

Earthworms affect plant growth and resistance against herbivores: A meta-analysis

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Abstract

1. Subterranean detritivores such as earthworms can increase soil nutrient availability through their burrowing and casting activities. A number of recent studies have explored whether these changes caused by earthworms may in turn affect plant performance and resistance to herbivores, but no formal synthesis of this literature has been conducted to date.
2. We tested for the effects of earthworms on plant growth, resistance and chemical defences against insect herbivores by performing a meta-analysis of the existing literature up to 2016. We also explored ecological factors that might explain among-studies variation in the magnitude of the earthworm effects on plant growth and resistance.
3. We found that earthworm presence increases plant growth (by 20%) and nitrogen content (by 11%). Overall, earthworms did not affect plant resistance against chewing herbivores (caterpillars, slugs and rootworms), and even led to a 22% decrease in plant resistance against phloem-feeding herbivores (aphids). However, earthworm presence increased production of chemical defences by 31% when plants were attacked by cell-feeders (thrips), and resulted in an 81% increase in resistance against thrips. The magnitude of earthworm effects was stronger when earthworm inoculations consisted of a mix of species and ecological types, and when densities of earthworms were high.
4. These results suggest that earthworm presence is an important factor underlying natural variation in plant defences against herbivores, and call for a better integration of the soil fauna in the studies of plant-herbivore interaction, both for applied and fundamental research.

KEYWORDS

chemical defences, detritivore diversity, endogeic earthworms, herbivore-feeding guilds, meta-analysis, plant growth-defence trade-off, plant nutrients, plant resistance

1 | INTRODUCTION

In response to the constant threat imposed by herbivores, plants have evolved a broad range of defensive strategies, including mechanical and chemical barriers that reduce herbivore performance (Agrawal, 2007;

Johnson, 2011; Schoonhoven, Van Loon, & Dicke, 2005). The effect of defensive traits on herbivore performance and fitness is termed plant resistance (Karban & Baldwin, 2007), while the ability of the plants to recover from tissue loss is termed tolerance (Núñez-Farfán, Feroni, & Valverde, 2007; Strauss & Agrawal, 1999; Tiffin, 2000). Understanding

the factors driving variation in plant anti-herbivore strategies remains a core question in ecology (Walling, 2000), and advances in this area could be used to inform crop protection (Lyon, Newton, & Walters, 2014).

It is generally assumed that plant ability to defend itself is costly, and thus it should trade off with other life history traits such as growth and reproduction (Coley, Bryant, & Chapin, 1985; Herms & Mattson, 1992; Koricheva, 2002). Nonetheless, the consequences of differences in allocation between plant growth and defences against herbivores vary depending on environmental conditions, such as variation in soil nutrients (Coley et al., 1985; Fine et al., 2006).

For optimal plant growth, soil nutrients must be available in sufficient and balanced amounts (Aerts & Chapin, 1999). While soils generally contain a relatively large stock of nutrients, these reserves are usually present in the forms of complexed organic compounds, rendering nutrients inaccessible for plants. The turnover and release of nutrients from soil organic matter (SOM) depend on the rate of decomposition and mineralisation of elements through biogeochemical processes (Prescott, 2005; Seastedt, 1984). Therefore, the efficiency of SOM decomposition and mineralisation will influence the magnitude of soil nutrient availability, in turn affecting plant growth and performance (Ladha, Khind, Khera, & Bueno, 2004; Yoshitake, Soutome, & Koizumi, 2014). Among the highly diverse soil fauna, the invertebrates of the meso- and macrofauna are the key organisms participating in SOM turnover and nutrient release (Bardgett & Chan, 1999; Bhaduria & Saxena, 2010; Edwards, 2004), owing to their critical role in breaking down detrital inputs and priming detritus for microbial decomposition (Prescott, 2005; Seastedt, 1984).

Earthworms are among the most important detritivores within soil food webs and are commonly considered as ecosystem engineers (Blouin et al., 2013; Cunha et al., 2016; Edwards, 2004). Through their burrowing and casting activities, earthworms improve soil nutrient availability via greater mineralisation and/or humification of soil organic matter, modifications of soil porosity and aggregation, and the stimulation of soil microflora (Bertrand et al., 2015; Brown, Edwards, & Brussaard, 2004; Cunha et al., 2016; Scheu, 2003; van Groenigen et al., 2014). In addition to these proven growth-promoting effects (e.g. van Groenigen et al., 2014), recent studies have highlighted that earthworms can also benefit plants by increasing their ability to resist herbivore attacks (Lohmann, Scheu, & Muller, 2009; Trouve, Drapela, Frank, Hadacek, & Zaller, 2014; Wurst, 2013; Wurst, Allema, Duyts, & Van Der Putten, 2008).

The mechanisms of earthworm-mediated plant resistance include, for example, an increase in plant tolerance to herbivores by stimulating plant biomass production during herbivore attack (Blouin et al., 2005; Wurst et al., 2008). Additionally, earthworms can alter plant resistance by influencing the expression of stress-responsive genes, and subsequently, the production of toxic secondary metabolites (Blouin et al., 2005; Jana et al., 2010; Lohmann et al., 2009). Nonetheless, earthworm effects on plant resistance against herbivores range from negative to positive (e.g. Johnson, Staley, McLeod, & Hartley, 2011; Loranger-Merciris, Cabidoche, Deloné, Quénehervé, & Ozier-Lafontaine, 2012; Scheu, Theenhaus,

& Jones, 1999). For instance, the endogeic earthworm *Aporrectodea caliginosa* had a negative effect on the aphid *Rhopalosiphum padi* (Ke & Scheu, 2008), while the anecic earthworm *Lumbricus terrestris* had a positive effect on the same aphid species (Eisenhauer & Scheu, 2008). Moreover, the positive impact of earthworms on plant growth could interact with defence allocation (Coley et al., 1985; Herms & Mattson, 1992; Koricheva, 2002). Therefore, earthworm effects on plant resistance against herbivores seem to be highly context dependent (Wurst, 2010, 2013), but are there general trends that emerge from the literature?

We here performed a meta-analysis to formally quantify the effects of earthworms on plant growth and resistance against herbivores, and to identify ecological factors, such as earthworm ecological types and diversity in the soil and herbivore feeding guilds, driving variation in the magnitude of earthworm effects among studies.

Earthworm species are classified into three major ecological types (anecic, epigeic and endogeic), which have distinct burrowing patterns. Epigeic earthworms live in litter or topsoil layers where they forage primarily on plant residues. Anecic earthworms live in permanent deep vertical burrows, and endogeic earthworms live in the soil and forage on soil organic matter (Bouché, 1977). Distinct burrowing patterns and food preferences, as well as variation in earthworm density and species richness have been shown to differentially affect soil nutrient mobilisation and plant nutrient uptake (Andriuzzi, Schmidt, Brussaard, Faber, & Bolger, 2016; Bossuyt, Six, & Hendrix, 2006; Curry & Schmidt, 2007; Spurgeon, Keith, Schmidt, Lammertsma, & Faber, 2013). We therefore hypothesised that the combination of different earthworm ecological types should result in better resource acquisition via niche partitioning, and therefore favour plant growth and nutrient content more than a single earthworm type (Newington, Setälä, Bezemer, & Jones, 2004).

In addition, earthworms could modify plant eco-physiological status, in turn affecting the ability of plants to respond to herbivore attack. For instance, *Arabidopsis thaliana* plants growing in the presence of *A. caliginosa* showed that enhanced expression of genes involved in phytohormone signalling (e.g. auxin, ethylene, jasmonic acids or salicylic acid), known to respond to biotic and abiotic stresses (Puga-Freitas, Barot, Taconnat, Renou, & Blouin, 2012; Puga-Freitas et al., 2016). Generally, plants activate the jasmonic acid (JA)-dependent signalling pathways in response to tissue-chewing herbivores such as caterpillars and cell-content-feeding herbivores such as thrips (Howe & Jander, 2008), whereas salicylic acid (SA)-dependent defences are activated in response to phloem-feeders such as aphids (Onkokesung, Reichelt, van Doorn, Schuurink, & Dicke, 2016; Stam et al., 2014). We therefore hypothesised that earthworms could enhance plant resistance against a variety of herbivore types by simultaneously activating several phytohormonal pathways.

Finally, given that selection for increased yield in domesticated crops often leads to reduced levels of resistance to herbivores as compared to wild relatives (Rosenthal & Dirzo, 1997; Rosenthal & Welter, 1995; Whitehead, Turcotte, & Poveda, 2017), we postulated that the magnitude of earthworm effects on plant growth would be stronger for wild plants, whereas the effects of earthworms on resistance to herbivores would be stronger for crop plants.

We specifically asked the four following questions: (1) Do earthworms increase plant growth and nutrient content? (2) Do earthworms increase plant resistance and defences against herbivores? (3) Which ecological factors (plant type; herbivore feeding guild; earthworm ecological type, earthworm density and species richness) lead to variation in earthworm-mediated plant resistance/defence? (4) Is there a trade-off between earthworm-mediated plant growth and resistance/defence under herbivore attack? We predicted that: (1) earthworm presence increases plant growth and nutrient content, (2) earthworm presence reduces plant resistance due to increased plant nutritional quality, (3) earthworm effects on plant defences are context dependent, and (4) earthworms have opposing effects on plant growth and resistance.

2 | MATERIALS AND METHODS

2.1 | Data collection

The dataset was compiled by conducting keyword searches in the ISI Web of Science up to December 2016, using combinations of relevant terms ("earthworm", "decomposer invertebrate", "ecosystem engineers", "plant growth or tolerance", "herbivore or herbivory or insect or nematode", "defence or defense or resistance"). Additional searches using the same keywords were conducted in the Google Scholar and reference lists of individual papers were screened to finally obtain a list of studies that met all the following inclusion criteria: (1) plants were subjected to at least two treatments: an earthworm inoculation treatment and control treatment without earthworm; (2) plants in both treatments were under herbivore attack; (3) Concerning plant growth, the study included at least one parameter of plant growth (e.g. above-ground biomass, below-ground biomass or total biomass) was measured; concerning plant resistance, the study included at least one measured parameter of plant resistance (i.e. herbivore performance parameters such as growth rate, mass, fecundity, development time, consumption, oviposition preference, density, or the degree of plant damage), and/or plant chemical defences (i.e. secondary metabolite production); and (4) the data included means, some measure of variance, and at least three independent replicates of each treatment. In total, the search yielded 20 papers published between 1999 and 2016 that met our criteria (See Appendix S1). However, meta-analyses exclusively based on published studies may produce biased results since the probability of the study to be published could depend upon the statistical significance, magnitude and/or direction of research findings (Koricheva, Gange, & Jones, 2009). It has been recommended, therefore, whenever possible, to include unpublished studies and grey literature (e.g. dissertations) in a meta-analysis (Møller & Jennions, 2001). By searching in Google using the same keywords as in Web of Science and by contacting individual researchers, we obtained one published PhD thesis (Kadir, 2014), in which the effects of 18 different earthworm combinations on *Brassica rapa* growth and resistance were tested. Finally, we also included two own unpublished studies (Xiao et al., unpublished data shown on Figure S1). Overall, this grey literature based-dataset includes work done on tomato and corn

plants, and represents 15%, 13%, 4% and 48% of the total sample size for growth, nutrient, resistance, and defence-related effect sizes, respectively (Appendix S1, Figure S1). To test whether inclusion of our own unpublished datapoints affected the results of the analysis, we performed sensitivity analyses by excluding these data and reanalysing the overall effects for all major variables (see Table S1). Overall, we found no significant differences in results (Table S1 vs. Tables S2–S5), therefore we report the results of analyses, including the unpublished data.

In total, our full searches yielded 79, 64 and 23 datapoints for plant responses in terms of growth, resistance, and defence, respectively (Appendix S1). When available, we also included data that measured earthworm effects on plant nutritional elemental composition (i.e. total carbon, nitrogen and phosphorous concentration), as a measure of how earthworms might modify plant nutrient content ($n = 65$ datapoints, Appendix S1).

Finally, because of our initial search constraints, earthworm effects on plant growth were assessed when plants were infested with herbivores. We thus aimed at confirming that earthworm effects on plant growth we observed were not masked by the presence of herbivores feeding on the plants. In addition, when available, we collected a subset of datapoints on plant growth parameter when plants were left herbivore-free, but only if these datapoints came from the same experiments as the dataset described above ($n = 25$, Appendix S1, Figure S2). This allowed a direct comparison of the magnitude of earthworm effects on plant growth in the presence and absence of herbivores.

Earthworm effects on plant growth were computed by including any measurements of plant biomass, such as above-ground biomass, below-ground biomass, and/or total biomass. When fresh and dry mass were both reported, dry mass was chosen. Earthworm effects on plant resistance against herbivores were assessed by including measures of herbivore growth and development and plant damage imposed by herbivores (Karban & Baldwin, 2007). Earthworm effects on plant chemical defences were assessed by including all data on plant secondary metabolites (Appendix S1).

We included multiple outcomes per study when data were reported from several independent experiments, tested on different plant species, or reported for treatments with different ecological type, species richness and density of earthworms. However, if repeated measurements of plant growth and/or resistance were available from the same experiment, only the last date of the measurements was used. If the experiments included additional treatments (e.g. manipulative drought and ambient rainfall patterns), only data of the ambient (control) condition were used. For each observation, we extracted the means of the control treatment (without earthworm) and the experimental treatment (with earthworms), as well as their *SD* and sample size (n). When *SE* was reported, we transformed it to *SD*, using formula $SD = SE * \sqrt{n}$. If data were presented in graphical form, we extracted data points using the GETDATA software (<http://www.getdata-graph-digitizer.com>).

Following van Groenigen et al. (2014), our initial dataset included five categorical moderating variables that were used to explore

additional sources of variation across the treatments: (1) herbivore feeding guild (three levels: cell-feeding herbivores including nematodes and thrips; chewing herbivores including slugs, caterpillars and rootworms; and phloem-feeding herbivores including aphids), (2) plant type (two levels: wild plants vs. crops), (3) earthworm ecological type (four levels: epigeic alone, endogeic alone, anecic alone and mixtures of the three ecological categories), (4) earthworm density (four levels: <100, 100–199, 200–400, >400 earthworms per m² of soil), and (5) earthworm species richness (two levels: single species vs. multi-species) (Appendix S1).

2.2 | Meta-analysis

Effect sizes for earthworm effects were calculated, using the natural logarithm of the response ratio (lnR) (Hedges, Gurevitch, & Curtis, 1999) of the mean responses in the presence (+E) and the absence (−E) of earthworm such that $\ln R = \ln(+E/-E)$. For interpretation of the results, mean effects and confidence intervals were back-transformed, using the formula: $(\text{EXP}(\ln R) - 1) \times 100$ and reported as the percentage changes between control and earthworm additions.

Because higher herbivore performance (e.g. abundance, larva mass, etc.) means that plants are less resistant to herbivores whereas higher levels of plant secondary metabolites mean that plants are better defended, the effect sizes for plant resistance and plant defence had different initial signs. In order to compare resistance and defence effect sizes within the same analyses, all resistance effect sizes, beside the development time of herbivores, were calculated as inverse of lnR such as: $\ln R_{\text{resistance}} = \ln(+E/-E)^{-1}$. Therefore, for all our analyses, effect sizes with positive values indicate that earthworm presence increased plant growth, nutrient content, resistance and defences against herbivores. The variance associated with effect size was calculated from the SD and sample size (*n*) associated with each mean value of plant growth, nutrients, resistance and chemical defences, respectively (Koricheva, Gurevitch, & Mengersen, 2013).

Meta-analysis was performed with the 'metafor' package (Viechtbauer, 2010) in R (R Development Core Team 2015). First, we estimated the overall effects of earthworms on plant growth, nutrients, resistance and chemical defences, using a random-effects model. The random-effects model was selected because of the across-studies variability and in order to partition the variance into within- and between-studies. In this analysis, individual effect sizes are weighted by the reciprocal of the sum of the variance between-study and sampling variance within study. The restricted maximum likelihood method (REML) was used to estimate between-study variance. The mean effect size was considered as significantly different from zero if its 95% confidence intervals (CIs) did not include zero (Koricheva et al., 2013).

We assessed potential publication bias in the overall database, using funnel plot and the "trim and fill" method (Jennions, Lortie, Rosenberg, & Rothstein, 2013). In order to assess the robustness of the observed overall effects of earthworm presence on plant growth, nutrients and resistance/defences, fail-safe numbers (Nfs) were calculated, using Rosenberg's weighted method ($\alpha = 0.05$) (Rosenberg, 2005) (See Tables S2–S5). Rosenberg's Nfs indicates how many studies

reporting zero effect size would need to be added to the meta-analysis to render the observed effect non-significantly different from zero (Rosenberg, 2005).

Next, we performed meta-regressions to explore how multiple moderator variables could affect the earthworm-mediated effect size on plant resistance and defences. Meta-regressions are more effective than standard meta-analytic techniques at examining the impact of moderator variables for studying effect sizes (Benton, 2014). To avoid potential non-independence between moderators, their effects were tested hierarchically as described in Figure S3. Moderator analyses were performed only when there were at least two levels with large enough sample size ($n > 3$, Figure S3). We used mixed-effects models to estimate the effect of each moderator (herbivore type, plant type, earthworm ecological type, earthworm density, and earthworm species richness) on the magnitude of earthworm presence. This model assumes that differences among studies within a group are due to random variation, whereas variation between groups is fixed. With this model, the between-group homogeneity (Q_B) was used to estimate the significance of each categorical moderator (Koricheva et al., 2013). If the Q_B was significant, we inferred that the mean effect size differed between moderator levels, and two moderator levels were considered to be significantly different from one another if their 95% CIs did not overlap.

Finally, we computed correlations between: (1) the effect of earthworms on plant growth versus plant resistance/defences, and (2) the effect of earthworms on plant resistance versus plant nutritional parameters using Pearson's correlation analysis (Tables S6–S8). Each data point of the correlation corresponded to an lnR value as calculated above. A significant positive correlation means that an increase in plant resistance in the presence of earthworms is associated with an increase in plant growth and/or plant nutritional parameters.

3 | RESULTS

3.1 | Earthworm effects on plant growth

Overall, earthworm presence increased plant biomass by 20% (Figure 1a, Table S2). Specifically, earthworm presence significantly increased plant above-ground biomass by 16%, below-ground biomass by 29% and total biomass by 22% (Figure 1a, Table S2). The 'trim and fill' method detected three missing studies to the left of the grant mean. The addition of three missing cases to the dataset produced a new grand mean effect size of 19% (95% CIs 13% to 26%, $n = 82$), suggesting a robust positive overall effect of earthworms on plant growth in the presence of herbivores (Table S2). The Rosenberg's Nfs for the overall database is 6,420, which is 15 times higher than the threshold of 405 ($5 \times 79 + 10$), also indicating a robust mean effect size (Table S2).

Additionally, by directly comparing the magnitude of earthworm effects on plant growth in the presence and absence of herbivores, using a balanced subset (i.e. datapoints come from the same study, $n = 25$), we found that earthworm presence increased overall plant

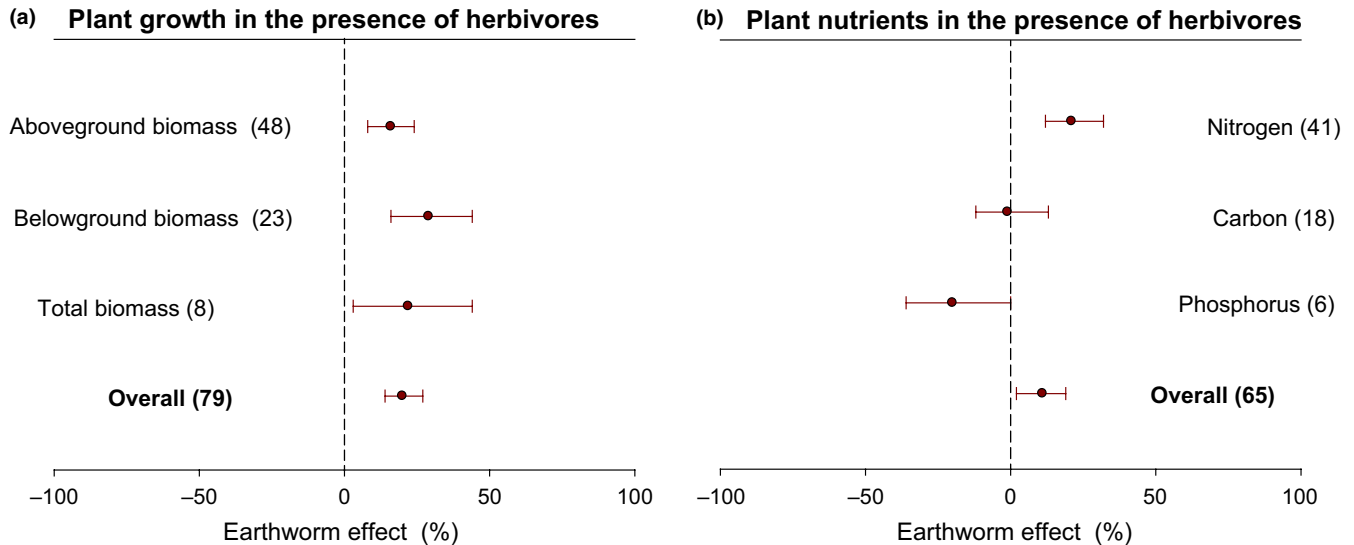


FIGURE 1 The effect size of earthworms on plant growth (a) and nutrients (b) in the presence of herbivores. Error bars denote 95% bias-corrected confidence intervals (CIs). Sample sizes are shown in brackets. The individual effect is significant if the 95% CI does not include zero

biomass by 14% and by 11% when plants grew in the presence and absence of herbivores, respectively (Figure S2).

3.2 | Earthworm effects on plant nutrient content

Earthworm presence stimulated an overall 11% increase in plant nutrient content in the presence of herbivores (Rosenberg's $N_f = 19035$, $n = 65$, Figure 1b, Table S3). The addition to 14 missing cases to the dataset by the "trim and fill" method produced a new grand mean effect size of 21% (95% CIs 12% to 31%, $n = 79$), suggesting a robust positive overall effect of earthworms on plant nutrient content in response to herbivory (Table S3). This result was mainly driven by a 21% increase in plant nitrogen content, while we detected a 20% decrease in phosphorus and a 1% decrease in carbon content when earthworms were present (Figure 1b, Table S3).

3.3 | Earthworm effects on plant resistance

Overall, earthworm presence decreased plant resistance to herbivores by 15% (95% CIs -24% to -4%, $n = 64$). After 6 missing cases were added to the analysis by the "trim and fill" method, the new grand mean effect size was -9% (95% CIs -19% to 3%, $n = 70$) (Table S4). Between-study variation explained 83% of the observed variation in the magnitude of the effect. While plant cultivation type did not influence earthworm effects on plant resistance ($Q_B = 0.04$, $df = 1$, $p = .844$), we found a strong effect of herbivore type ($Q_B = 12.098$, $df = 2$, $p = .002$). Earthworm presence increased plant resistance to cell-feeders by 34% (and by 50% after adding two missing cases with the "trim and fill" method; Table S4). This result was mainly driven by 80% increase in plant resistance to thrips and 11% increase in resistance to root-feeding nematodes (Figure 2a, Table S4). In contrast, earthworm presence had no significant effect on plant resistance to chewing herbivores (Figure 2b, Table S4), and decreased plant

resistance to phloem-feeders by 22% (Figure 2c, Table S4). We therefore proceeded to explore the possible causes of this heterogeneity using moderator analyses (including earthworm ecological type, species richness and density) with chewing and phloem-feeding herbivores separately (Figure S3).

Earthworm ecological type and species richness did not affect earthworm effects on plant resistance against chewing herbivores (Figure 2b, Table S4). Plant resistance against phloem-feeders was particularly decreased when a mixture of the three earthworm ecological types or a mixture of different species of earthworms (multi-species) was added in the experiments, and when earthworm densities were high (i.e. above 400 individuals per m^2) (Figure 2c, Table S4).

3.4 | Earthworm effects on plant chemical defences

Overall, earthworm presence did not significantly affect plant defence compounds (Figure 3). Between-study variation explained 81% of the observed variation in the magnitude of the effect. Again, while plant type did not affect earthworm effects on plant chemical defences ($Q_B = 2.659$, $df = 1$, $p = .103$), we found a strong effect of herbivore type ($Q_B = 12.139$, $df = 2$, $p = .002$). Specifically, we found that earthworms had no effect on chemical defences in the presence of chewing herbivores (Table S5). However, earthworm presence increased overall chemical defences by 32% in the presence of cell-feeding herbivores; this result was driven by a 38% increase in defensive compounds in the presence of nematodes and a 31% increase in the presence of thrips (Table S5). Additionally, earthworm presence decreased chemical defences by 48% in the presence of phloem-feeders (Table S5), although this result was driven by one data-point only.

Because of lack of data for phloem-feeding and chewing herbivores (Figure S3), we proceeded to perform moderator analyses only for the cell-feeding herbivores (thrips). We found that single-species earthworm inoculations significantly increased plant chemical defences in

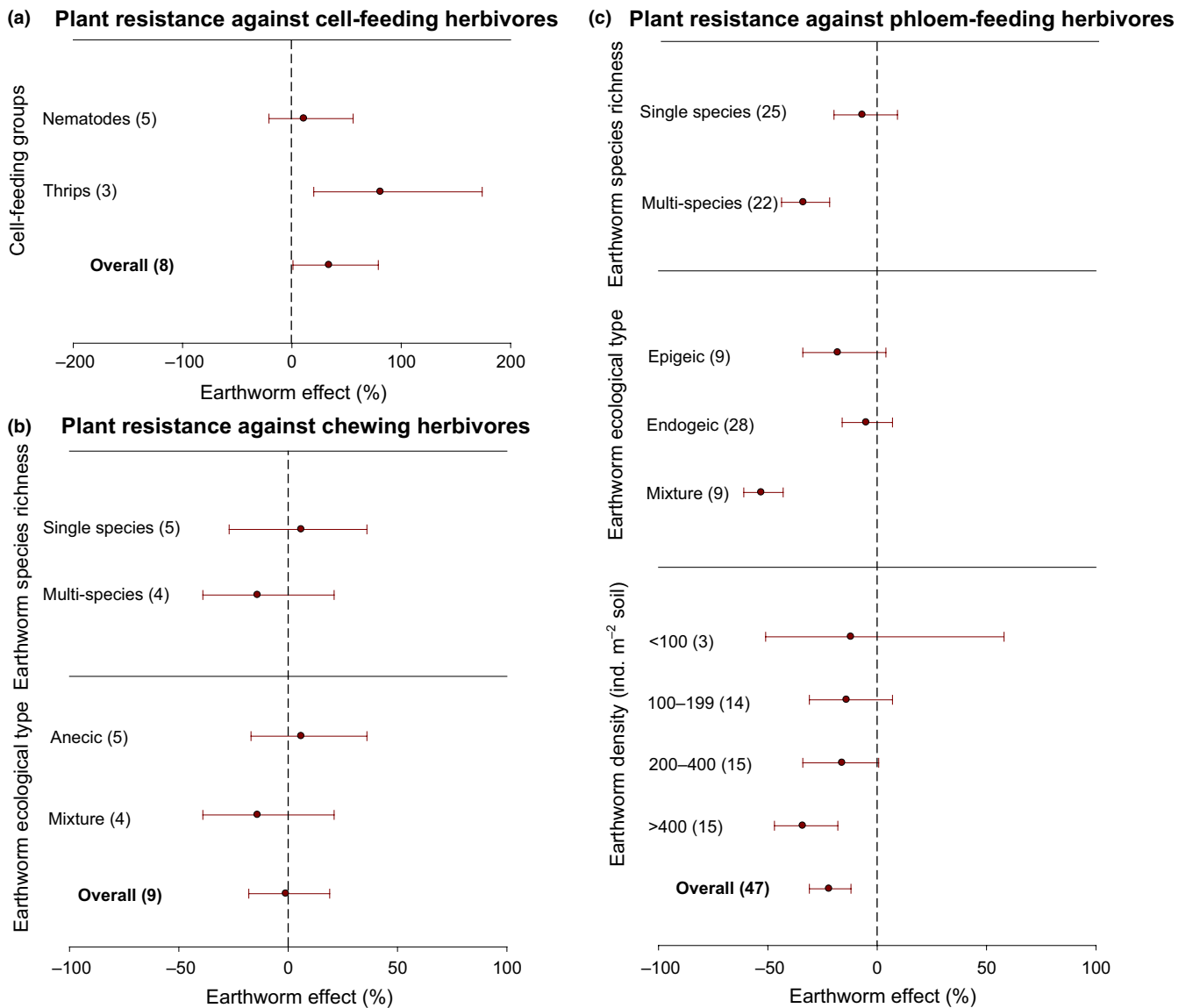


FIGURE 2 Moderator analyses of the effect size of earthworm presence on plant resistance against (a) cell-feeders, (b) chewing herbivores and (c) phloem-feeders. Error bars denote 95% bias-corrected confidence intervals (CIs). Sample sizes are shown in brackets. The individual effect is significant if the 95% CI does not include zero

the presence of cell-feeding thrips (Table S5). In addition, earthworm-mediated plant chemical defences against thrips were not dependent on earthworm ecological type (Table S5).

3.5 | Earthworm-mediated relationship between plant growth, nutrients, resistance and defences

Effects of earthworm presence on plant resistance were negatively correlated with earthworm effects on plant growth (Figure 4a, Table S6). However, this relationship was affected by herbivore type, plant type, earthworm ecological type, density, and species richness (Table S7). Negative correlations between earthworm effects on plant resistance and growth were strongest against phloem-feeders ($r = -.48$, $p = .008$), in wild plants ($r = -.51$, $p = .009$), with endogeic earthworm inoculations ($r = -.53$, $p = .008$),

with earthworm density below 100 individuals per m^2 ($r = -.95$, $p = .012$) and with earthworm multi-species inoculations ($r = -.52$, $p = .022$) (Table S7). On the other hand, earthworm presence mediated an overall positive relationship between plant growth and chemical defences ($r = .48$, $p = .021$, Figure 4b, Table S6). This positive earthworm-mediated relationship was strongest in crop plants ($r = .52$, $p = .025$, Table S7), with earthworm single species treatment ($r = .49$, $p = .045$, Table S7), and with earthworm multi-species treatment ($r = .97$, $p < .001$, Table S7). Effects of earthworm presence on plant resistance were negatively correlated with earthworm effects on plant nutrients only when earthworms were endogeic species ($r = -.42$, $p = .032$), and their density was less than 100 individuals per m^2 ($r = -.98$, $p = .003$) and 200–400 individuals per m^2 ($r = -.61$, $p = .026$) (Table S8). Effects of earthworm presence on plant phosphorus content were negatively correlated with earthworm effects

on plant chemical defences (Table S6). Finally, effects of earthworm presence on plant growth were positively correlated with earthworm effects on plant nutrient content, total nitrogen and carbon in particular. (Table S6).

4 | DISCUSSION

We found that earthworm presence had an overall positive effect on plant growth and nutritional content, and variable overall effects on plant resistance and chemical defences. The results were strongly dependent on the herbivore feeding guild, as well as on the ecological type, density and species richness of earthworms.

Plant chemical defences in the presence of different herbivores

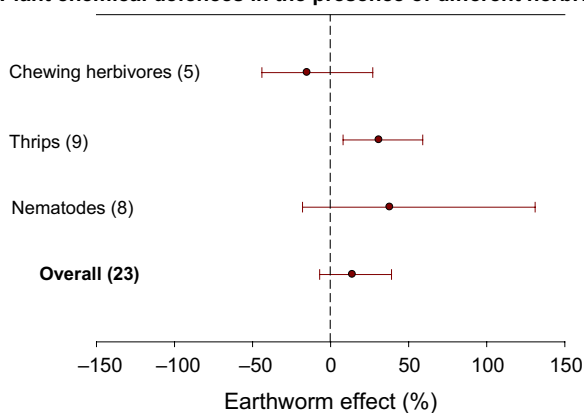


FIGURE 3 The effect size of earthworms on plant chemical defences in the presence of different herbivores. Error bars denote 95% bias-corrected confidence intervals (CIs). Sample sizes are shown in brackets. The individual effect is significant if the 95% CI does not include zero

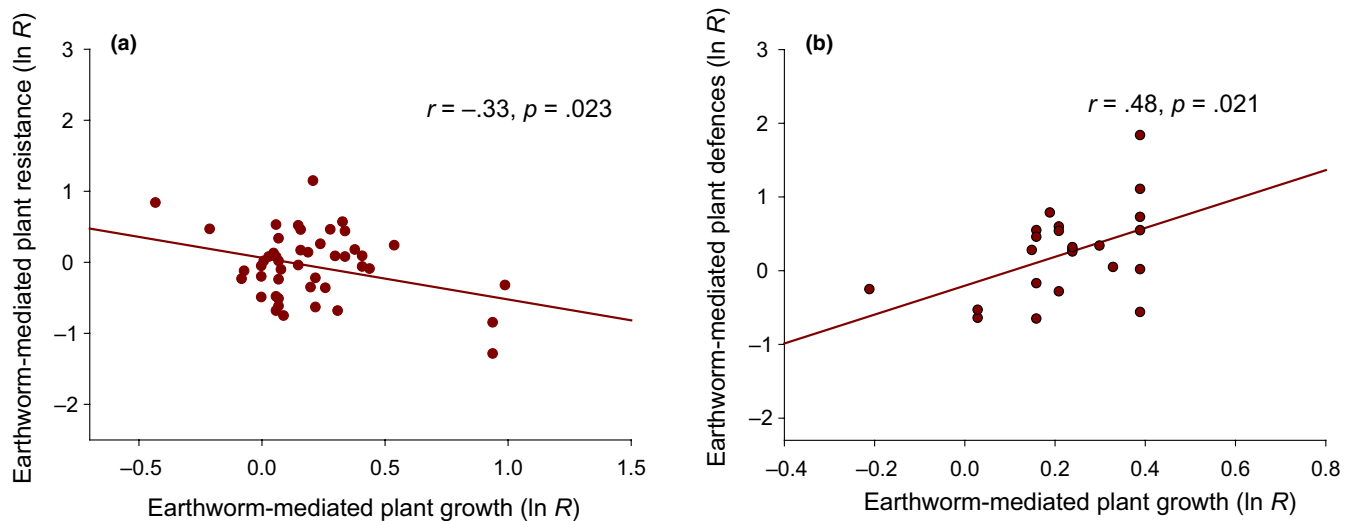


FIGURE 4 Correlations between the effects of earthworms on (a) plant resistance and growth, (b) chemical defences and growth. Each data point of the correlation corresponded to an lnR. For instance, a significant negative correlation between growth and resistance means that positive effect of earthworm on growth is correlated with negative effect of earthworms on plant resistance and vice versa

4.1 | Earthworm effects on plant growth

We found an overall positive effect of earthworms on plant biomass gain against herbivores (20% more biomass on plants inoculated with earthworms) (Figure 1a). This is in line with previous results that extrapolated the positive effects of earthworms on plant production (e.g. van Groenigen et al., 2014). In addition to the previous studies, our subset data enabled a direct comparison of the effects of earthworms on plant growth in the presence or absence of herbivores. We found that the magnitude of the relative change in biomass of plants that experienced herbivores (14%) was similar to that of herbivore-free plants (11%) (Figure S2), indicating that herbivores did not attenuate the effects of earthworms on plant growth.

Because herbivores are generally thought to decrease plant biomass, these results might be suggestive of an earthworm-mediated tolerance in plants under herbivore attack. While the meta-analysis could not tease apart the mechanisms behind plant growth enhancement in the presence of earthworms, the compensatory continuum hypothesis (CCH) asserts that plants have a greater potential for compensating for herbivore damage under resource-rich conditions (Maschinski & Whitham, 1989). Therefore, earthworms could favour tolerance responses of plants by increasing soil nutrient availability.

4.2 | Earthworm effects on plant resistance

Plant resistance against herbivores is generally mediated by changes in nutritional quality and/or production of toxic secondary metabolites. Earthworms have been shown to affect primary and secondary metabolism in plants, as well as the expression of stress-responsive genes in both above-ground and belowground parts of plants, thus potentially impacting herbivore performance (Blouin et al., 2005; Jana et al., 2010; Lohmann et al., 2009). We found that earthworms increased plant susceptibility to phloem feeders, but increased resistance to

cell-feeding herbivores, and had no effect on resistance to chewing herbivores.

Across the studies involving the phloem feeders (aphids), we observed an overall increase in abundance of the herbivores when earthworms were present. Nonetheless, these results were context-dependent. In particular, only high densities and higher levels of species and functional diversity of earthworms decreased plant resistance against aphid herbivores. Under aphid attack, plants activate the SA pathway for stimulating chemical and physical barriers such as callose deposition and the production of defensive secondary metabolites, which are transported into the phloem to increase toxicity (Elzinga & Jander, 2013; Züst & Agrawal, 2016). In turn, aphids could inject effector proteins to prevent callose deposition, and deal with toxic metabolites by metabolism or excretion (Elzinga & Jander, 2013; Kim & Jander, 2007; Züst & Agrawal, 2016). Earthworms, therefore, could favour plant susceptibility to aphids by inhibiting the SA signalling pathway. While earthworms have been shown to affect plant defence signalling pathways and gene expression (Puga-Freitas et al., 2012, 2016), we are not aware of studies directly linking earthworm presence to plant physiological and molecular mechanisms for deterring aphid attack, but this should be considered for future avenues of research.

In addition, accessible nutrients, such as sugars, amino acids and nitrogen are also important determinants for the growth and development of herbivores including aphids (Caillaud, Pierre, Chaubet, & Pietro, 1995; Cao, Liu, Zhang, & Liu, 2016; Mattson, 1980). Therefore, the positive effects of earthworms on plant nutritional quality (e.g. higher nitrogen content), might also cause increased plant susceptibility to aphids. This idea is corroborated by the fact that in a more complex earthworm community, earthworm species act synergistically to increase soil fertility (Bertrand et al., 2015; Curry & Schmidt, 2007; Spurgeon et al., 2013) and plant nutrient content (e.g. Laossi et al., 2009), in turn increasing plant susceptibility to aphid attack.

Contrary to the aphids, earthworms mediated increased plant resistance against cell-feeders. This was particularly true when measuring resistance against thrips (Figure 2a), while the effects were more variable when measuring resistance against soil-dwelling nematodes. While the effects of earthworms on nematodes could partially be explained by direct interference (i.e. earthworms could ingest nematodes while ingesting the surrounding substrate Boyer, Reversat, Lavelle, & Chabanne, 2013), the effects of earthworms on thrips are likely to be mediated by changes in aboveground plant functional traits. Our unpublished study, as described in Figure S1, showed that earthworm-inoculated plants under thrips attack had higher concentrations of total carbon and nitrogen, lower concentrations of total phosphorus, and higher levels of jasmonic acid and total phenolic compounds (Figure S1d,e). Earthworm-mediated increase in resistance against thrips can thus be due to the activation of the JA signalling pathway. In addition, we speculate that stimulation of the soil microbial community by earthworms could have enhanced defence priming in plants (Blouin et al., 2005; Jana et al., 2010; Pineda, Zheng, van Loon, Pieterse, & Dicke, 2010; Puga-Freitas et al., 2012), and ultimately increase resistance by promoting chemical defence accumulation in the plants. This, however, has never been specifically tested so far.

4.3 | Earthworm effects on plant chemical defences

We found that overall, earthworm presence did not significantly affect plant chemical defences when chewing herbivores were on plants, but notably increased chemical defences when cell-content feeders, particularly thrips were present. For example, earthworm presence promoted the induction of defence compounds such as jasmonic acid and phenolics in tomato leaves when under thrips attack (Figure S1e). Similarly, earthworms significantly increased concentrations of total glucosinolates, a nitrogen-based defence compound class, in leaves of *Sinapis alba* (Lohmann et al., 2009). Therefore, in these cases, earthworm presence could favour plant resistance by increasing plant chemical defences. On the other hand, Wurst, Langel, Rodger, and Scheu (2006) showed that concentrations of two glucosinolates (glucoiberin and glucoraphanin) in shoots of *Brassica oleracea* decreased when the endogeic earthworm *Octolasion tyraeum* was added to the system. Similarly, earthworms could induce a decline of root sesquiterpene (*E*)- β -caryophyllene when rootworms are present (Figure S1j).

The inconsistent effects of earthworms on plant chemistry might be due to the interactive effects of plant growth and nutrient uptake on plant secondary metabolism. For instance, it was shown that phytosterol concentration in *Plantago lanceolata* plants was not affected by earthworms directly, but increased with increasing nitrogen concentration of the leaves (Wurst, Dugassa-Gobena, Langel, Bonkowski, & Scheu, 2004), which is mediated by earthworm presence (Wurst & Jones, 2003). Additionally, several studies have shown that the initial soil nutrient content and the distribution of soil organic matter could influence plant defensive secondary metabolites (Ke & Scheu, 2008; Wurst, Dugassa-Gobena, & Scheu, 2004; Wurst, Langel, Reineking, Bonkowski, & Scheu, 2003). For instance, earthworms favoured an increase in total phytosterol content of *P. lanceolata* shoots, but only when the spatial distribution of organic residues/litter was mixed homogeneously with soil (Wurst et al., 2004). Only few studies in our meta-analysis addressed the effects of differences in initial soil properties such as distribution of organic litter, or the changes in soil available nutrients (e.g. mineral nitrogen), driven by earthworm presence. This prevented the use of soil bio-chemical properties as a moderator in this study. Nonetheless, an increasing number of studies demonstrate that soil nutrients and microorganisms both modify the synthesis of defensive secondary metabolites (e.g. Badri, Zolla, Bakker, Manter, & Vivanco, 2013; Ohkama-Ohtsu & Wasaki, 2010), and ultimately influence plant-herbivore interactions (Badri et al., 2013; Pineda, Dicke, Pieterse, Pozo, & Biere, 2013; Pineda, Soler, Pozo, Rasmann, & Turlings, 2015). This indeed calls for a better integration of earthworms living in different soil conditions and with different ecologies into plant-herbivore interaction studies.

4.4 | Earthworm effects on the trade-offs between plant performance, resistance and chemical defences

We found that the effects of earthworms on growth and resistance of plants under herbivory were overall negatively correlated

(Figure 4a), as would be predicted by classic plant defence theory (Herms & Mattson, 1992; Züst & Agrawal, 2017). An increasing number of studies indicate that earthworms could indirectly influence the performance of herbivores such as phloem-feeders by predominantly affecting plant size, vigour and nutrient content (Eisenhauer & Scheu, 2008; Scheu et al., 1999; Trouve et al., 2014), and to a lesser extent by changes in plant secondary chemistry (Francis, Lognay, Wathelet, & Haubruge, 2001; Katsanis, Rasmann, & Mooney, 2016; Wurst et al., 2004). For example, Cao et al. (2016) showed that the green peach aphid (*Myzus persicae*) performed better on an enhanced amino acid: sugar ratio and enhanced absolute amino acid concentration in the phloem, but also activated genes responsible for glucosinolates synthesis in the leaves of Chinese cabbage. Similarly, Wurst et al. (2004) showed that *A. caliginosa* earthworm presence decreased the concentration of the defence compound catalpol in *P. lanceolata* leaves, but this was not positively correlated with the performance in term of development time of the aphid *M. persicae*.

Contrary to expectations, earthworm presence simultaneously increased both plant growth and chemical defences (Figure 4b). These effects were particularly strong on crop plants. Because of lack of data, we could not highlight a particular combination of factors explaining these results, besides the fact that bigger plants had higher level of secondary metabolites, independently of any particular plant by herbivore by earthworm combination. Several studies have shown that the assumed growth-defence trade-off might be modified (i.e. reduced or even reversed) by different levels of nutrients in the soil (Coley et al., 1985; Donaldson, Kruger, & Lindroth, 2006; Lind et al., 2013), or not detected due to the failure to address the appropriate measure of growth-related traits (Züst, Joseph, Shimizu, Kliebenstein, & Turnbull, 2011; Züst, Rasmann, & Agrawal, 2015). Overall, these different patterns suggest that earthworm effects on defence allocation in plants are in part dictated by resource allocation, and are highly context dependent in terms of categories of defence compounds. However, this needs to be systematically addressed in future manipulative studies.

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AUTHORS' CONTRIBUTIONS

Z.X., M.L., F.H. and S.R. designed the study. Z.X., X.W. and A.K. collected data and performed the meta-analysis. J.K. assisted with the

meta-analysis. Z.X. and S.R. wrote the first draft of the manuscript and all authors contributed to revisions.

DATA ACCESSIBILITY

All data used in the meta-analysis are present in the manuscript or online supporting information and deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.382k1> (Xiao et al., 2017).

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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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