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RESEARCH ARTICLE

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Invasive earthworms erode soil biodiversity: A meta-analysis

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Abstract

1. Biological invasions pose a serious threat to biodiversity and ecosystem functioning across ecosystems. Invasions by ecosystem engineers, in particular, have been shown to have dramatic effects in recipient ecosystems. For instance, invasion by earthworms, a below-ground invertebrate ecosystem engineer, in previously earthworm-free ecosystems alters the physico-chemical characteristics of the soil. Studies have shown that such alterations in the soil can have far-reaching impacts on soil organisms, which form a major portion of terrestrial biodiversity.
2. Here, we present the first quantitative synthesis of earthworm invasion effects on soil micro-organisms and soil invertebrates based on 430 observations from 30 independent studies.
3. Our meta-analysis shows a significant decline of the diversity and density of soil invertebrates in response to earthworm invasion with anecic and endogeic earthworms causing the strongest effects. Earthworm invasion effects on soil micro-organisms were context-dependent, such as depending on functional group richness of invasive earthworms and soil depth. Microbial biomass and diversity increased in mineral soil layers, with a weak negative effect in organic soil layers, indicating that the mixing of soil layers by earthworms (bioturbation) may homogenize microbial communities across soil layers.
4. Our meta-analysis provides a compelling evidence for negative effects of a common invasive below-ground ecosystem engineer on below-ground biodiversity of recipient ecosystems, which could potentially alter the ecosystem functions and services linked to soil biota.

KEYWORDS
biodiversity change, biological invasion, ecosystem engineer, soil invertebrates, soil micro-organisms

*These authors contributed equally to this work.

1 | INTRODUCTION

Biological invasions trigger dramatic changes in ecosystems (Simberloff et al., 2013; van Kleunen et al., 2015; Walther et al., 2009). For example, invasive species reduce biodiversity of native species by altering their favoured environments (Molnar, Gamboa, Revenga, & Spalding, 2008; Vila et al., 2011). The extent of invasion effects on ecosystems, however, depends on the biological characteristics (e.g. life-history traits) of invading species (Pyšek & Richardson, 2008; Strayer, Eviner, Jeschke, & Pace, 2006). Invasion by ecosystem engineers, in particular, causes notable impacts on ecosystems via substantial alterations in local environments (Cameron, Vilà, & Cabeza, 2016; Craven et al., 2017; Crooks, 2002; Cuddington & Hastings, 2004; Ehrenfeld, 2010; Wardle, Bardgett, Callaway, & Van der Putten, 2011).

Invasion by earthworms in regions like North American forests is one of the well-studied cases of invasion by ecosystem engineers (Frelich et al., 2006; Hendrix & Bohlen, 2002; Hendrix et al., 2008). Earthworms change the physical structure and chemical characteristics of soils through bioturbation with important implications for the biotic interactions in the soil (Blouin et al., 2013; Bohlen et al., 2004; Eisenhauer, 2010). Thus, many studies have concentrated on investigating earthworm invasion effects on soil biota including soil micro-organisms and soil invertebrates. However, the evidence from different studies is mixed (see, for example, Straube, Johnson, Parkinson, Scheu, & Eisenhauer, 2009), and a general consensus is still lacking. Addressing this knowledge gap is crucial for advancing the invasive ecology of animal ecosystem engineers.

Earthworm effects on ecosystems are mainly driven by their litter feeding and soil-burrowing activities (Edwards, 2004). Ecosystems adapted to earthworms (i.e. where they are native) depend primarily on earthworms in terms of fragmentation and decomposition of organic matter (Hendrix & Bohlen, 2002). In contrast, earthworm-free ecosystems have slower decomposition rates and thus thicker organic layers (Hendrix et al., 2008). When earthworms invade into previously earthworm-free sites, greater organic substrate availability promotes the population of earthworms (Frelich et al., 2006; Hendrix et al., 2008). In turn, decomposition rates increase rapidly together with changes in soil structure with a notable decline of organic layers (Ashton, Hyatt, Howe, Gurevitch, & Lerdau, 2005). These earthworm effects are further manifested via changes in the soil chemical environment (Eisenhauer, Partsch, Parkinson, & Scheu, 2007), spatial distribution of soil micro-organisms (McLean, Migge-Kleian, & Parkinson, 2006), soil fauna movements (Cameron, Proctor, & Bayne, 2013) and plant community composition (Craven et al., 2017; Dobson & Blossey, 2015).

Invasive earthworms affect other soil biota in numerous ways (Frelich et al., 2006; Hendrix et al., 2008; McLean et al., 2006). Soil micro-organisms benefit from earthworm invasion when earthworms increase microbial access to remotely available substrates via soil mixing (McLean et al., 2006). Furthermore, earthworm casts and burrow walls are hotspots of nutrient availability in the soil, which have been shown to shift microbial community structure (Blouin et al., 2013). Specifically, invasive earthworms detrimentally affect fungal communities by disrupting their hyphal networks, whereas earthworm effects on bacterial communities are less conspicuous (Dempsey, Fisk, & Fahey, 2011; Eisenhauer, Schlaghamerský, Reich, & Frelich, 2011). Earthworms additionally disrupt mycorrhizal networks in the soil, with important implications for nutrient mineralization and plant nutrient uptake (Frelich et al., 2006; Paudel et al., 2016).

Soil invertebrate communities also vary in their responses to earthworm invasion (Eisenhauer, 2010; Eisenhauer et al., 2007; Schlaghamerský, Eisenhauer, & Frelich, 2014; Straube et al., 2009). The body size and spatial niche of soil invertebrates are crucial determinants of earthworm effects (Eisenhauer, 2010; Migge-Kleian, McLean, Maerz, & Heneghan, 2006). Earthworms are usually a superior competitor at detritus consumption than other detritivore soil invertebrates, such as micro-arthropods (Brown, 1995). Larger soil predators (macrofauna, such as ground beetles) benefit when they can feed on earthworms, but are negatively affected by earthworm-induced habitat modifications (Migge-Kleian et al., 2006). The response of smaller body sized microbe-feeding soil invertebrates (mesofauna, such as Collembola or oribatid mites) may depend on earthworm effects on microbial communities (Migge-Kleian et al., 2006). In general, invasive earthworms are detrimental to litter-dwelling and -feeding soil invertebrates due to habitat removal (Eisenhauer et al., 2007).

A major determinant of differential effects of invasive earthworms on soil biota is related to their three functional groups: epigeic, endogeic and anecic earthworms (Eisenhauer, 2010; McLean et al., 2006). These functional groups represent three different feeding strategies and ecological niches (in terms of habitat use) of earthworms (Bouché, 1977; Lavelle, 1988). Anecic earthworms live in vertical burrows in the soil and feed on soil surface litter that is dragged into the burrows, whereas endogeic earthworms feed and live in the mineral soil layer (soil dwellers). Epigeic earthworms live in the litter layer and primarily dwell on the soil surface (litter dwellers). Due to their different feeding behaviour, their impacts on ecosystems differ considerably (Hale, Frelich, & Reich, 2005). For instance, anecic and endogeic earthworms produce stable organo-mineral complexes in their casts, which may constrain soil microbial growth (McLean et al., 2006). In contrast, epigeic earthworms foster microbial growth by conditioning litter materials (partial digestion of litter materials in earthworm guts) (McLean et al., 2006). Litter removal by epigeic species may reduce the population of litter-inhabiting and -feeding invertebrates (Eisenhauer et al., 2007).

Earthworm invasion effects may also vary with soil depth (Bohlen et al., 2004; Frelich et al., 2006). Invasive earthworms may negatively affect microbial communities in the litter and organic layers compared to the mineral soil layer (Eisenhauer et al., 2007). However, microbial growth in mineral layers could be stimulated when anecic earthworms transport surface litters that are pre-processed by epigeic earthworms deeper into the soil, whereas microbial growth in organic layers may decrease due to mixing of organic matter with mineral soil. Soil layer-specific microbial responses can further cascade to soil invertebrate communities that primarily feed on micro-organisms (Eisenhauer et al., 2007).

In the present study, we conducted a meta-analysis of earthworm invasion effects on soil micro-organisms and soil invertebrates. We hypothesized earthworm invasion effects on soil biota to be overall negative. However, we expected the direction and the strength of the effect to depend on functional group richness (FGR) of invasive earthworms and soil layers.

2 | MATERIALS AND METHODS

2.1 | Data search and selection

We created a dataset collecting published studies to explore the effects of exotic earthworm species on soil biota. For this, we conducted a search in the Web of Science database in June 2016 within papers published between 1945 and 2016 using the keywords (‘lumbric*’ OR ‘earthworm*’) AND (‘invasi*’ OR ‘exotic’ OR ‘non-native’ OR ‘peregrine’ OR ‘alien’ OR ‘introduce*’) AND (‘soil biot*’ OR ‘soil org*’ OR ‘soil micro*’ OR ‘soil macro$arthropod*’ OR ‘soil animal*’ OR ‘soil arthropod*’ OR ‘soil invert*’ OR ‘soil fauna*’ OR ‘soil meso$fauna’ OR ‘soil macro$fauna’ OR ‘soil divers*’ OR ‘soil biodivers*’ OR ‘soil fung*’ OR ‘soil bact*’ OR ‘mycorrhiza*’). These keywords were selected to encompass the maximum number of published studies, which often use a variety of expressions for describing earthworms, soil fauna and soil micro-organisms in different taxonomic resolutions. Additionally, we included studies found in the references of the papers returned by the database and unpublished studies from doctoral theses as well as published ones found via personal communication. The initial Web of Science search returned 187 studies (with the search terms above), which were screened for the following two inclusion criteria: (1) studies reporting the effects of invasive earthworms (with and without earthworms treatment) and (2) studies reporting either density/biomass, species diversity or richness of soil invertebrates or any soil microbial parameter. The number of studies was reduced to 81 after applying these two inclusion criteria. Among the 81 studies, several review and opinion papers were excluded. In the end, we were able to include 28 published studies and 2 theses (one doctoral thesis and one master thesis) for our meta-analysis (Appendix S1: Table A1, also see Data Sources). We requested the raw data of the two studies, which did not report variance and the absolute values of bacterial and fungal biomass (Appendix S1: Table A1).

Data were mainly extracted from tables, figures and main text. From each study, means, variances and sample sizes of treatments with (treatment) and without earthworms (control) were extracted. Where means and variances were only illustrated in figures, we used the software Plot Digitizer (Huwaldt & Steinhorst, 2015) for data extraction. Studies on effects of exotic earthworms on micro-organisms reported a multitude of different microbial measures/response variables, such as microbial biomass C, basal respiration, microbial diversity, fungal diversity, fungal species richness, total bacterial and fungal biomass, and colonization rates of mycorrhizal fungi. In addition, we collected information on the functional groups of earthworm species, the taxon (only fauna) of the response variable, whether it was a laboratory or a field study, and if data were obtained from the organic or mineral soil layer from each study. Measurements in humus and the top 5 cm soil were assigned to the organic layer. The most frequently studied earthworm species were *Lumbricus terrestris* (Linnaeus), *L. rubellus* (Hoffmeister), *Octolasion tyrtaeum* (Savigny), *Dendrobaena octaedra* (Savigny), *Pontoscolex corethrurus* (Müller) and *Aporrectodea* sp. (Orley). The studies on earthworm effects on soil fauna comprised faunal density and diversity data for not only macro- and mesofauna in general, but also for higher resolution taxonomic groups, such as enchytraeids, mites, single mite taxa, Collembola, spiders, beetles, diplurans, julid millipedes, nematodes, pauropods, proturans and pseudoscorpions.

2.2 | Data preparation

We assembled three datasets according to three key response variables: soil fauna density, soil fauna diversity (taxa richness) and microbial properties. Studies that reported effects at different experimental durations, with different earthworm species or response taxa or in different soil layers were treated as separate observations. The same study ID was given to multiple observations from one study to account for the dependence of observations. Multiple observations within one study that resulted from measurements at different sites (only field studies) were coded as independent studies. We included a variable on the earthworm functional group identities being represented in the studies (after Bouché, 1977) and a variable indicating FGR (1, 2 and 3).

In total, we identified 54 observations for the analysis of fauna diversity, 207 observations for the analysis of fauna density and 169 observations for microbial responses. Field studies were comprised of 199 observations, whereas 231 observations were from the laboratory studies (Appendix S1: Table A1).

2.3 | Data analysis

Effect sizes for earthworm invasion effects on soil biota responses were calculated using log response ratio (LRR) as:

$$\mathrm{LRR} = \ln \frac{x_i}{x_u}$$

where x_i and x_u are the sample means of the two groups (earthworm invaded and uninvaded/lightly invaded respectively). The variance of LRR was calculated as:

$$V = S^2_{\mathrm{pooled}} \left(\frac{1}{n_i (x_i)^2} + \frac{1}{n_u (x_u)^2} \right)$$

where S_{pooled} is the pooled standard deviation and n_i and n_u are the number of observations of the two groups (invaded and uninvaded/lightly invaded respectively). We calculated LRR and its variance using random-effects models. Random-effects model allows the true effect to vary from one study to the other (Borenstein, Hedges, Higgins, & Rothstein, 2012). Hence, random-effects model suited our analyses best as we included data from studies differing in terms of, for example, duration, experimental design, location and study type (laboratory vs. field). We used restricted maximum likelihood estimators in random-effects models due to their greater efficiency in providing unbiased estimates (Viechtbauer, 2005). The confidence intervals (CI) for each estimate of effect size were calculated using bias-corrected bootstrapping methods, which corrects for non-normality of data and non-constant standard error (Efron & Hastie, 2016). The effect sizes were considered significant when bias-corrected 95% CI did not overlap with zero. We also estimated total heterogeneity and a test-statistic for it for each random-effects model to test how heterogeneous the effect sizes were across studies for a given response variable (Koricheva, Gurevitch, & Mengersen, 2013). Significant heterogeneity indicates a greater variance among studies than expected when accounted for the sampling error (from the random-effects models). In such cases, some additional unexamined factors might have influenced the estimated effect size and its variance. We also examined whether publication bias influenced our results using contour funnel plots (Koricheva & Gurevitch, 2014) with standard errors of the effect sizes as y-axis and the effect size (LRR) as x-axis (Sterne & Egger, 2001).

We further investigated the effects of FGR of invasive earthworms and soil layer in a separate multi-level meta-analysis. FGR and soil layers (organic and mineral) were used as covariates in separate models to explain the variations in the effect sizes of invasive earthworm effects on selected soil biota responses. We were only able to run multi-level meta-analyses for microbial biomass C, microbial diversity (also only for soil layer effects) and soil invertebrate density and diversity due to a lack of sufficient number of studies for other response variables. For the same reasons, we were also not able to test the interaction term between the two moderators (i.e. FGR and soil layer) except for soil invertebrate density. Study ID was used as a random factor in all the multi-level models. All analyses were performed in R statistical software (R Development Core Team, 2014) using the METAFOR package (Viechtbauer, 2010) for meta-analysis and the BOOT package (Canty & Ripley, 2016; Davison & Hinkley, 1997) for bootstrapping of confidence intervals.

3 | RESULTS

Visual inspection of funnel plots revealed negligible publication bias in reported soil biota responses to earthworm invasion (Appendix S2: Figures A1, A2 and A3).

3.1 | Earthworm invasion effects on soil micro-organisms

The overall response of microbial biomass C was neutral to earthworm invasion based on 53 observations in 11 studies (Figure 1, Table 1) with a significantly high heterogeneity among studies (Table 1). The effect size of earthworm invasion on microbial diversity was also non-significant based on 28 observations in 6 studies (Figure 1, Table 1).

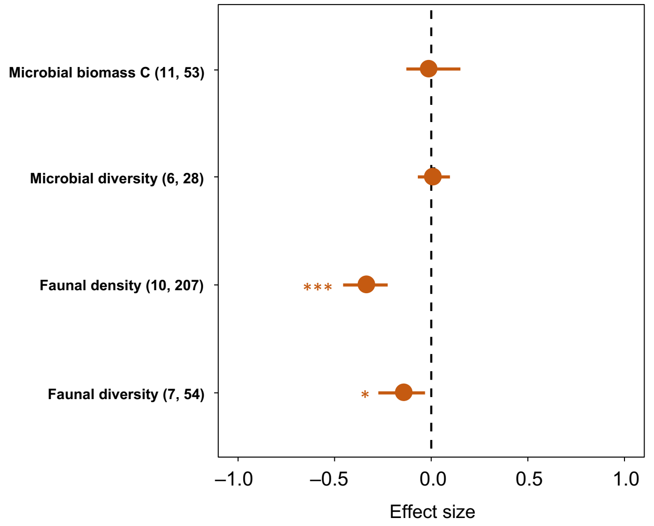

FIGURE 1 Effect size (Log response ratio) ± bias-corrected bootstrapped 95% confidence intervals for earthworm invasion effects on soil biota. Earthworm invasion effects are significant (indicated by asterisks) when confidence intervals do not overlap with zero. *$p < .05$ and ***$p < .001$ for the estimated effect size. The values next to response variables in parentheses stand for number of studies and number of observations respectively [Colour figure can be viewed at wileyonlinelibrary.com]

Moreover, we found a high degree of heterogeneity among observations (Table 1).

We found no significant effect of earthworm invasion on total bacterial and fungal biomass based on 18 observations in 6 studies and 9 observations in 3 studies respectively (Figure 2a, Table 1). However, mycorrhizal fungal colonization significantly decreased due to earthworm invasion (17 observations in 4 studies; Figure 2, Table 1). We found no significant effect of earthworm invasion on the basal respiration of soil micro-organisms (36 observations in 5 studies; Figure 2, Table 1). Model heterogeneity details are provided in Table 1.

3.2 | Earthworm invasion effects on soil invertebrates

Earthworm invasion significantly reduced soil invertebrate density based on 207 observations in 10 studies (Figure 1, Table 1). We also found a high degree of heterogeneity among observations of earthworm invasion effects on soil faunal density (Table 1). Soil invertebrate diversity was also significantly lower in sites invaded by earthworms based on 54 observations in 7 studies, with a significantly high heterogeneity (Figure 1, Table 1). Notably, among the three functional groups of earthworms, we found that densities of soil invertebrates were significantly reduced in endogeic and anecic earthworm monocultures, whereas densities did not show any significant change in epigeic earthworm monocultures (details in Appendix S3).

Among the soil invertebrate groups, the densities of Collembola and oribatid mites were significantly reduced by the presence of

TABLE 1 Results of meta-analysis for earthworm invasion effects on soil biota (soil micro-organisms and soil invertebrates). Effect size section includes log response ratio (LRR), bias-corrected bootstrapped 95% CIs and *SE*. Test statistics include estimates of the total heterogeneity (between studies) and test statistics based on Chi-square distribution and the respective *p*-value. *df* stands for degrees for freedom

	Effect size			Test statistics			
	LRR	95% CI	*SE*	Total heterogeneity (τ^2)	Test for heterogeneity (Q)	*df*	*p*-value
Microbial biomass C	−0.009	−0.138, 0.153	0.070	0.225	715.038	50	<.001
Microbial diversity	0.013	−0.070, 0.091	0.042	0.023	147.474	27	<.001
Faunal density	−0.335	−0.452, −0.217	0.065	0.480	2,952.171	187	<.001
Faunal diversity	−0.138	−0.278, −0.040	0.068	0.148	320.020	53	<.001
Microbial parameters							
Bacteria	0.066	−0.028, 0.160	0.045	0.015	32.091	17	.014
Fungi	−0.119	−0.386, 0.146	0.132	0.024	7.455	8	.488
Mycorrhizal fungi	−0.172	−0.510, −0.010	0.127	0.231	698.224	16	<.001
Basal respiration	−0.068	−0.218, 0.085	0.078	0.213	599.794	35	<.001
Soil invertebrate groups							
Astigmata	−0.086	−0.653, 0.844	0.345	0.848	29.086	12	.003
Collembola	−0.283	−0.512, −0.108	0.105	0.210	81.376	36	<.001
Gamasida	−0.173	−0.587, 0.130	0.183	0.110	17.007	19	.589
Oribatida	−0.649	−1.182, −0.336	0.201	1.038	501.094	34	<.001
Prostigmata	0.307	0.076, 0.589	0.124	0.003	12.635	14	.555

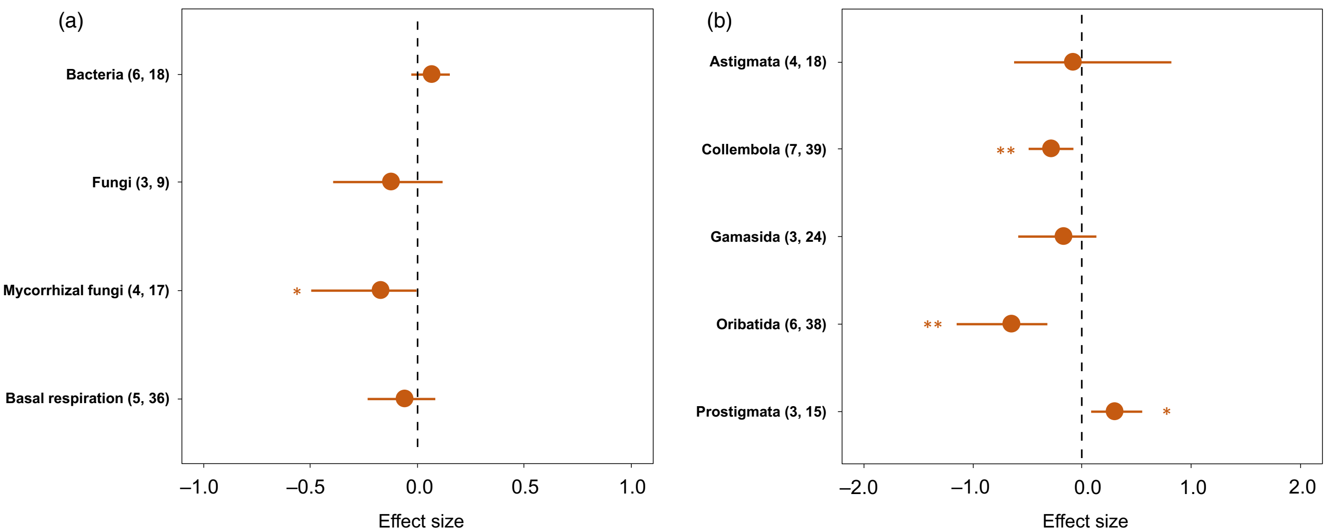

FIGURE 2 (a) Effect size (Log response ratio) ± bias-corrected bootstrapped 95% confidence intervals for earthworm invasion effects on soil microbial groups (density and colonization rates) and soil microbial basal respiration. (b) Effect size (Log response ratio) ± bias-corrected bootstrapped 95% confidence intervals for earthworm invasion effects on soil faunal group densities. Earthworm invasion effects are significant (indicated by asterisks) when confidence intervals do not overlap with zero. *p < .05 and **p < .01 for the estimated effect size. The values next to response variables in parentheses stand for number of studies and number of observations respectively [Colour figure can be viewed at wileyonlinelibrary.com]

invasive earthworms (Figure 2b, Table 1). In contrast, the density of prostigmatid mites was significantly higher in the presence of earthworms (Figure 2b, Table 1). Densities of other faunal groups (Astigmata and Gamasida) were not significantly affected by earthworm invasion (Table 1).

3.3 | Effects of earthworm functional group richness and soil layer

Multi-level meta-analysis revealed a significant positive effect of earthworm FGR on soil microbial biomass (Figure 3). That is, microbial

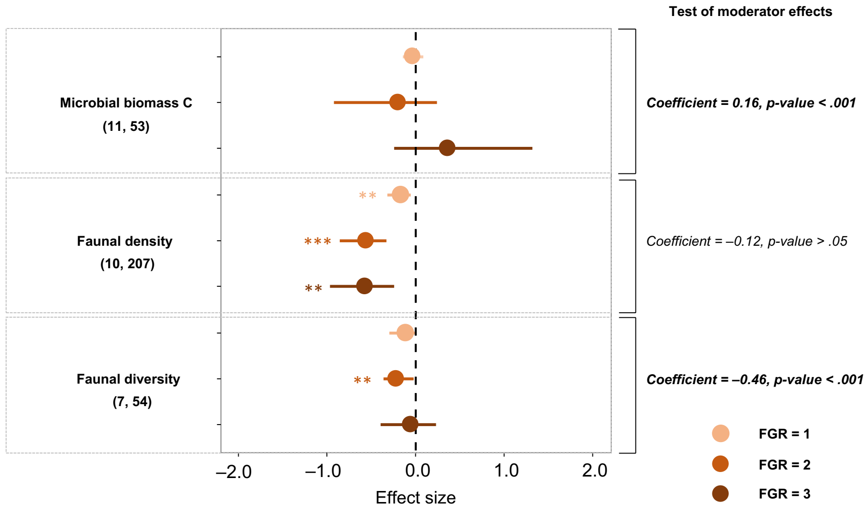

FIGURE 3 Effect size (Log response ratio) ± bias-corrected bootstrapped 95% confidence intervals for earthworm invasion effects on soil biota for different levels of functional group richness (FGR) of invasive earthworms. Results of multi-level meta-analysis are shown on the right-hand side of the figure as a test of moderator (or covariate) effect. Bold coefficients indicate significant moderator effect. Earthworm invasion effects are significant (indicated by asterisks) when confidence intervals do not overlap with zero. $^{**}p < .01$ and $^{***}p < .001$ for the estimated effect size. The values next to response variables in parentheses stand for number of studies and number of observations respectively [Colour figure can be viewed at wileyonlinelibrary.com]

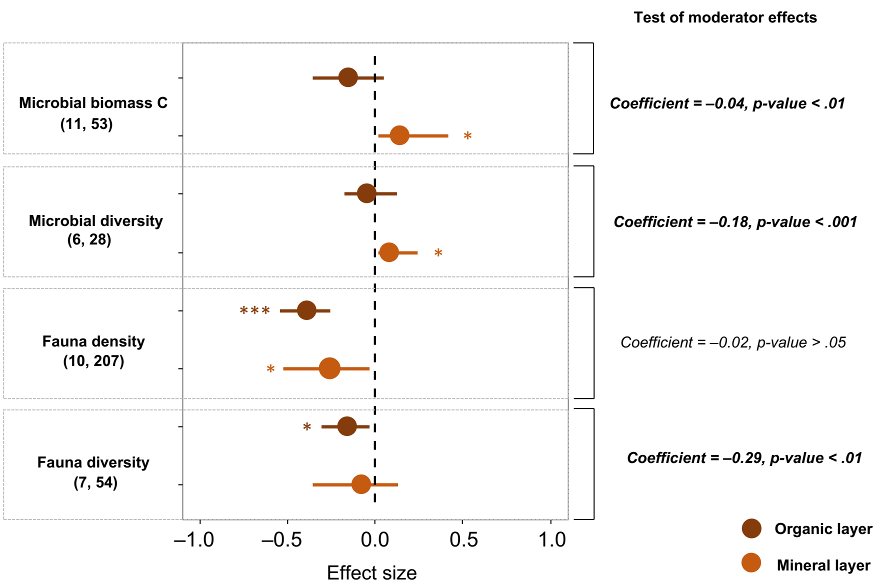

FIGURE 4 Effect size (Log response ratio) ± bias-corrected bootstrapped 95% confidence intervals for earthworm invasion effects on soil biota for two soil layers: organic and mineral. Results of multi-level meta-analysis are shown on the right-hand side of the figure as a test of moderator (or covariate) effect. Bold coefficients indicate significant moderator effect. Earthworm invasion effects are significant (indicated by asterisks) when confidence intervals do not overlap with zero. $^{*}p < .05$ and $^{***}p < .001$ for the estimated effect size. The values next to response variables in parentheses stand for number of studies and number of observations respectively [Colour figure can be viewed at wileyonlinelibrary.com]

biomass increased from slightly negative to slightly positive with FGR. Earthworm invasion effects on soil invertebrate density were independent of FGR of earthworms, whereas soil invertebrate diversity decreased most in the presence of two earthworm functional groups (Figure 3).

We found contrasting effects of earthworm invasion on microbial biomass and diversity between the mineral and the organic layer of the soil (Figure 4). Microbial biomass decreased in earthworm-invaded organic layer of the soil, while increased in earthworm-invaded mineral layers. A similar pattern was observed for microbial diversity (Figure 4). Earthworm invasion effects on soil invertebrate density were consistently negative. However, we found a significant interaction effect between FGR and soil layer on soil invertebrate density (coefficient = 0.32, *p*-value = .01, see Appendix S4 for the figure) indicating that FGR effects may vary between soil layers. That is, soil invertebrate density decreased with FGR in organic soil layers, whereas the opposite was true in mineral soil. Furthermore, we found a stronger negative effect of earthworm invasion on soil invertebrate diversity in the organic layer compared to the mineral layer of the soil (Figure 4).

4 | DISCUSSION

Our meta-analysis is the first quantitative synthesis of soil biota responses to invasive earthworms. The key findings of our study are: (1)

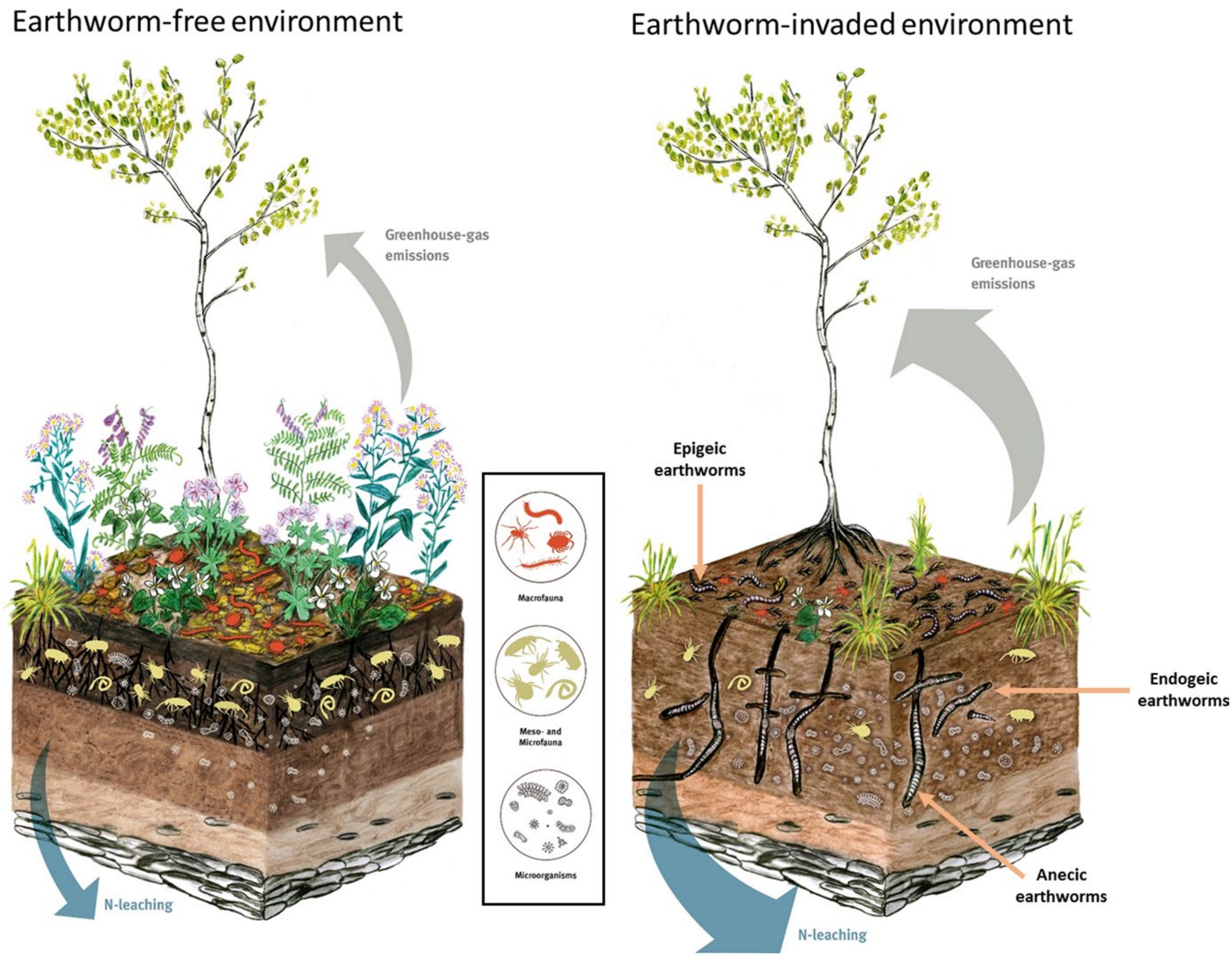

FIGURE 5 A schematic illustration of invasive earthworm effects on ecosystems that were free of earthworms (left figure). Because of earthworm's soil burrowing and litter feeding activities, earthworm-free ecosystems are dramatically altered after earthworm invasion. Previous meta-analyses have revealed shifts in plant communities in response to invasive earthworms (Craven et al., 2017), whereas earthworm effects are also known to enhance greenhouse gas emissions (Lubbers et al., 2013) and N-leaching (Bohlen et al., 2004). Our research highlights shifts in soil biodiversity (a major component of terrestrial biodiversity) in response to invasive earthworms (the response variables used in this study are inside the black rectangle and within the black circles) [Colour figure can be viewed at wileyonlinelibrary.com]

earthworm invasion reduced soil invertebrate density and diversity, in agreement with our general hypothesis; (2) soil microbial community responses to earthworm invasion were positive in the mineral soil layer; and (3) responses on soil microbial biomass C and invertebrate diversity depended on FGR of invasive earthworms, indicating potential interactive effects by different functional groups of invasive earthworms. We further report that invasive earthworms were detrimental to mycorrhizal colonization of plant roots. Among the soil invertebrate groups, invasive earthworms strongly reduced the density of Collembola and oribatid mites, while they increased the density of prostigmatid mites, indicating major shifts in soil invertebrate community composition (Figure 5 for a general overview of earthworm invasion effects).

4.1 | Earthworm invasion effects on soil microbial communities

Effects of invasive earthworms on soil micro-organisms were neutral when analysed across all soil layers. However, combining the organic and mineral soil layers masked differential responses of soil micro-organisms in these layers to earthworm invasion. Invasive earthworms tended to reduce soil microbial biomass and microbial diversity in the organic layer, whereas they increased both microbial variables in the mineral soil layer (Figure 4). The greater microbial biomass in the mineral layer of earthworm-invaded soils is likely to be driven by vertical transport of substrates from the organic layer and soil mixing by earthworms (bioturbation), whereas lower microbial biomass in the organic layer may be related to the upward transport of mineral material, which are usually comprised of less microbial resources compared to the organic layer (Groffman et al., 2015; McLean et al., 2006). Furthermore, this result coincides with the general notion that earthworm activity stimulates the relatively inactive microbial communities in the mineral soil layer (McLean et al., 2006) (see also Figure 5). Greater microbial biomass means greater carbon retention in the mineral layer (Groffman et al., 2015), and thus a higher sequestration of carbon in this layer (Zhang et al., 2013). However, invasive earthworms may also reduce soil carbon content independent of the soil layers (Eisenhauer et al., 2007). Our results thus encourage future studies to link the differential responses of microbial biomass in organic and mineral soil layers to carbon dynamics and the consequences for net carbon storage in earthworm-invaded soil.

Mycorrhizal fungi were among the most negatively affected microbial groups due to earthworm invasion, however, these results are based on relatively lower number of studies (Figure 2a). Invasive earthworms' burrowing activities and potentially direct feeding on fungal hyphae have been argued to detrimentally affect mycorrhizal fungi in the soil (Paudel et al., 2016). Such earthworm-induced reduction in mycorrhizal fungi are detrimental to plant communities (Paudel et al., 2016), such as for the performance of native plant species (Gundale, 2002) as confirmed by a recent meta-analysis (Craven et al., 2017). Due to a low number of studies, we were unable to assess how microbial groups may differentially respond to earthworm invasion effects in different layers of the soil.

Invasive earthworm effects on soil microbial biomass tended to get more positive with increasing FGR of earthworms (from slightly negative to slightly positive), which may indicate synergistic effects of the three functional groups of invasive earthworms. It is possible that three different feeding strategies of earthworms create relatively favourable soil conditions for microbial colonization and growth. For instance, anecic earthworms create greater heterogeneity in the soil by forming deep soil burrows, which enhances possibilities for a greater colonization by micro-organisms living on litter mixed by epigeic and endogeic earthworms (Groffman et al., 2015). However, it is also likely that FGR effects on microbial biomass could systematically vary between soil layers, given that the presence of functional groups of earthworms per se is a function of soil layers. The analysis of such potential interaction effects was not possible with the available data.

4.2 | Earthworm invasion effects on soil invertebrate communities

One of the key results of our meta-analysis is the decline of soil fauna density and diversity in response to invasive earthworms (only the response of soil fauna diversity was not significant in mineral soil). However, the greater heterogeneity in earthworm invasion effects on soil fauna density (Table 1) indicates a higher variation among studies regarding the direction of earthworm effects. The existing literature comprises both positive and negative effects of invasive earthworms on soil invertebrate communities. For instance, several studies have argued for short-term benefits to soil micro-arthropod communities in earthworm-invaded soils due to increased habitat complexity (reviewed in Migge-Kleian et al., 2006). The long-term effects of invasive earthworms on soil invertebrates, on the other hand, are widely accepted to be negative due to a substantial loss of organic layers (Migge-Kleian et al., 2006). A majority of soil invertebrate communities reside in the organic layers of the soil. Habitat loss thus may force soil invertebrates to disperse deeper into soil or their densities eventually would decline (Brown, 1995). Indeed, our results show that soil invertebrate diversity largely declined in the organic soil layer. Furthermore, reduced microbial biomass C in the organic layer could detrimentally affect microbial-feeding invertebrate fauna (Thakur & Eisenhauer, 2015). Our results of lower invertebrate faunal density and diversity could thus be related to lower availability of micro-organisms in earthworm-invaded organic soil layers (Eisenhauer et al., 2007; Migge-Kleian et al., 2006).

The decline of soil fauna density in response to FGR of invasive earthworms was most pronounced in organic soil layers, while the effect was slightly positive in mineral soil layers (Appendix S4). These interactive effects between FGR and soil layer on soil invertebrate density provide insights on how the presence of three functionally different earthworms may alter the resource availability for other soil invertebrate fauna. The presence of all three groups can dramatically reduce the organic material in the organic layer of the soil leading to a substantive depletion of resources for soil invertebrates (Figure 5). Furthermore, our results also confirm that endogeic and anecic earthworms are more detrimental to other soil invertebrates than epigeic earthworms (Appendix S3), agreeing with previous studies (Eisenhauer, 2010; Migge-Kleian et al., 2006). Hence, we speculate that the greater detrimental effects of earthworm FGR on soil invertebrates in organic soil layers could be primarily due to synergistic effects of endogeic and anecic earthworms, which progressively become weaker in mineral soil layers.

Densities of two key soil invertebrate groups—Collembola and oribatid mites—were significantly lower in the presence of invasive earthworms. These two groups are the most commonly studied soil fauna groups in earthworm invasion literature (Migge-Kleian et al., 2006) and critical detritivores in the litter and soil (Coleman, Crossley, & Hendrix, 2004). These key groups of soil invertebrates are assumed to be highly vulnerable to habitat destruction in the organic soil layer due to bioturbation by earthworms (Eisenhauer et al., 2007; Migge-Kleian et al., 2006). However, despite a general decline in densities of these faunal groups, prostigmatid mites benefited from the presence of invasive earthworms (Figure 2B). Studies have previously reported densities of prostigmatid mites to associate with soil carbon content (Hasegawa et al., 2013; Noble, Whitford, & Kaliszweski, 1996), which when increased due to earthworm activity can potentially benefit them.

In conclusion, our study provides evidence for negative effects of invasive earthworms on soil fauna density and diversity (see Figure 5 for an overview). Moreover, invasive earthworms shifted the community composition of soil micro-organisms and invertebrates as well as the spatial distribution of microbial biomass along the soil profile (Figure 5). Given the tremendous roles soil micro-organisms and invertebrate fauna play in regulating ecosystem functions (Bardgett

& van der Putten, 2014; Wagg, Bender, Widmer, & van der Heijden, 2014), we speculate that earthworm invasion effects can potentially alter important ecosystem functions, such as soil carbon storage (Groffman, Bohlen, Fisk, & Fahey, 2004) and nutrient dynamics (Bohlen et al., 2004), in recipient ecosystems. Moreover, the context-dependent effects on microbial communities could be crucial for how soil communities may get restructured spatially and temporally in earthworm-invaded soil (Eisenhauer et al., 2011). In congruence to a recent meta-analysis that revealed negative effects of invasive earthworms on native plant communities of recipient ecosystems (Craven et al., 2017), our study highlights shifts in the diversity, density and taxonomic composition of soil invertebrate communities, with the potential for dramatic alterations in the structure and function of earthworm-invaded ecosystems (Figure 5).

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AUTHORS' CONTRIBUTIONS

N.E., M.P.T. and O.F. conceived the study. O.F., M.P.T., N.E., M.A., M.C., I.R., F.S. and K.T. assembled the data for the meta-analysis. M.P.T. and O.F. analysed the data. M.P.T. wrote the manuscript. All authors contributed in revisions.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.v1c28 (Ferlian et al., 2017).

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List of published and unpublished studies used for the meta-analysis. Further details of these studies are also reported in Appendix S1 (Table A1).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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