REVIEW AND SYNTHESIS

Invasive plants differentially affect soil biota through litter and rhizosphere pathways: a meta-analysis

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Abstract

Invasive plants affect soil biota through litter and rhizosphere inputs, but the direction and magnitude of these effects are variable. We conducted a meta-analysis to examine the different effects of litter and rhizosphere of invasive plants on soil communities and nutrient cycling. Our results showed that invasive plants increased bacterial biomass by 16%, detritivore abundance by 119% and microbivore abundance by 89% through litter pathway. In the rhizosphere, invasive plants reduced bacterial biomass by 12%, herbivore abundance by 55% and predator abundance by 52%, but increased AM fungal biomass by 36%. Moreover, CO_2 efflux, N mineralisation rate and enzyme activities were all higher in invasive than native rhizosphere soils. These findings indicate that invasive plants may support more decomposers that in turn stimulate nutrient release via litter effect, and enhance nutrient uptake by reducing root grazing but forming more symbioses in the rhizosphere. Thus, we hypothesise that litter- and root-based loops are probably linked to generate positive feedback of invaders on soil systems through stimulating nutrient cycling, consequently facilitating plant invasion. Our findings from limited cases with diverse contexts suggest that more studies are needed to differentiate litter and rhizosphere effects within single systems to better understand invasive plant-soil interactions.

Keywords

Biological invasions, trophic groups, nutrient cycling, effect size, above-belowground interactions, plant-soil feedback.

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INTRODUCTION

Plant invasion is an important component of ongoing global change and can potentially alter the structure and functions of recipient ecosystems (Vitousek *et al.* 1997; Ehrenfeld 2010; Ricciardi *et al.* 2017). Many studies have examined the effects of plant invasion on terrestrial ecosystems focusing mainly on their aboveground components, and found that invasive plants often increase primary productivity and litter input, and suppress the growth of native plants, altering the diversity of native plant communities (Ehrenfeld 2010; Vilà *et al.* 2011). Because soil biota play vital roles in shaping plant communities and functioning of terrestrial ecosystems (Wardle *et al.* 2004), more attention has recently been directed towards assessing invasion impacts on soil biota and their potential feedbacks to plant invasion (Callaway *et al.* 2004; Reinhart & Callaway 2006; Inderjit & van der Putten 2010; Dawson & Schrama 2016). Most studies have found that the effects of invasive plants on the diversity and abundance of soil communities, both the directions and magnitudes, are case-specific (Belnap & Phillips 2001; Kourtev *et al.* 2003; Callaway *et al.*

2004). Vilà *et al.* (2011) synthesised the ecological impacts of plant invasion and found that invasive plants generally reduce the abundance of animal species, but have varying effects on their diversity. In contrast, Meisner *et al.* (2014) analysed the effects on the below-ground subsystems and showed that invaders favour invertebrates and nematodes, and have neutral effects on soil bacteria and fungi. These uncertainties highlight the need to carefully re-examine invasion effects on multiple trophic groups of soil biota and their functions (Ricciardi *et al.* 2017).

Soil biota play pivotal roles in modulating primary production by controlling decomposition and nutrient availability, as well as affecting root grazing and plant nutrient uptake (Wardle *et al.* 2004; Bardgett & Wardle 2010). Invasive plants may interrupt interactions between soil communities and native plants, consequently driving invasion success (Reinhart & Callaway 2006; Suding *et al.* 2013; Dawson & Schrama 2016; Ricciardi *et al.* 2017). The interruptions act mainly through two pathways: litter effect through modifications of detritus inputs and the physical environment, and rhizosphere effect through modulations of root exudation and root-biota

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interactions (Wolfe & Klironomos 2005). Although there are exceptions (e.g. Ehrenfeld *et al.* 2001; Jo *et al.* 2016), most successful invaders produce more litter that often decomposes faster than litter of native plants, providing more resources to decomposers (Ehrenfeld 2003; Prescott & Zukswert 2016). Alterations in the amount and palatability of detritus impact soil organisms including detritivores, bacterivores and fungivores (Reinhart & VandeVoort 2006; Bastow *et al.* 2008; Wolkovich *et al.* 2009). Moreover, changes of litter quantity and quality can modify the habitat heterogeneity and properties (e.g. soil moisture, pH or light), which affect the performances of soil biota (Kappes *et al.* 2007; McGrath & Binkley 2009; Robson *et al.* 2009; Wolkovich 2010). In turn, decomposers, as well as microbivores, can liberate nutrients locked in organic matters and in microbes via grazing on soil microbes and stimulating the turnover of microbes, potentially increasing nutrient availability for plants (Anderson *et al.* 1983; Ingham *et al.* 1985; Bonkowski 2004; Moore *et al.* 2004; Wardle *et al.* 2004).

At the same time, living roots function as an important driver for soil communities and ecosystem processes through provision of carbon sources for microbes while competing for nutrients or even water with microbes (Kaye & Hart 1997; Högberg *et al.* 2001; Pollierer *et al.* 2007; Bardgett *et al.* 2014). The root tissues, root exudates and leakages of some plant invaders can be different from those of natives, which cause rhizosphere effects on soil biota in the invaded systems (Wolfe & Klironomos 2005; Coats & Rumpho 2014). Invasive plants can produce distinct organic acids, allelochemicals and hormones, disrupting the structure of soil microbial communities in the rhizosphere and altering patterns of nutrient cycling that favour the invasive plants (Kourtev *et al.* 2002; Blank & Young 2004; Caldwell 2005; Lankau 2012; Morris *et al.* 2016). In particular, root exudates from some invasive species contain allelopathic compounds that may be detrimental to some components of soil biota (Callaway & Ridenour 2004; Lankau 2012). The alternations of soil microbial communities that regulate nutrient availability in soil may feedback positively to the growth of invasive plants, probably through affecting their ability of exploring resource and nutrients (Dawson *et al.* 2012; Schrama & Bardgett 2016). In the new habitats, invasive plants often encounter few soil-borne pathogens or root herbivores, as the result of enemy release, thereby gaining competitive advantages over native plants (van der Putten *et al.* 2005; Reinhart *et al.* 2010; Morriën *et al.* 2012). Besides, roots of invasive plants enhance or reduce their mutualistic associations with different mycorrhizal fungi or N-fixing bacteria (Jin *et al.* 2004; Reinhart & Callaway 2006; Pringle *et al.* 2009; Vogelsang & Bever 2009; Sun & He 2010), which potentially feedback to plant invasion by enhancing N uptake of invaders (Pringle *et al.* 2009) or by lowering the dependence of plant invaders on arbuscular mycorrhizal fungi (AMF) compared to natives (Vogelsang & Bever 2009).

Hence, the litter and rhizosphere of an invasive plant may have different, even contrasting effects on specific species or trophic groups of soil biota (Elgersma *et al.* 2011), obscuring the general picture and precluding us from understanding the mechanisms by which the invasive plants interact with soil biota. Considering that different groups of soil biota play distinctive roles in soil nutrient cycling and plant growth (Wardle *et al.* 2004), differentiating litter and rhizosphere effects of invasive plants on specific components of soil biota may provide new insights into the underlying mechanisms of plant invasion effects. Yet, no synthesis has been conducted to specifically tease apart litter and rhizosphere effects on multiple trophic groups of soil biota.

In this study, we undertook a global synthesis to assess the effects of plant invasion on different trophic groups of soil biota and their functions using meta-analysis. In particular, we differentiated the effects of litter and rhizosphere on soil biota in an attempt to better ascertain the potential mechanisms involved in invasions and identify the possible linkages between these two pathways. We tested the following three hypotheses. First, invasive plants increase the abundance of decomposers and support a more biodiverse food web through the litter pathway, which in turn increases nutrient release or/and mineralisation. Second, the living roots of plant invaders attract fewer root grazers but more symbiotic soil organisms while outcompeting microbes in the rhizosphere, which is likely to be beneficial to nutrient uptake of roots. Third, litter and rhizosphere effects of invasive plants are linked through enhanced nutrient cycling, which jointly determine the net impacts of plant invasion on soil ecosystems.

MATERIAL AND METHODS

Literature search and data extraction

We conducted a literature search on the Web of Science on 03 February 2017 without restriction on publication year, using the following two search term combinations: (litter OR debris OR residues) AND (plant invas* OR alien plant OR exotic plant) AND (soil community OR soil biota OR soil fauna OR soil invertebrate OR soil trophic OR soil microb* OR soil C cycle OR soil N cycle); (living root OR root exudates OR rhizosphere* OR rhizodepositi*) AND (plant invas* OR alien plant OR exotic plant) AND (soil community OR soil biota OR soil fauna OR soil invertebrate OR soil trophic OR soil microb* OR soil C cycle OR soil N cycle). These two search combinations were used to search articles on the litter and rhizosphere effects of invasive plants on soil biota and their functions respectively. Papers were also surveyed based on the reference lists in the relevant articles (including reviews). Therefore, we believe that our searches should have achieved a relatively good coverage of the literature on litter and rhizosphere effects of invasive plants on soil biota, not restricted to publications indexed in Web of Science.

In this meta-analysis, we focused on studies that compared the impacts of litter or/and rhizosphere on soil biota between invasive and co-occurring native plants. The invasion impacts on soil biota were classified into four groups (soil microbes, soil fauna, C and N cycle) including 18 specific variables: biomass of total microbes, bacteria, fungi and AMF, microbial biomass carbon (MBC), abundance of soil invertebrates, herbivores, detritivores, microbivores and predators, richness of soil fauna, CO_2 efflux, N mineralisation and nitrification rate, NH_4^+ and NO_3^- concentrations and enzyme activities related to C and N cycles. In our analysis, the soil invertebrates were

classified into four major groups, i.e. herbivores, detritivores, microbivores (including bacterivores and fungivores) and predators. The classification of each faunal group in the assessed studies was derived from the descriptions of the original authors. For some studies that did not indicate the feeding habits of soil fauna directly, we also surveyed other peer-reviewed publications to confirm their trophic attributes.

Each article was examined to evaluate if its data met the following criteria of selection. (1) Only studies examining litter and/or rhizosphere effect of invasive plants on biomass, abundances or/and functions of soil biota were included. Specifically, litter effect of invasive plants in our analysis referred to the differences in soil biota between plant invaders and natives induced by litter. Most studies examined litter effect by burying litter (or litterbags) of invasive and native plants in the soil or on the soil surface. The rhizosphere effect on soil biota comes from root tissues, root exudates and leakages of invasive plants, and the relevant experiments are usually conducted by planting invasive and native plants in the greenhouse. Since the plant materials (including litter) were picked out from the soil in advance, these studies only examined rhizosphere effect of invasive plants. Studies that examined the whole-invasive plant effects (i.e. litter and rhizosphere effects are mixed) were excluded. (2) Studies comparing the differences of soil biota under the same plant species between the invaded and native soils were excluded. Therefore, papers which studied home-field advantages of soil communities were not included. (3) Non-experimental studies (such as modelling and reviews) were excluded. (4) Studies with isotopic data without abundance, biomass or richness of soil biota were excluded. (5) Studies in which fauna was neither collected from soil ground nor buried litter (such as rivers, leaves and stems) were excluded. (6) If the invasive plant litter was buried in the invaded habitats, data were excluded to avoid the interference of rhizosphere effects from invasive plants. For litter studies conducted only in the non-invaded habitats, there was no rhizosphere effect from invasive plants. These studies were also included to examine the litter effect. (7) If a response variable was measured at different times, only data from the last time were considered. (8) Data with replicates (n) smaller than two or if replication was not reported were excluded. (9) Data without statistical variation were excluded. (10) If a study had other manipulations (e.g. N addition, CO_2 elevation), only data from non-manipulated plots were considered.

These criteria yielded a total of 52 studies for further analysis. For each variable, means, statistical variation (standard error, standard deviation or confidence interval) and sample size (n) were extracted for both invasive and native plants. For those studies that were conducted at more than one site, we treated values obtained from the experiment at each site as an individual observation, and used the plot number at each site as the replicate number (i.e. n). These data were retrieved directly from tables and data sets provided by the authors, or from graphs using GetData Graph Digitizer (version 2.25.0.32).

Effect size

The log response ratio (RR) was used as a measurement of effect size and calculated according to Hedges *et al.* (1999):

$\ln \mathrm{RR} = \ln(\bar{X}_t) - \ln(\bar{X}_c)$, where $\bar{X}_t$ and $\bar{X}_c$ represent the means of the treatment (i.e. plots with invasive species) and control (i.e. plots with native species) groups respectively. The variance of log response ratio (v) was calculated as $v = \frac{S_t^2}{n_t \bar{X}_t^2} + \frac{S_c^2}{n_c \bar{X}_c^2}$, where S and n represent the standard deviation and number of replicates respectively; and the subscript 't' and 'c' refer to the treatment and control group respectively. We chose response ratio because it is easy to get back-transformed value and quantify proportionate changes between treatment and control groups (Hedges *et al.* 1999; Hawkes & Sullivan 2001). For certain studies, some variables within a study considered more than one individual effect size; for example, multiple taxa that were included in one trophic group. To avoid pseudoreplication of effect sizes, a pooled effect size and its variance per variable within a study were calculated using a fixed-effect model (Borenstein *et al.* 2009). The pooled effect size of each response variable assigned to each case study (M) was computed according to Borenstein *et al.* (2009): $M = \frac{\sum_{i=1}^{k} \frac{1}{v_i} Y_i}{\sum_{i=1}^{k} \frac{1}{v_i}}$, and the Y_i and v_i represent the individual effect size and its variance in each case study (i); and k is the number of individual effect size per variable per case study (e.g. the number of taxa in each trophic group per case study). The variance of pooled effect size for each response variable (V_M) was calculated with the formula (Borenstein *et al.* 2009): $V_M = \frac{1}{\sum_{i=1}^{k} \frac{1}{v_i}}$.

Data analysis

The weighted mean of effect size for each variable was computed and analysed using mixed-effects models with restricted maximum likelihood estimator (REML) (Borenstein *et al.* 2009). Plant pathway (i.e. litter vs. rhizosphere) was treated as a categorical moderator to compare their differences in log response ratio. The weighted mean of log response ratio (RR++) and its 95% confidence intervals for each plant pathway (i.e. litter and rhizosphere effect) were calculated individually. The calculation of RR++ followed the equation (Hedges *et al.* 1999): $\mathrm{RR}{++} = \frac{\sum_{i=1}^{m} \sum_{j=1}^{n} \frac{1}{v_{ij}} \mathrm{RR}_{ij}}{\sum_{i=1}^{m} \sum_{j=1}^{n} \frac{1}{v_{ij}}}$, where superscripts of 'm' and 'n' represent the number of treatment and control group respectively; and RR_{ij} and v_{ij} represent the pooled effect size and its variance per response in each case study respectively. The Q_M test was used to estimate the difference in the weighted mean of log response ratio between levels of moderators, and Q_E tests were computed to determine whether the variability in the effect sizes which cannot be explained by the moderators is larger than sampling error (i.e. residual heterogeneity) (Rosenberg 2013). Random-effect models were fitted to estimate the mean effect size of the biomass of AMF, abundances of detritivores and herbivores, NH_4^+ and NO_3^- concentrations; because we collected only adequate case studies for statistical analysis under either the litter or rhizosphere effect. Percent changes of variables influenced by invasion were estimated as $(e^{\mathrm{RR}{++}} - 1) \times 100\%$ (Liao *et al.* 2008). The percent changes are different from response ratios, with the former quantifying the magnitude of invasion impacts and the latter assessing whether plant invasions have significant effects on response variables.

Funnel plots for each variable were drawn to visualise the influence of publication bias (Duval & Tweedie 2000). We also excluded one outlier with high standard error for the abundance of predators. The results including and excluding the outlier were reported in the Appendix S1 and S3 Table 1.

In addition, we carried out separate meta-analyses to test the possible effects of growth form of invasive plants (woody vs. herbaceous), and to examine whether the plant invaders were reported to have allelopathic effects on the effect sizes through the litter and rhizosphere pathway respectively. Due to the limited number of case studies, we only examined the effects of growth form on two variables (i.e. biomass of bacteria and fungi), and allelopathic effects on the biomass of bacteria, using mixed-effects models. Fourteen studies were included in the subgroup analysis. Percentages of changes followed by invasions of woody and herbaceous plants were also calculated respectively.

All of our analyses were performed in R 3.4.0 using the 'metafor' package (version 1.9-9).

RESULTS

Overview of database

Our analysis included comparisons of 42 invasive species vs. 46 native plant species. The numbers of case studies reported for litter (27 studies) and rhizosphere (26 studies) effects were similar. The geographical distribution of studies was globally uneven, with 48% studies being conducted in North America, followed by Europe (21%) and Asia (21%) (Appendix S2

Table 1 Percent changes of soil biota and their functions in response to litter and rhizosphere effects of plant invasion. Data were shown with mean ± 95% CIs

Variables	Percent changes $(e^{RR} - 1) \times 100\%$	
	Litter effect	Rhizosphere effect
Biomass		
Microbes	27.52 ± 34.31	6.28 ± 10.63
Bacteria	16.07 ± 11.84	−12.06 ± 15.45
Fungi	−2.87 ± 29.20	4.20 ± 20.77
AMF	—	36.18 ± 34.40
MBC	14.65 ± 21.26	−29.20 ± 58.44
Abundance		
Soil invertebrates	71.48 ± 85.81	−40.37 ± 98.45
Detritivores	119.31 ± 76.30	—
Herbivores	—	−55.03 ± 98.31
Microbivores	89.38 ± 33.25	−14.49 ± 67.27
Predators	0.39 ± 81.07	−51.87 ± 72.91
Richness		
Soil fauna	14.08 ± 15.44	−7.92 ± 27.79
C cycle		
CO_2 efflux	18.09 ± 23.91	21.92 ± 18.75
Enzyme activities	0.76 ± 51.48	27.30 ± 100.14
N cycle		
Mineralisation rate	14.53 ± 133.24	194.85 ± 132.30
Nitrification rate	1.90 ± 38.70	4.22 ± 28.40
Enzyme activities	23.20 ± 35.73	74.00 ± 77.74
NH_4^+ concentration	—	20.91 ± 28.40
NO_3^- concentration	—	−44.33 ± 151.01

'—' denotes data are not adequate to calculate percent changes.

Table 1). Complete list and detailed information of studies used in the meta-analysis are given in the Appendix S2.

Litter effects

Litter of invasive plants significantly impacted specific microbial groups, abundances of certain trophic groups and richness of soil fauna (Fig. 1). Specifically, bacterial biomass was higher under invasive plant litter treatment than that under natives (log response ratio = 0.15, 95% CI = (0.03, 0.26)) (Fig. 1). Litter of invasive plants had positive effects on primary consumers (i.e. detritivores and microbivores). The abundances of detritivores and microbivores were respectively 119 and 89% higher under invaders' treatment than natives through the litter pathway (Table 1), and the richness of soil fauna also tended to be higher under invasive than native plant litter treatment (log response ratio = 0.13, 95% CI = (−0.02, 0.28)) (Fig. 1). Litter of invasive plants did not have significant effects on any variables related to C and N cycles (Fig. 1).

Rhizosphere effects

Rhizosphere of invasive plants had different impacts on the biomass/abundances of soil biota compared with litter of invasive plants (Table 2, Fig. 1). Unlike positive effects of invasive plant litter on bacterial biomass, living roots of invasive plants reduced the biomass of bacteria in the rhizosphere (log response ratio = −0.13, 95% CI = (−0.28, 0.02)) (Fig. 1). Compared to native plants, invasive plants increased the biomass of AMF in the rhizosphere by 36% (Table 1). Living roots of invaders had negative effects on both primary (i.e. herbivores) and secondary consumers (i.e. predators) (Fig. 1). The abundances of herbivores and predators in invaded rhizosphere soils were 55% and 52% lower than those in native soils respectively (Table 1). Neither litter nor rhizosphere of invasive plants had discernable effects on fungal biomass and total microbial biomass (e.g. microbial biomass carbon) (Table 2, Fig. 1), probably due to the high variability among studies (i.e. data residual heterogeneity) in the database (Appendix S3 Table 2). This indicates that fungal biomass and MBC changed inconsistently with plant invasion across different case studies.

Overall, living roots of invasive plants had greater impacts on nutrient cycling than plant litter, increasing CO_2 efflux (log response ratio = 0.20, 95% CI = (0.02, 0.38)), N mineralisation rate (log response ratio = 1.08, 95% CI = (0.07, 2.09)) and tended to enhance the enzyme activities related to N cycling (log response ratio = 0.55, 95% CI = (−0.10, 1.21)) (Fig. 1). The N mineralisation rate was 195% higher in invasive than native rhizosphere soils; however, the magnitude of response might be overestimated because of the possible influence of publication bias (shown in the Appendix S1). The concentrations of NH_4^+ and NO_3^- were not significantly affected by plant invasion (Table 1).

Impacts of growth form and allelopathy of invaders

Effect sizes of some response variables had great variability among studies (see Appendix S3 Table 2). The possible contributing factors, i.e. growth form of invaders and allelopathic
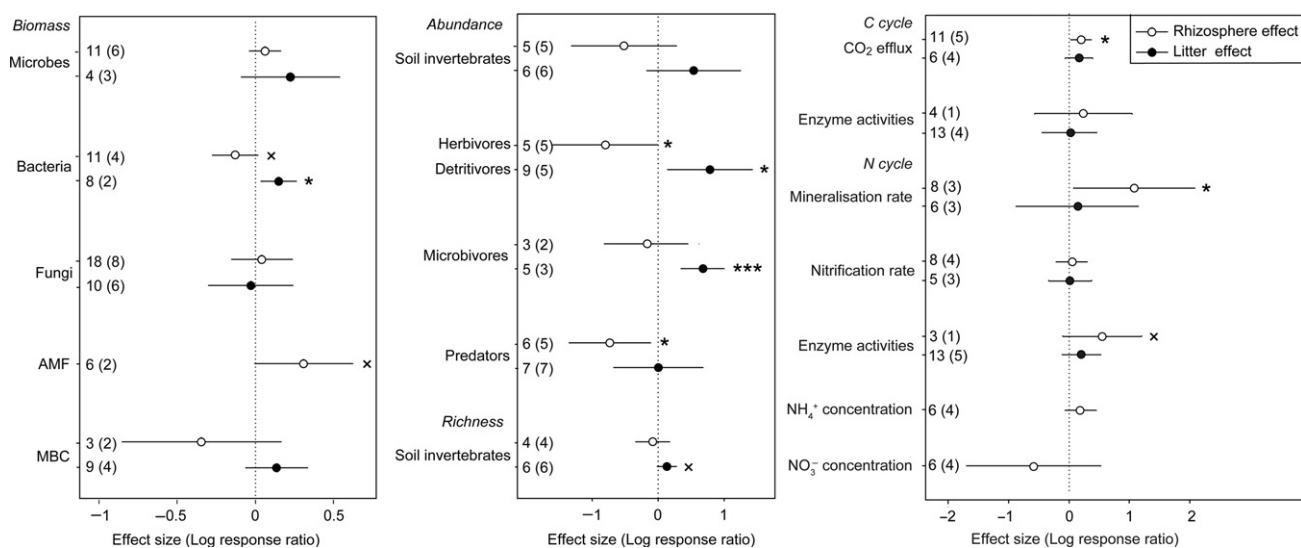
Figure 1 Mean effect size (log response ratio) of litter (solid circle) and rhizosphere (open circle) effects of plant invasion on soil biota and their functions. Positive effect sizes means that the values under invasive plants are higher than those under native plants, and negative effects sizes means the values are lower under invasive plants than native plants. Means of log response ratio are shown with 95% CI; number of plant species pairs and number of studies (in the bracket) for each variable are shown in front of each means. *** denotes $P < 0.001$; * denotes $P < 0.05$; × denotes $P < 0.1$.

Table 2 Results from the mixed-effects models with plant pathway (litter vs. rhizosphere) as a categorical moderator. Q_M and the *P*-value for the tests of moderators are given for each model. Significances ($P < 0.1$) are highlight in bold

Variables	Q_M	*P*-value of model
Biomass		
Microbes	3.60	0.166
Bacteria	**9.32**	**0.009**
Fungi	0.21	0.900
AMF*	—	—
MBC	3.51	0.173
Abundance		
Soil invertebrates	3.82	0.148
Detritivores*	—	—
Herbivores*	—	—
Microbivores	**16.89**	**0.0002**
Predators	**5.35**	**0.069**
Richness		
Soil fauna	3.40	0.183
C cycle		
CO_2 efflux	**6.79**	**0.034**
Enzyme activities	0.34	0.842
N cycle		
Mineralisation rate	4.47	0.107
Nitrification rate	0.10	0.949
Enzyme activities	4.30	0.117
NH_4^+ concentration*	—	—
NO_3^- concentration*	—	—

*Denotes the variable fit random-effect models.

effects, partially explained the highly variable effects of plant invasion on the biomass of bacteria or/and fungi.

Herbaceous invaders (litter: log response ratio = 0.15; rhizosphere: log response ratio = −0.14) had a greater impact on the biomass of bacteria than woody invaders (litter: log response ratio = 0.11; rhizosphere: log response ratio = −0.06),

irrespective of plant input pathways (Appendix S3 Fig. 1a,b). The invasion of woody plants increased the biomass of fungi by 77% through the rhizosphere pathway, which was greater than that of herbaceous invaders (0.17%) (Appendix S3 Table 3).

No matter whether the invasive plants are reported to have allelopathic effects, they appeared to suppress the biomass of bacteria in the rhizosphere (Appendix S3 Fig. 2). However, invasive plants with reported allelopathic effects (log response ratio = −0.14, 95% CI = (−0.30, 0.02), $P = 0.091$) had a greater negative impact on the bacterial biomass in the rhizosphere than those without reported allelopathic effects (log response ratio = −0.09, 95% CI = (−0.40, 0.21), $P = 0.546$) (Appendix S3 Fig. 2).

DISCUSSION

We synthesised the impacts of plant invasion on the trophic group structures and functions of soil communities and ascribed them to two distinct biotic loops, the litter-based loop and the living root-based loop. Our results show that litter and rhizosphere of invasive plants affected different trophic groups of soil biota at different magnitudes and/or directions, which reinforced the net impacts of plant invasion on the abundances/biomass of some components in the soil communities. Although the litter-based loop and the living root-based loop were differentially affected by invasive plants, they jointly enhance nutrient cycling via nutrient release and uptake that may further facilitate invasion (Fig. 2).

Invasive plant litter increases decomposers' abundance and promotes nutrient release

Our results showed that invasive plant litter favoured decomposers, increasing the biomass of bacteria, detritivores and microbivores by 16, 119 and 89% respectively (Table 1).
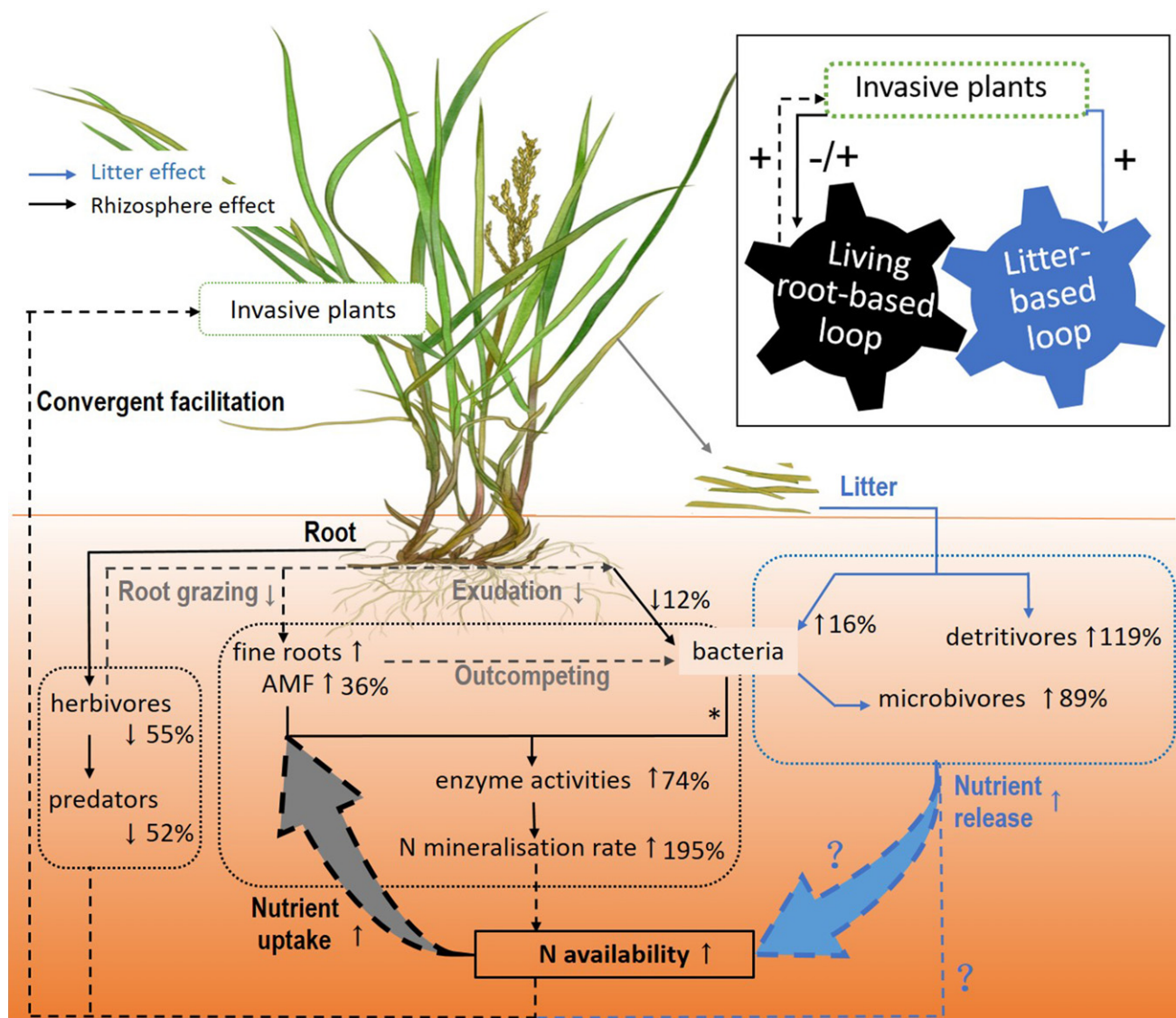
Figure 2 A conceptual model illustrating how differential litter and rhizosphere effects of invasive plants on soil biota in converge to facilitate plant invasion. Blue and black arrows mean litter and rhizosphere effects respectively. Solid and dashed arrows represent determined (i.e. statistically significant) and possible effects/feedbacks (either non-significant or not directly tested, but likely important) respectively. '↑', positive effect; '↓', negative effect; '?', unknown. *In face of plant competition for N, bacteria may have to produce more exoenzymes to degrade N-containing organic compounds, which will increase the N enzymatic activities.

Litter provides energy and food sources for the soil community and the amount of resources usually determines the complexity and stability of the soil detritus-based food web (Moore *et al.* 2004). Invasive plants generally produce more litter than natives (Ehrenfeld 2003; Liao *et al.* 2008). Liao *et al.* (2008) synthesised the results of 16 experimental studies and reported that the invasive plants produced 49% more litter than their native counterparts. Moreover, litter of invasive plants often decays faster than that of native plants (Ehrenfeld 2003; Liao *et al.* 2008; Prescott & Zukswert 2016). The higher litter decomposition rate of invasive plants is usually related to higher litter quality (indicated by the lower C:N ratio and/or lignin:N ratio) (Lee *et al.* 2017). With greater quantity and quality of litter materials, invasive plants generate more available C and other resources for soil biota than natives (Prescott & Zukswert 2016), leading to more abundant decomposers and supporting a more biodiverse soil community (Table 1; also see Mayer *et al.* 2005; Podgaiski & Rodrigues 2010). In turn, more abundant decomposers and microbivores induced by invasive plant litter can induce faster nutrient cycling and provide more plant-available nutrients, via grazing on soil microbes and the turnover of microbes (Anderson *et al.* 1983; Ingham *et al.* 1985; Bonkowski 2004; van der Putten *et al.* 2007; Meisner *et al.* 2011). For example, bacterial-feeding nematodes were found to cause considerable N release to soil in the form of NH_4^+ or amino-N through consuming bacteria in the short-term inoculation experiment (Anderson *et al.* 1983; Ingham *et al.* 1985). Thus, invasive plant litter may stimulate nutrient release by supporting more abundant decomposers and microbivores.

Our results also showed that secondary consumers (i.e. predators) were less sensitive than primary consumers (i.e. detritivores and microbivores) to alterations in litter types (Table 1). This lower sensitivity of the higher trophic groups to plant invasion has previously been documented by McCary *et al.* (2016) who examined the overall effects of invasive plants on aboveground food web in wetlands. Basal detritus resources can affect predators in the food web through altering the food source via the bottom-up cascading effect (Pace *et al.* 1999). However, soil animals at higher trophic levels may utilise diverse types of food resources and not only limited to litter-derived resources (Eissfeller *et al.* 2013). For instance, some soil animals grouped as predators (e.g. taxa in Hymenoptera, see Appendix S2 Tables 1) in our database are reported to feed on plant tissues directly when primary food resources (e.g. beetle larvae) are less available (Adachi 1983). Furthermore, movement and predatory activities of some invertebrates in the novel habitat may be impeded by invasive plant litter. Wolkovich *et al.* (2009) found the addition of invasive grass litter decreased the abundance of entomophagous *Pheidole vistana* Forel, probably because of limited movements of *P. vistana* through thick litter with long legs. Besides, the short duration of litter manipulation in the most studies included can also be a possible reason for the weaker response of higher trophic levels to plant invasion compared with that of low trophic levels. Through burying litter containers of invasive and native plants' stems in the soil, Chen *et al.* (2007) found that the difference of predatory nematodes' abundance between invasive and native plants treatment reached the maximum after 32 days of litter burial, which lagged behind a more rapid response of bacterial-feeding nematodes. Therefore, how invasive plant litter affects high trophic groups likely depends on the degree by which soil animals rely on invasive plant litter as food resources or habitats (Gerber *et al.* 2008) and the duration of experiment (Chen *et al.* 2007).

Interestingly, there were no detectable changes in the functions of soil biota (i.e. C and N cycles) that may be expected in response to the significant impacts of invasive plant litter on the trophic structure of decomposer community (Fig. 1). In a previous meta-analysis, Vilà *et al.* (2011) also found that plant invasion had minor impacts on variables related to nutrient cycling although it substantially affected biotic indicators such as plant species and communities. There are at least two reasons to explain this discrepancy. First, the responses of ecosystem processes (e.g. C and N cycles) to plant invasion may lag behind those of biological communities (Vilà *et al.* 2011; Hulme *et al.* 2013; Castro-Díez *et al.* 2014). Biotic variables, such as abundance or diversity of biota, are among the first impacted by plant invasion, whereas the responses of ecosystem processes, such as C and N cycling, come later (Vilà *et al.* 2011; Hulme *et al.* 2013). More than 67% of studies in our database lasted for <6 months, which might be too short to cause detectable changes in nutrient cycling following litter decomposition of invasive plants. The litter effects of invaders on nutrient cycling (e.g. N mineralisation and nitrification) may become detectable only over a longer period. Second, litter can affect decomposers not only through providing additional food resource and

nutrition, but also through altering habitat heterogeneity and environmental properties (Reinhart & VandeVoort 2006; McGrath & Binkley 2009; Wolkovich *et al.* 2009). Litter additions from invasive plants can increase habitat heterogeneity by providing more foraging choices and shelter for soil biota, which may favour some groups of soil animals (Reinhart & VandeVoort 2006; Wolkovich 2010). Considering that most studies included in the litter experiments are manipulated via litter addition in the field and no significant changes in variables related to C and N cycles were found, we suggest in the short-term litter experiments, enhanced habitat heterogeneity due to invasive plants litter addition may also significantly contribute to the increased abundance of decomposers (Keith *et al.* 2009).

Roots of invasive plants alter soil biota in the rhizosphere and enhance plant nutrient acquisition capacity

Our results showed that in contrast to the stimulatory effects of litter on some trophic groups, living roots of invasive plants had negative effects on the biomass/abundance of soil biota (Fig. 1). The overall negative impacts were exerted on three major functional groups: bacteria (−12%), herbivores (−55%) and predators (−52%) (Table 1). Root tissues and exudates of invasive plants provide food resources for the soil biota, some of which may be allelopathic biochemicals that can suppress native plants and microbes (Hierro & Callaway 2003; Inderjit *et al.* 2008). Our study also found that invasive plants with allelopathic effect had greater suppressive impacts on bacterial biomass in the rhizosphere than those without allelopathy (Appendix S3 Fig. 2). About 67% of invasive plant species in our database were reported to have allelopathic effects (Appendix S2 Table 1), which may partially explain the suppressive effects of invaders' roots on the biomass of soil biota observed in our analysis (Fig. 1). Also, the invaders had fewer herbivores than natives (Fig. 1), which might reduce grazing on roots and allow more carbohydrate allocation to growth and reproduction of invasive plants (Joshi & Vrieling 2005; Blumenthal 2006). At the same time, physical damage to roots directly exerted by soil-borne herbivores can affect plant growth by enhancing root exudation and soil microbial activities (Bardgett *et al.* 1999). Therefore, less grazing and damage to roots potentially reduce root leakage and exudation, consequently reducing resources and nutrients for microbes (Blumenthal 2006; Coats & Rumpho 2014). Less biomass of bacteria in the invasive than the native rhizosphere (Fig. 1) also suggests that invasive plant roots may have less leakage and/or induce faster bacterial biomass turnover in the rhizosphere, benefiting root growth and nutrient uptake. Interestingly, the abundance of predators was significantly suppressed by the living roots of invaders, but not altered by the invasive plant litter (Fig. 1). This suggests that the rhizosphere pathway likely induces stronger cascading effects than the litter pathway.

Soil CO_2 efflux, the sum of heterotrophic (primarily microbial) and root respiration (George *et al.* 2003), increased in response to plant invasion (Fig. 1). Because total microbial biomass C remained unchanged (Fig. 1), the higher CO_2 efflux might have stemmed from increased root respiration and/or

microbial turnover and activities. Root respiration supports root growth and activities such as nutrient acquisition (Lambers *et al.* 1983), and greater root respiration under invasive plants implies higher root biomass (Liao *et al.* 2008) and/or greater nutrient uptake (Castro-Díez *et al.* 2014). Also, AMF increased by 36% in response to plant invasion based on a few case studies (Table 1). Whether invasive plants enhance their associations with mutualists (e.g. AMF) are controversial (Reinhart & Callaway 2006; Vogelsang & Bever 2009), depending on the functional groups of invaders and natives, and on whether the invasive and native plants relying on AMF were grown in competitive environments (Bunn *et al.* 2015). However, some studies in which invasive plants are colonised by more AMF when they are grown together with a native neighbour (Sun & He 2010; Bunn *et al.* 2015) support our finding. Since AMF are effective nutrient scavengers, more mutualistic AMF often enhance nutrient uptake and increase plant competitive ability, although whether they provide net positive, neutral or negative effects depends on the resource and habitat conditions in the environment (Pringle *et al.* 2009; Johnson *et al.* 2010; Cheng *et al.* 2012). In spite of less abundant bacteria in the rhizosphere of invaders, higher N enzymatic activities and N mineralisation rates were found under invasive plants than those under native plants (Fig. 1). We postulate that in face of plant competition for N, microbes may have to produce more exoenzymes to degrade N-containing organic compounds (Sinsabaugh & Moorhead 1994). It should be pointed out that N mineralisation rates are often measured via soil incubation in the absence of living plants, which may not fully reveal soil N cycling *in situ*. Although N mineralisation rate was indeed affected by roots of invaders, inorganic N in the rhizosphere soil did not accumulate (Fig. 1; also see Castro-Díez *et al.* 2014). With fewer competitors for nutrients (e.g. soil bacteria) and a functionally active root-symbiont system, invasive plants are believed to increase the competitive ability over natives, probably through absorbing and assimilating more nutrients from soil with faster N mobilisation rate. The finding that invasive plants exhibited more vigorous growth than natives especially in the soil of greater nutrient availability (Schrama & Bardgett 2016), also supported our suggestion.

Database limitations and future directions

Based on limited number of case studies, we synthesised the litter and rhizosphere effects of invasive plants on the trophic groups of soil biota and their functions, providing new insights into the importance of litter and living roots of invasive plants in altering soil communities. However, we realise that the current database and framework still have important limitations, which need to be overcome in the future studies. (1) The database in this analysis only had a limited number of individual studies (52 studies) and a small fraction of invasive plants (42 species) (Appendix S2 Table 1) from thousands of invasive species worldwide (Hulme *et al.* 2013), which brings about high variability of results in the meta-analysis (Borenstein *et al.* 2009). The estimated effect sizes of most response variables (72%, see Appendix S3 Table 2) in our analysis showed variability among different cases, probably because

studies in the database were conducted in diverse contexts (e.g. different plants species and ecosystems types). Although the growth form and allelopathic effects of invasive plants partially explained the high variability in the effect sizes of bacterial and fungal biomass (see Appendix S3 Figs 1 and 2), there is a need for synthesising more studies to test the effects of other explanatory factors (e.g. ecosystem type, invasion history, soil nutrient conditions). Here, it should be emphasised that few studies included in the analysis were designed to differentiate litter or rhizosphere effects of invasive plants (only Elgersma *et al.* 2011 in our database). Therefore, we did not compare the relative importance of litter and rhizosphere effects of invasive plants on soil systems. More studies that explicitly differentiate litter and living root effects of invaders within single systems should be conducted to validate our hypothetic framework and determine contributing factors. Moreover, in the funnel plots of detritivores' abundance, soil invertebrates' richness and N mineralisation rate (Appendix S1), we did not find a data point with small effect size and large SE. This means that studies with a small effect size but large SE (c.f., not statistically significant) probably might not have been published, which may suggest an overestimation of the invasion effects on these three variables. (2) The majority of studies in our database were carried out under controlled conditions in the greenhouse, usually lasting <6 months and lacking repeated measures (see Appendix S2 Table 1), which may not fully manifest long-term ecological processes in the field (Vilà *et al.* 2011; Strayer 2012). In the future, more long-term studies under more realistic environmental conditions need to be conducted, paralleling to manipulative studies, to validate our framework. (3) Effects of plant invasions on the soil food web need to be investigated simultaneously across multi-trophic organisms, i.e. both microbes and soil fauna; however, only two studies (Wolkovich *et al.* 2009; Kulmatiski & Beard 2011) met this criterion in our database. Different components in the soil biota are intrinsically linked, whose ecological interactions are tightly coupled with biogeochemical cycles (Scheu 2002; Högberg & Read 2006). In addition, different trophic groups may respond differently, even in contrasting directions, to plant invasion (Fig. 1, also see McCary *et al.* 2016). Therefore, considering the invasion impacts both on soil microbes and fauna simultaneously will enhance our mechanistic understanding of invasive plant-soil biota interactions.

CONCLUSIONS

Based on our meta-analysis, we provide a conceptual framework in which the effects of invasive plants on soil biota and their functions are grouped into two interconnected biotic loops, i.e. the litter-based loop and the living root-based loop (Fig. 2). The distinction between litter and rhizosphere effects may allow us to reconcile contrasting results observed when the above- and below-ground effects of plant invasion are considered together. The present compartmentalisation helps us understand the interactions between invasive plants and soil biota and improves the predictive power of invasion effects on soil ecosystems through coupling different C and N pools and processes mediated by soil biota. Because soil organisms are

generally C-limited but plants are nutrient-limited, high C input from invasive plant litter supports more abundant decomposers to stimulate nutrient release, and a functionally active root-symbiont system and accelerated nutrient cycling is beneficial to nutrient uptake of invaders, which may positively feedback to plant invasion. Considering that our framework is built on limited number of case studies with diverse contexts, more studies differentiating litter and rhizosphere effects of invasive plants within single systems are obviously needed to validate and improve our conceptual framework.

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AUTHORSHIP

PZ, JW and SH conceived the study. PZ extracted the data from the literature, constructed the database and performed the statistical analyses. PZ, BL, JW and SH constructed the conceptual framework. PZ wrote the first draft of manuscript, and all authors contributed substantially to revisions.

DATA ACCESSIBILITY STATEMENT

The data supporting this article can be found in electronic supplementary material and Dryad Digital Repository (https://doi.org/10.5061/dryad.8k57d86).

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SUPPORTING INFORMATION

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