CI analysis on subsets of focal invasiveness and taxonomic distance tested whether invaders benefited from soils conditioned by distant relatives.

To address the question: (2) Do functional traits correspond to soil biota effects? We analyzed the soil biota effect (lnR) as a function of the interaction between focal invasiveness status and trait collected from the TRY database (i.e. SLA and SRL).

To address the question: (3) Do focal and conditioning status interact to influence soil biota effects? We incorporated the phylogenetic distance between focal species and conditioning species. Given a lack of statistical power to include noninvasive species (no invasive species and noninvasive species growing in heterospecific noninvasive soil), we dropped noninvasive species. We modeled the soil biota effect (lnR) as a function of focal invasiveness, conditioning invasiveness, taxonomic distance and their three−way interaction. We followed this global model with contrasts within the three−way interaction. In addition, the 95% CI analysis estimated the averaged soil biota effect (lnR) of each subset of focal and conditioning invasiveness. This detected the interaction of focal and conditioning invasiveness status, and whether or not invaders benefited from soils conditioned by native species.

Results

Our literature search generated 396 measures of the soil biota effect (lnR) across 103 focal species (76 native, 15 invasive and 13 noninvasive) and 88 conditioning species (58 native, 18 invasive and 12 noninvasive) from 29 papers (Table S1). One focal

species *Solidago canadensis* is native in 2 studies in North America, while it is invasive in 1 study in East Asia (Table S1). We used the soil biota effect (lnR) to measure soil microbial effects to plants. The mean effect size was lnR = 0.099, which was significantly positive (95% CI= [0.0266, 0.1714]), indicating that plants generally performed better in live soils than they did in sterile soils.

The preliminary test showed 97% of total variance was due to heterogeneity among estimates ($I^2 = 97.82$; Q (df = 374) = 4460.6290, $P < 0.0001$). The median of the number of estimates per reference was 2 ± 0.5, with a range from 1 to 24. For 36 out of 103 focal species, they come from a single reference, supporting our use of a model without the random effect of reference (but see Appendix 1 for the alternative models with a random effect of reference, Table AS1).

(1) *Do invasive species differ from noninvasive introduced and native species in soil biota effects?*

The effect of "focal plant invasiveness" was a significant predictor of the soil biota effect (lnR) (QM (df = 2) = 289.63, $P < 0.0001$). The soil biota effect (lnR) among invasive species was significantly 3.2× higher than that among native species (Table S2, Fig. 1a). The soil biota effect (lnR) of invasive species was also significantly higher than that of noninvasive species (Table S2). However, we did not find a significant difference of the soil biota effect (lnR) between native and noninvasive species (Table S2). The 95% CI indicated that native species had a significantly positive soil biota effect (lnR), while lnR for invasive and noninvasive species were not significantly different from 0 (Table 1a).

Invasive and native species responded differently to phylogenetic distance from the conditioning species (QM (df = 2) = 108.8703, $P < 0.0001$). Invasive species showed a positive correlation between the soil biota effect (lnR) and phylogenetic distance (Estimate = 0.0017 ± 0.0001, $P < 0.0001$), where invasive species had a higher lnR when they grew in the soil from distant species (Fig. 1b). However, neither native (Estimate = 0.0001 ± 0.0001, $P = 0.3303$) nor noninvasive species (Estimate = 0.0013 ± 0.0010, $P = 0.1926$) showed any significant correlation between the soil biota effect (lnR) and phylogenetic distance.

In addition, we tested the soil biota effect (lnR) as a function of focal invasiveness, taxonomic distance (i.e. conspecific, congeneric, confamilial, and distant), and their interaction, to determine at what taxonomic scale the phylogenetic distance effect occurred. The interaction of focal invasiveness and taxonomic distance was also significant (QM (df = 6) = 125.6365, $P < 0.0001$). In a comparison across taxonomic distances, we also found that invasive species had a more positive response to soil biota in soils from more distant relatives (Table S3a), whereas native species did not generally differ across taxonomic distances in native soils (Table S3b). Further, consistent with our alternative analysis, we also found that invasive species generally responded more positively to soil biota than their native relatives (Table S3c). The 95% CI analysis showed that invaders benefited from conspecific soils, while they encountered a negative soil biota effect from invader congeneric soils (Table 1b). The soil biota effect (lnR) of native species showed a significantly positive soil biota effect in distant soils, while they were not different from 0 at other taxonomic distance scales (Table 1b).

We found no significance of years since introduction of focal species (QM (df = 1) = 0.4684, $P = 0.4937$), while we detected a significant effect of years since introduction of conditioning species (QM (df = 2) = 12.6281, $P = 0.0018$). We found the soil biota effect (lnR) of native and invasive species were both negatively correlated with the years since introduction of conditioning species, such that plants had a more positive soil microbial effect when growing in the soil conditioned by more recently introduced species (Fig. 1c). Among native, invasive and noninvasive species, invasive species had a more negative correlation (Estimate= -0.0054 ± 0.0021, $P = 0.0098$) than native species (Estimate= -0.0028 ± 0.0006, $P < 0.0001$), while noninvasive species showed no significant correlation (Estimate = 0.0029 ± 0.0042, $P = 0.4876$).

We tested the interaction of focal plant invasiveness and soil pooling approach (e.g. pooled or unpooled) and found a marginally significant interaction between pooling and invasiveness on the soil biota effect (lnR) (QM (df = 2) = 5.3115, $P = 0.0702$) and a significant main effect of pooling (Estimate = 0.6734 ± 0.2264, $P = 0.0029$). Plants growing

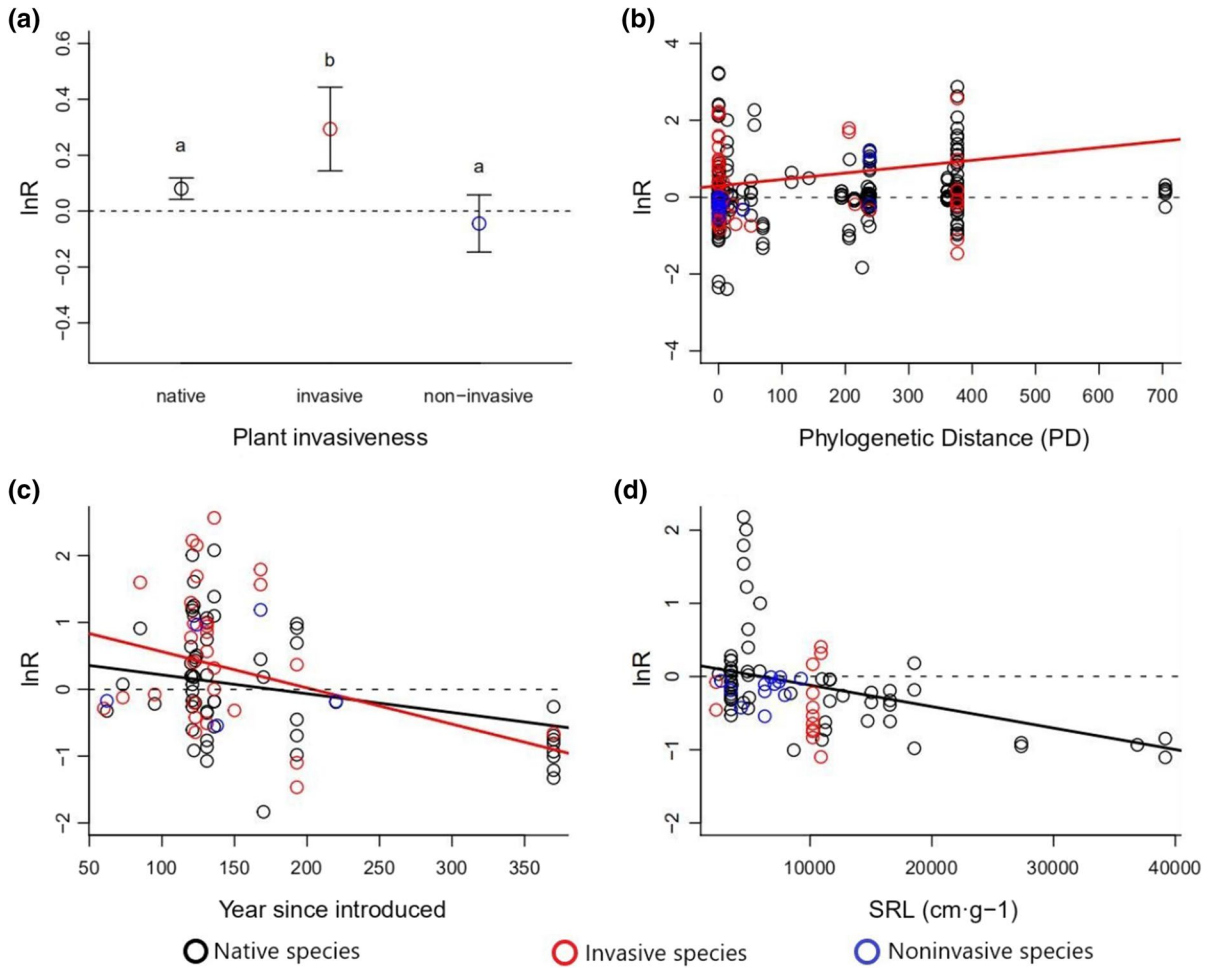

Fig. 1 The log−response ratio (lnR) to soil biota ([ln(live)−ln(sterile)] for native, invasive and noninvasive introduced species. A positive log−response ratio indicates that soil biota benefits plant growth. **a** Contrast across plant invasiveness (Means ± 1 SE), where means that share a letter are not significantly different in posthoc comparisons; **b** versus phylogenetic distance; **c** versus the year since each *conditioning* species was introduced; note that native focal (responding) species are responding to conditioning introduced species, each of which has a time since introduction. **d** versus specific root length (SRL). Regression lines are only shown for significant relationships

in unpooled soil (Estimate = 0.1128 ± 0.0486) generated a higher the soil biota effect (lnR) than those in pooled soil (Estimate = 0.0192 ± 0.0542). We detected no significant interaction of plant invasiveness and inoculum type (QM (df = 1) = 2.0059, $P = 0.1567$).

(2) *Do functional traits correspond to soil biota effects?* We included an interaction of focal plant invasiveness and each of two functional traits (SLA and SRL) into our mixed−effect phylogenetic meta−analysis models. We found no significant interaction of plant invasiveness and SLA (QM (df = 2) = 2.4917, $P = 0.2877$). We found the main effect of SLA had a marginally significantly negative correlation with the soil biota effect (lnR) (Estimate= − 0.0691 ± 0.0377, $P = 0.0667$).

We tested SRL within the interaction and found a significant interaction between invasiveness and SRL on the soil biota effect (lnR) (QM (df = 2) = 15.5277, $P = 0.0004$). The soil biota effect (lnR) of native species had a significantly negative correlation with SRL (Estimate = − (2.93 ± 0.61) × 10^5, $P < 0.0001$),

Table 1 The average estimate and its 95% CI of each subset of focal factors or combinations. This methodology tests hypotheses of (a) Enemy Escape, (b) Biotic Resistance and (c) Darwin's naturalization. Estimates in bold are significantly different from 0 (not overlapping with 0)

Subset	Estimate	95% CI− (Lower, Upper)
(a) Hypothesis: Invasive species might escape from soil enemies in soil biota; therefore, they might not have a significantly negative lnR.		
Focal species: Native	0.08046	(0.00514, 0.15578)
Focal species: Invasive	0.29356	(− 0.00866, 0.59578)
Focal species: Noninvasive	−0.04442	(−0.26017, 0.17132)
(a) Analysis: The lnR of Invasive species are not significantly different from 0, consistent with a lack of suppression by enemies in the soil. In addition, native species have a positive lnR, suggesting that they are benefiting from soil biota.		
(b) Hypothesis: Invasive species might benefit from taxonomically distant relatives, consistent with Darwin's naturalization hypothesis; therefore, invasive species might have a significantly positive lnR in soils from distant conditioning species.		
Focal species: Invasive Taxonomic Novelty: Conspecific	0.49601	(0.08390, 0.90811)
Focal species: Invasive Taxonomic Novelty: Congeneric	−0.57733	(−0.81688, −0.33779)
Focal species: Invasive Taxonomic Novelty: Confamilial	−0.11453	(−1.56964, 1.34057)
Focal species: Invasive Taxonomic Novelty: Distant	0.44011	(−0.23737, 1.11759)
Focal species: Native Taxonomic Novelty: Conspecific	0.01543	(−0.15047, 0.18133)
Focal species: Native Taxonomic Novelty: Congeneric	0.15739	(−0.19795, 0.51274)
Focal species: Native Taxonomic Novelty: Confamilial	−0.03863	(−0.31714, 0.23988)
Focal species: Native Taxonomic Novelty: Distant	0.12706	(0.04265, 0.21147)
Focal species: Noninvasive Taxonomic Novelty: Conspecific	−0.17033	(−0.27709, −0.06357)
Focal species: Noninvasive Taxonomic Novelty: Congeneric	−0.19010	(−1.23963, 0.85943)
Focal species: Noninvasive Taxonomic Novelty: Distant	0.65007	(−1.20618, 2.50632)
(b) Analysis: Invasive species have an insignificantly positive lnR in distant soils. The soil biota effect of invasive species is positive in their own soils (conspecific), but it is negative in soils from their congeners. Native species show a positive lnR in distant soils, while noninvasive introduced species have a negative lnR in distant soils.		
(c) Hypothesis: Invasive species might have a positive response to invader soil biota, if invaders facilitate other invaders. Invasive species might encounter a belowground biotic resistance from native species; therefore, they might have a negative lnR in native soils.		
Focal species: Invasive Conditioning species: Invasive	0.52705	(0.12919, 0.92492)
Focal species: Invasive Conditioning species: Native	−0.12964	(−0.55250, 0.29321)
Focal species: Native Conditioning species: Native	0.07371	(−0.00543, 0.15286)
Focal species: Native Conditioning species: Invasive	0.12147	(−0.09871, 0.34165)
Focal species: Native Conditioning species: Noninvasive	−0.25940	(−1.10309, 0.58429)
Focal species: Noninvasive Conditioning species: Native	−0.22725	(−0.37731, −0.07719)

Table 1 (continued)

Subset	Estimate	95% CI− (Lower, Upper)
Focal species: Noninvasive Conditioning species: Noninvasive	−0.17033	(−0.27709, −0.06357)
(c1) Analysis: The soil biota from invasive species might facilitate subsequent invasive species through positive effects of soil biota. Invasive species do not have a significantly negative soil biota effect in native soils, inconsistent with biotic resistance. Noninvasive species show significantly negative lnR in both native and noninvasive soils, which might explain the weak invasiveness of these introduced species.		
Focal species: Invasive Conditioning species: Native Taxonomic Novelty: Congeneric	−0.57733	(−0.81688, −0.33779)
(c2) Analysis: Invasive species had a significantly negative lnR in the soils from their native congeners. Native congeneric soil biota might suppress the invaders.		

while neither invasive (Estimate = − (2.09 ± 3.78) × 10^5, $P = 0.5807$) nor noninvasive species (Estimate = − (1.64 ± 1.37) × 10^5, $P = 0.2309$) were significant in such a correlation (Fig. 1d).

(3) *Do focal and conditioning status interact to influence soil biota effects?* To test biotic resistance predictions, we included an interaction between focal plant invasiveness, conditioning plant invasiveness, and taxonomic scale. The model showed a significant three−way interaction (QM (df = 1) = 13.4848, $P = 0.0002$). We found invasive species had more negative soil biota effect (lnR) in native congeneric and confamilial soils than native distant soils (Table S4). The 95% CI analysis reported that invasive species responded positively to soil biota from their own species and other invasive species (Table 1b, c). The soil biota effect (lnR) of native species not significantly different from 0, for native, invasive and noninvasive conditioning species (Table 1c). When growing in native soils, invaders responded negatively to soil biota from native congeners, while the response to native distant relatives' soils was not different from zero (Table 1c).

Discussion

While numerous studies have found evidence for enemy escape aboveground as a possible driver of biological invasions (reviewed in Liu and Stiling 2006; Hawkes 2007; Bajwa et al. 2016), we present a phylogenetic meta−analysis to add on the growing understanding of belowground soil biota effects. We find results consistent with predictions of enemy escape belowground combined with probable benefits of mutualists. Our comparison of invasive with noninvasive introduced species tests enemy escape as a mechanism governing the differential success of introduced species (sensu Grotkopp et al. 2002; Burns 2004), suggesting that more invasive species may be of greater escape from belowground enemies. Consistent with previous studies of escape from herbivore enemies (Hawkes 2007) and plant soil feedbacks (Diez et al. 2010), enemy escape was weaker for older conditioning species (those introduced at an earlier data) in our study. Native species responding to this conditioning effect similarly experience more positive responses to soil biota when the conditioning introduced species had been in the introduced range for longer. Further, benefits of soil biota were greater in the soils of distant relatives (both native and introduced), suggesting that conservation of soil pathogens (Parker and Gilbert 2004; Liu et al. 2012; Sweet and Burns 2017) may enhance the success of phylogenetically distant invaders (Diez et al. 2010; El−Barougy et al. 2020). We also found evidence consistent with growth−defense tradeoffs for native species (Lemmermeyer et al. 2015), but not for introduced species, consistent with enemy escape reducing allocation constraints on invader growth (but see Heckman et al. 2019). Further, we found evidence that pooled soil might exaggerate negative soil biota effects by exaggerating the effects of rare soil pathogens (Smith-Ramesh and Reynolds 2017).

In contrast with soil biota effects, plant−soil feedbacks measure the relative plant performance in home versus away soils, and pairwise plant−soil feedbacks indicate the contrast of plant additive performance in their own soils versus each other's soils (Bever et al. 1997; Bever 2003; Van der Putten et al. 2013; Crawford et al. 2019). Reviews of plant−soil feedbacks also suggest that distant relatives might be more likely to escape from enemies (Crawford et al. 2019). Compared with native−native species pairs, nonnative species generally have weaker (less negative) plant−soil feedbacks (Crawford et al. 2019), also consistent with escape from soil pathogens. Our work adds to this by isolating the effects of soil biota compared with sterilized soils, quantifying time since introduction, and comparing introduced invasive with noninvasive species, all of which are possible because of a substantial number of recent papers.

Darwin proposed that phylogenetically distant relatives might become more invasive upon introduction (Darwin 1859), a pattern that has been called "Darwin's naturalization hypothesis" (Daehler 2001). This pattern has been found in some empirical studies (e.g. Strauss et al. 2006). However, other studies found the opposite pattern (e.g. Daehler 2001; Li et al. 2015), a contradiction that has been called Darwin's naturalization conundrum, and contrasting patterns might be detected with different measures of invasion success. Invader establishment may be greater with closer phylogenetic distance (e.g. due to niche conservation), whereas invader performance (e.g. biomass) may be greater with further phylogenetic distance (e.g. due to escape from conserved pathogens) (Li et al. 2015). Some reviews suggest that phylogenetic relatedness does not correlate with plant−soil feedbacks (Mehrabi and Tuck 2015; but see Crawford et al. 2019), however, phylogeny is a strong predictor of soil biota effects in some studies (Brandt et al. 2009). Our synthesis focused on individual invader performance measures through a comparison of plant performance with live and sterile soil microbial communities, consistent with Li et al.,'s finding of potential greater performance at greater phylogenetic distances (Li et al. 2015). Here, we find general evidence that more phylogenetically distant invaders experience more positive responses to soil biota (Fig. 2), which might act as a mechanism explaining Darwin's naturalization hypothesis (Diez et al. 2010; but see Zheng et al. 2018).

Escape from soil pathogens is not the only possible mechanism for the soil biota effects observed here. A whole soil inoculation methodology cannot separate soil mutualists from soil enemies, so our meta−analysis is unable to tease apart these types of mechanisms. In addition, sterilization methods can have artifacts (Wolf et al. 1989; Wolf and Skipper 1994), potentially leading to greater performance in some sterilized soils (Mahmood et al. 2014), though small amounts of inoculant, as in most of the studies used here, are thought to minimize this artifact (Brinkman et al. 2010). Further, mycorrhizal fungi and other soil mutualists can negatively influence plant performance (Johnson et al. 1997), though mycorrhizal mutualists are unlikely to lead to the patterns we found in soil biotic effects over time or phylogenetic distance (Diez et al. 2010). The generally positive effect size observed here is consistent with a role for mutualists, especially for invaders.

We also explored plant functional traits. As expected, invasive species might escape their soil pathogens, and thus their growth might no longer be constrained by the tradeoffs with defense allocation (Lemmermeyer et al. 2015), although the difference of statistical power between our native and invasive samples might limit our ability to detect the tradeoffs across invaders. In contrast to SRL, SLA did not interact with plant invasive status to influence soil biota effects, but might correlate with invasiveness for other reasons, i.e. high SLA might reflect a faster growth strategy overall in invaders (Burns 2006).

We found evidence for a congeneric biotic resistance, where performance of invasive species might be constrained by native congeners because of competition or shared soil pathogens, consistent with the literature among terrestrial plant−based studies (Jeschke et al. 2012; but see Levine et al. 2004). Biotic resistance has implications for native restoration following invader removal. Because congener's soils suppress invader performance, planting native congeners after removing invaders might reduce re−invasion.

Plant invasions are likely a result of multiple mechanisms, including enemy escape (Keane and Crawley 2002; Bajwa et al. 2016). Here, we demonstrate that soil biota effects are generally more positive for invasive than noninvasive species, implicating enemy escape belowground as a mechanism governing difference in invasion success amongst introduced species. Prior meta−analysis finds invasive species

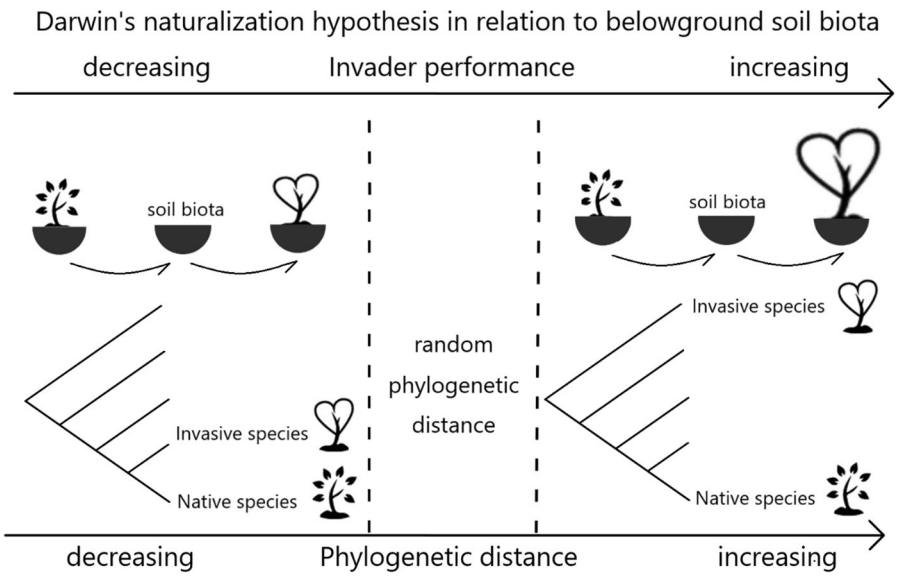

Fig. 2 Conceptual diagram of species naturalization and phylogenetic distance. The soil biota from distantly related native species could benefit the growth of invasive species, consistent with the Darwin's naturalization hypothesis. We find greater belowground enemy escape in the soils of distant relatives. Left panel shows a pair of closely related native and invasive species, corresponding to a moderate performance of the invader (negative or neutral lnR). Right panel depicts a pair of distantly related native and invasive species, corresponding to an increased performance of invaders (more positive lnR)

are not different from native species in arbuscular mycorrhizal colonization rate but differ in arbuscular mycorrhizal fungal community composition (Bunn et al. 2015), suggesting that differences in community composition could drive some of the effects. Further, the strength of such effects might attenuate over time, and this analysis provides a test of this prediction belowground. Our results also add to a growing body of evidence that phylogenetically distant invaders may benefit from soil mutualists and escape from conserved pathogens (Kempel et al. 2018; Crawford et al. 2019). Mechanistic studies of enemy escape are still needed to identify soil biota communities and compare stages of invasion (Li et al. 2015).

Acknowledgements We thank the Gaurav Kandlikar, Robin Snyder, Karen Abbott, the Ecology and Evolution reading group and the Burns lab group at Case Western Reserve University for constructive comments on this paper. Thanks also for Nicholas Prewett for contributions to data collection.

Author's contribution JHB, Y−LZ and YL contributed to the study conception and design. Material preparation, data collection and analysis were performed by YL, Y−LZ, LVJ and JHB. The first draft of the manuscript was written by Yu Liu and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding The authors declare that no funds, grants, or other support were received during the preparation of this manuscript.

Data availability We archived the data and R code for analysis with the Open Science Framework (available for review at: https://osf.io/p7wvq/?view_only=17030392d46544e5bc8294b0dea63a23).

Declarations

Conflict of Interests The authors have no relevant financial or non−financial interests to disclose.

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