

Global Change Biology (2017) 23, 1065–1074, doi: 10.1111/gcb.13446

The unseen invaders: introduced earthworms as drivers of change in plant communities in North American forests (a meta-analysis)

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Abstract

Globally, biological invasions can have strong impacts on biodiversity as well as ecosystem functioning. While less conspicuous than introduced aboveground organisms, introduced belowground organisms may have similarly strong effects. Here, we synthesize for the first time the impacts of introduced earthworms on plant diversity and community composition in North American forests. We conducted a meta-analysis using a total of 645 observations to quantify mean effect sizes of associations between introduced earthworm communities and plant diversity, cover of plant functional groups, and cover of native and non-native plants. We found that plant diversity significantly declined with increasing richness of introduced earthworm ecological groups. While plant species richness or evenness did not change with earthworm invasion, our results indicate clear changes in plant community composition: cover of graminoids and non-native plant species significantly increased, and cover of native plant species (of all functional groups) tended to decrease, with increasing earthworm biomass. Overall, these findings support the hypothesis that introduced earthworms facilitate particular plant species adapted to the abiotic conditions of earthworm-invaded forests. Further, our study provides evidence that introduced earthworms are associated with declines in plant diversity in North American forests. Changing plant functional composition in these forests may have long-lasting effects on ecosystem functioning.

Keywords: introduced earthworms, plant communities, plant diversity, biological invasions, earthworm invasion, community composition, meta-analysis

Received 10 May 2016 and accepted 15 July 2016

Introduction

Species invasions are among the strongest drivers of environmental change globally (Sala *et al.*, 2000;

Murphy & Romanuk, 2014) and can have large effects on biodiversity and ecosystem processes, functions and services (Wardle *et al.*, 2004; Vilà *et al.*, 2011; Walsh *et al.*, 2016). Understanding the full extent of invasive species impacts is a fundamental challenge in ecology (Simberloff *et al.*, 2013); species invasions can have cascading effects across trophic levels (Estes *et al.*, 2011)

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and facilitate future invasions (Simberloff & Von Holle, 1999). While the ecological importance of linkages between above- and belowground communities and ecosystem processes is recognized (de Deyn & van der Putten, 2005), the impacts of introduced belowground organisms, such as earthworms, on aboveground communities are less understood than those of introduced aboveground organisms (Wardle *et al.*, 2004; Cameron *et al.*, 2016).

Introduced earthworms, which have been invading northern North American forests with little or no native earthworm fauna since the time of European settlement (Hendrix & Bohlen, 2002), have a profound influence on ecosystem functioning and services in North American forests. By re-engineering soil physical and chemical characteristics (Bohlen *et al.*, 2004; Hendrix *et al.*, 2008; Eisenhauer, 2010), they accelerate nutrient cycling (Szlavec *et al.*, 2006; Sackett *et al.*, 2013; Ewing *et al.*, 2015) and water infiltration (Eisenhauer *et al.*, 2012; Capowiez *et al.*, 2014) and may increase CO₂ emissions to the atmosphere (Lubbers *et al.*, 2013). Significant impacts of introduced earthworms on ecosystem functioning could also be mediated through changes in biodiversity, given the wide range of above- and belowground organisms with which they interact (Edwards, 2004). Previous studies have documented effects of introduced earthworms on ecological communities in forests (Hale *et al.*, 2006; Eisenhauer *et al.*, 2007; Frelich *et al.*, 2012; Fisichelli *et al.*, 2013), but the generality or variability of such effects has yet to be systematically quantified. Here, we synthesize the impacts of invasive earthworms on the diversity and composition of understory plant communities in North American forests.

Previous studies have documented a range of effects of introduced earthworms on plant communities (e.g., Hale *et al.*, 2006), including changes in both species diversity and composition. Introduced earthworms cause these changes in a number of ways: by predated and ingesting seeds and seedlings (Zaller & Saxler, 2007; Asshoff *et al.*, 2010; Forey *et al.*, 2011; Drouin *et al.*, 2014; Clause *et al.*, 2015; Cassin & Kotanen, 2016), altering seedbank composition (Eisenhauer *et al.*, 2009; Nuzzo *et al.*, 2015), modifying microhabitats where seeds germinate by removing leaf litter (Frelich *et al.*, 2006), and accentuating drought events by accelerating drainage via constructing burrows (Larson *et al.*, 2010; Eisenhauer *et al.*, 2012). Furthermore, disturbances associated with introduced earthworms might confer a competitive advantage to graminoids (Hale *et al.*, 2006; Holdsworth *et al.*, 2007a; Nuzzo *et al.*, 2009; Fisichelli *et al.*, 2013; but see Dobson & Blossey, 2015), or facilitate invasion by other species (e.g., Heneghan *et al.*, 2007; Nuzzo *et al.*,

2009). Other common stressors in North American forests, for example, deer browsing or allelopathic invasive plants, also may interact with introduced earthworms, potentially intensifying compositional changes in plant communities (Fisichelli *et al.*, 2013; Dávalos *et al.*, 2015; Hale *et al.*, 2016). The overall impact of ecosystem engineers on plant diversity is generally considered to be positive (Romero *et al.*, 2015) but has yet to be systematically investigated for earthworms across North American forests.

Variation in the impacts of introduced earthworms on biodiversity could reflect differences in invasion history. Different assemblages of introduced earthworms have been strongly correlated with distinct stages of invasion (Hale *et al.*, 2005; Holdsworth *et al.*, 2007b; Loss *et al.*, 2013). Recently invaded forests are usually dominated by epigeic earthworms, such as *Dendrobaena octaedra*, while forests with longer invasion histories also have endogeic and anecic species where environmental conditions, for example, soil pH, texture and moisture, permit their presence (Hale *et al.*, 2005; Frelich *et al.*, 2006; Holdsworth *et al.*, 2007b; Loss *et al.*, 2013). The combined impact of multiple earthworm ecological groups on forest understories can be dramatic, as these earthworm assemblages can completely remove surface leaf litter, reduce organic matter in upper soil horizons (Hale *et al.*, 2005; Nuzzo *et al.*, 2009; Resner *et al.*, 2015), and cause significant declines in plant diversity (Hale *et al.*, 2006; Holdsworth *et al.*, 2007a). Therefore, accounting for earthworm invasion history is essential for reaching a general understanding of how diversity and composition of plant communities are affected by introduced earthworms.

Changes in biodiversity due to introduced earthworms could lead to significant alterations in the provisioning of vital ecosystem functions in North American forests, such as nutrient and water cycling, which has important implications for the development of future management and conservation strategies. In the present study, we assessed for the first time impacts of introduced earthworms on plant diversity and composition across North American forests using meta-analytic techniques. We predict that the presence and abundance of introduced earthworms (i) decrease plant species diversity (Bohlen *et al.*, 2004) and (ii) systematically favor graminoids (Frelich *et al.*, 2012; Fisichelli *et al.*, 2013) and non-native plant species (Heneghan *et al.*, 2007; Nuzzo *et al.*, 2009). Further, we expect that the magnitude of all abovementioned effects will increase with the number of earthworm ecological groups, reflecting a greater variety of potential disturbance mechanisms likely to result in changes in plant communities (Hale *et al.*, 2006).

Materials and methods

Data selection

To create a database of the effects of earthworm invasion on understory plant communities in North American forests, we performed a search in July 2014 in the ISI Web of Science database using the keywords ('earthworm*') AND ('exotic' OR 'invasive'). These search terms were selected in order to include a wide array of studies that addressed the effects of introduced earthworms on aboveground communities. From the initial list of 359 studies (see PRISMA diagram; Appendix S1), we examined each title and abstract to determine whether they met the inclusion criteria. Our inclusion criteria were that each study: (i) was performed in a North American forest ecosystem, (ii) reported density, biomass, or presence/absence of introduced earthworms that were identified either to species or earthworm ecological group and (iii) reported the cover or presence/absence of plant species (or plant functional groups) in the forest understory. Subsequently, we communicated with authors of the selected studies to obtain raw data for earthworm and plant communities. When raw data were not available, means or effect sizes were extracted directly from figures and tables. Through personal knowledge of the authors, we also obtained data from three Masters theses. In total, we identified 14 unique studies meeting our inclusion criteria (Appendix S2 and Table S1) that allowed us to examine associations of introduced earthworm community properties (density, biomass, and ecological group richness) with understory plant community properties (diversity, species richness, and evenness: 13 studies, 233 effect sizes) and with cover of plant growth forms and native or non-native status (11 studies, 412 effect sizes). As most studies used hierarchical sampling designs, effect sizes were calculated at the site level for each combination of earthworm and plant community measures to capture within-study variation.

Data description and preparation

Studies meeting the inclusion criteria were published between 2006 and 2015 and were predominantly located in the Upper Midwest and Mid-Atlantic regions of the United States, from Indiana, the United States to Alberta, Canada (Table S1). Plant communities were typically assessed using plots (median area = 1.4 m²; range = 0.25–100 m²) in which identity and percent cover were recorded for each species. Most studies assessed plant communities once; for those that did so over multiple years, we calculated the mean percent cover of each plant species over the study period. Species richness (number of species), diversity (Shannon–Wiener diversity), and evenness (Evar; Smith & Wilson, 1996) of the understory plant community (usually all species less than 1 m tall) were calculated at the plot level. Plant growth habits and plant native status were extracted from the USDA plant database (USDA, 2014) for each species and categorized into three functional groups; woody, herbaceous, and graminoid (grasses and sedges), and either native or non-native. Cover of each plant functional group or plant native status was calculated as the summed percent of total cover in a plot.

In general, earthworm communities were sampled in subplots (0.06–0.25 m²) nested within vegetation plots. Earthworms were extracted using a variety of techniques, for example, liquid mustard, cover boards, or formalin (Table S1), sorted to species or earthworm ecological group, counted, and/or weighed. For each plot, we calculated three measures of introduced earthworm communities: total biomass (g m⁻²), total density (number of individuals m⁻²), and richness of earthworm ecological groups (0–3). Introduced earthworm species were categorized into three ecological groups, anecic, epigeic, and endogeic (Table S2), which reflect differences in habitat and feeding preferences (Bouché, 1977; Bohlen *et al.*, 2004). While widely used, this classification system may not be optimal as earthworm ecological groups cover a range of sizes and feeding behaviors (Lavelle, 1983; Brown, 1995). For example, *Lumbricus rubellus* and *Aporrectodea longa* are typically classified as epigeic and anecic, respectively, but their feeding behavior places them between different ecological groups ('epi/endogeic' and 'anecic-endogeic', respectively; Eisenhauer *et al.*, 2008; Ferlian *et al.*, 2014). As earthworm communities were sampled with different frequencies across studies (Table S1), we calculated the mean of each measure of earthworm communities per plot across sampling periods.

Effect sizes

To estimate the direction and strength of the relationships between introduced earthworm and plant communities, Spearman's rank correlation coefficients were calculated because most data were not distributed normally (Myers & Sirois, 2014). Spearman's correlation coefficients were transformed to Pearson's correlations and then converted to Fisher's *z* transformation of *r* for analysis to normalize the distribution of data (Koricheva *et al.*, 2013). Sampling variance for Fisher's *z* transformation of *r* was calculated using unbiased estimates following Hedges (1989). Differences in data collection in particular studies prevented effect sizes from being calculated for all possible combinations of plant and earthworm community measures (Table S1).

Data analysis

We used multilevel, meta-analytic regression models to estimate mean effect sizes of the relationships between introduced earthworm and plant communities in North American forests with the 'metafor' package (Viechtbauer, 2010). These models account for the nonindependence of measures taken from the same study (Nakagawa & Santos, 2012; Koricheva *et al.*, 2013). For all models, we used a random intercept term where 'site' was nested within 'study'. Observations from studies were weighted by the inverse of the sampling variance (Viechtbauer, 2010). Separate models using restricted maximum likelihood estimation were fitted for each measure of plant diversity and each plant functional group or native status. In all models, introduced earthworm community measures were included as a categorical moderator variable to test whether these measures had similar or

contrasting effects. Model assumptions were checked by visually inspecting residuals for homogeneity and Pearson residuals for normality. To assess whether publication bias affected the results of our analyses, we visually inspected contour funnel plots (Koricheva & Gurevitch, 2014). We assessed the sensitivity of our analyses to the type of earthworm sampling technique, for example, formalin, liquid mustard, or cover boards. To do so, we added earthworm sampling technique as a fixed effect and its interaction with earthworm community measures to our original models. All analyses were performed using R 3.2.3 (R Core Team, 2015). Effect sizes and sampling variances used for all analyses are included as Supporting Information (for metadata, see Appendices S3 & S4).

Results

Plant diversity

We found that plant species diversity was significantly and negatively correlated with richness of earthworm ecological groups (Fig. 1; 95% confidence intervals did not overlap with zero), but was not significantly correlated with earthworm biomass or density. Plant species evenness and richness were not significantly correlated with any measure of introduced earthworm communities (Fig. 1). For each plant community variable, effect sizes were similar for earthworm biomass, density, and ecological group richness (Table 1).

Plant community composition

Graminoid cover was significantly positively correlated with introduced earthworm biomass, density, and ecological group richness (Fig. 2). In contrast, cover of neither herbaceous nor woody plants was significantly correlated with any measure of introduced earthworm communities. Non-native plant cover exhibited a significant, positive correlation with introduced earthworm biomass (Fig. 3), but not with introduced earthworm density or richness of earthworm ecological groups. Native plant cover decreased, albeit nonsignificantly (mean effect size = -0.24 ; 95% confidence interval = -0.49 – 0.01), with increasing introduced earthworm biomass.

Effect sizes for the relationships of native and non-native plants with introduced earthworm communities differed significantly depending on the earthworm community measure (Table 1). Native plant cover and non-native plant cover were more strongly related to introduced earthworm biomass than to either earthworm density or richness of earthworm ecological groups (Fig. 3).

Across-study variation

For all models testing the association between plant diversity and community composition with introduced

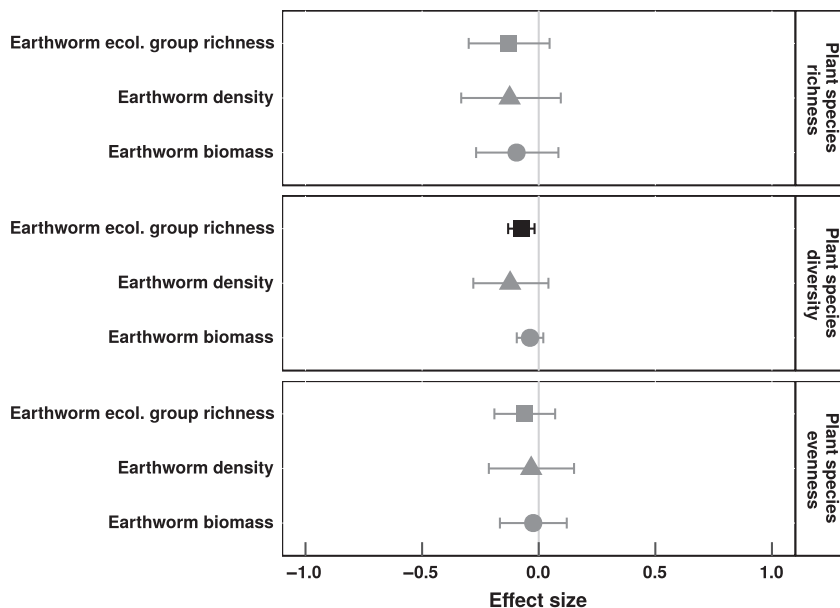


Fig. 1 Mean effect sizes of relationships between introduced earthworm communities and plant species richness, diversity, and evenness of forest understory communities in North America. Whisker bars are 95% confidence intervals: Black whisker bars did not overlap with zero. Mean effect sizes are Pearson's correlation coefficients. Plant species diversity was calculated using Shannon–Wiener diversity, and plant species evenness was calculated using Evar (Smith & Wilson, 1996). Earthworm biomass is biomass of introduced earthworms (g m^{-2}), earthworm density is number of introduced earthworms ($\text{individuals m}^{-2}$), and earthworm ecological group richness is the number of introduced earthworm ecological groups.

Table 1 Summary of meta-analytic mixed-effects models testing the relationships between introduced earthworm biomass, density, and ecological group richness and plant diversity, native and non-native status, and functional group cover of forest understory communities in North America

| Response variable | Studies | Observations | AICc | Residual heterogeneity | L |
|--------------------------------|---------|--------------|-------|------------------------|-----|
| <i>Plant diversity</i> | | | | | |
| Plant species richness | 13 | 83 | 56.1 | 209.2 | 0.4 |
| Plant species diversity | 10 | 75 | 43.0 | 112.8 | 0.4 |
| Plant species evenness | 10 | 75 | 28.2 | 98.0 | 0.5 |
| <i>Plant functional groups</i> | | | | | |
| Herbaceous cover | 11 | 102 | 35.5 | 188.8 | 3.4 |
| Graminoid cover | 9 | 88 | 37.1 | 203.9 | 1.2 |
| Woody cover | 11 | 102 | 458.6 | 816.6 | 3.4 |
| <i>Plant native status</i> | | | | | |
| Native plant cover | 10 | 61 | 67.1 | 262.0 | 7.9 |
| Non-native plant cover | 9 | 59 | 60.5 | 221.4 | 8.7 |

Meta-analytic mixed-effects models evaluated the size effects representing the association between a measure of introduced earthworm community abundance or structure (density, biomass, richness of earthworm ecological groups) and plant diversity, plant native and non-native status, or cover of plant functional groups. Plant species diversity is Shannon–Wiener diversity, plant species evenness is Smith and Wilson’s evenness measure (‘Evar’; Smith & Wilson, 1996). Residual heterogeneity shows if the variability of the effect sizes not captured by the moderator variables is heterogeneous. The moderator variable in all models was a categorical factor representing measures of introduced earthworm communities. L is the likelihood ratio test statistic for model coefficients. Values of residual heterogeneity and L in black italics indicate statistical significance ($\alpha = 0.05$).

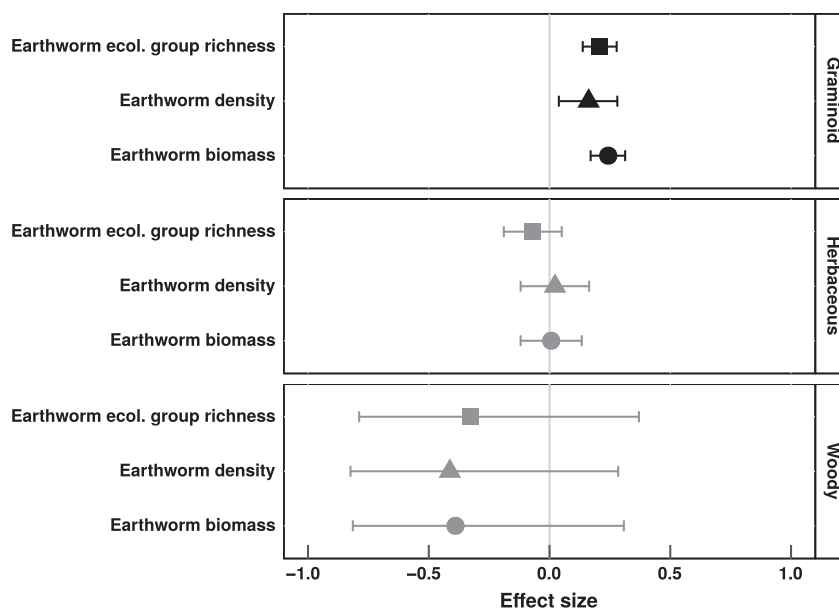


Fig. 2 Mean effect sizes of relationships between introduced earthworm communities and cover of plant functional groups in forest understory communities in North America. Whisker bars are 95% confidence intervals: Black whisker bars did not overlap with zero. Effect sizes are Pearson’s correlation coefficients. Earthworm biomass is biomass of introduced earthworms (g m^{-2}), earthworm density is number of introduced earthworms ($\text{individuals m}^{-2}$), and earthworm ecological group richness is the number of introduced earthworm ecological groups.

earthworm communities, the results showed a consistent and statistically significant amount of residual heterogeneity among studies (Table 1). In other words, our analysis detected that additional, unmeasured variables would be important for explaining the association

between plant and earthworm communities. Visual inspection of contour funnel plots did not reveal publication bias toward over-reporting relationships between plant diversity or community composition with non-native earthworm abundance or community

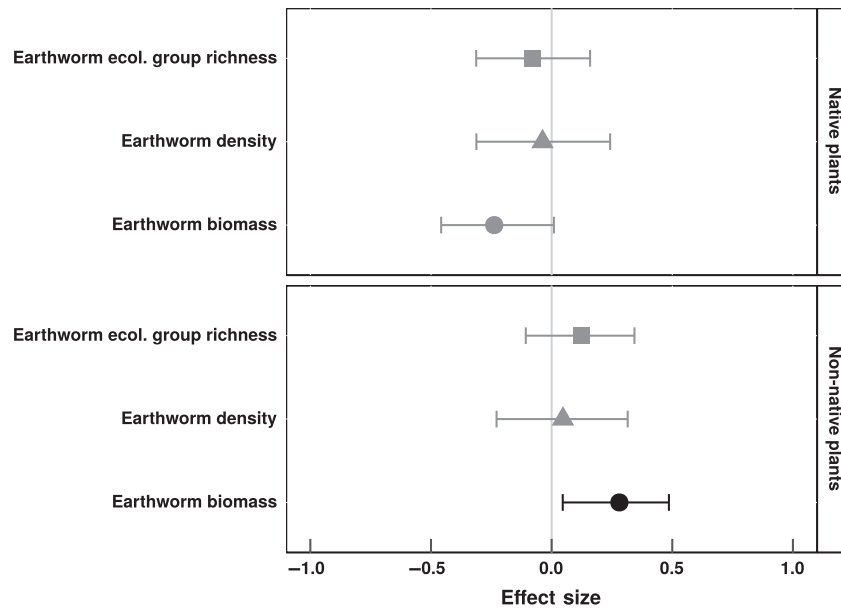


Fig. 3 Mean effect sizes of relationships between introduced earthworm communities and cover of native and non-native plants in forest understory communities in North America. Whisker bars are 95% confidence intervals: Black whisker bars did not overlap with zero. Effect sizes are Pearson's correlation coefficients. Earthworm biomass is biomass of introduced earthworms (g m^{-2}), earthworm density is number of introduced earthworms ($\text{individuals m}^{-2}$), and earthworm ecological group richness is the number of introduced earthworm ecological groups.

composition. Results from the sensitivity analyses indicated that different earthworm sampling techniques did not influence the association between plant diversity and community composition with introduced earthworm communities. For all models, the interaction of earthworm sampling technique and earthworm community measures was not statistically significant ($P > 0.10$).

Discussion

The extensive effects of introduced ecosystem engineers, such as earthworms, in North American forests could have transformative impacts on biodiversity and diversity-dependent ecosystem functions (Ehrenfeld, 2010). Here, we present the first quantitative meta-analysis showing that introduced earthworms are significantly associated with declines in plant species diversity and changes in plant community composition across multiple studies in North American forests.

Changes in plant diversity

Our analysis showed that earthworm invasion significantly influences plant species diversity. Forests with multiple earthworm ecological groups had significantly lower plant diversity than forests with fewer earthworm ecological groups. While particular earthworm species or ecological groups may have specific effects

on seed fate and seedling growth and mortality (e.g., Asshoff *et al.*, 2010; Eisenhauer *et al.*, 2012; Fahey *et al.*, 2013; Drouin *et al.*, 2014; Groffman *et al.*, 2015), our results highlight the combined impacts of multiple earthworm ecological groups on plant communities (Hale *et al.*, 2005). Changes in plant species diversity likely occurred through a number of direct mechanisms, such as seed or seedling ingestion (Eisenhauer *et al.*, 2010; Clause *et al.*, 2015; Cassin & Kotanen, 2016), and indirect mechanisms, including altering water or nutrient availability, mycorrhizal associations, and soil structure (Hale *et al.*, 2005; Holdsworth *et al.*, 2007b; Dobson & Blossey, 2015; Resner *et al.*, 2015; Paudel *et al.*, 2016). While richness of earthworm ecological groups was positively and significantly correlated with earthworm density and biomass (Fig. S1 and Table S3), neither of the latter surrogates for earthworm activity exhibited significant associations with plant species diversity. In contrast to richness of earthworm ecological groups, variation in earthworm density or biomass may not fully capture the progression of earthworm invasion impacts (Loss *et al.*, 2013) and, rather, may reflect changes in dominance of particular earthworm species, such as small-bodied *D. octaedra*, large-bodied *L. terrestris* (Hale *et al.*, 2004) or entire ecological groups (Hale *et al.*, 2005; Eisenhauer *et al.*, 2007; Holdsworth *et al.*, 2007b).

In line with recent global meta-analyses on local-scale changes in species richness (Vellend *et al.*, 2013;

Dornelas *et al.*, 2014; but see Gonzalez *et al.*, 2016), we found that plant species richness was robust to earthworm invasion. Despite no average change in plant species richness or evenness, there were clear changes in plant diversity and community composition. This result also could reflect scale-dependent effects of earthworm invasions on plant diversity (Powell *et al.*, 2013); similar to plant invasions, earthworm invasion may alter the slope and intercept of the species–area relationship by changing species abundance distributions.

Changes in plant community composition: native versus non-native plant species

We provide clear evidence that non-native plant cover is positively associated with biomass of introduced earthworms, thus supporting the ‘invasional meltdown’ hypothesis (Simberloff & Von Holle, 1999). Plant species that coevolved in the presence of earthworms, that is plant species of European and Asian origin, could have adaptations that confer tolerance to the presence of earthworms. Non-native plant species may be adapted to similar soil conditions as those found in earthworm-invaded forests, such as high soil pH and sparse litter cover (Nuzzo *et al.*, 2009; Beauséjour *et al.*, 2014; Whitfield *et al.*, 2014). The bioturbation of the forest floor associated with earthworm invasion also may favor non-native plant species without obligate mycorrhizal associations (Lawrence *et al.*, 2003; Paudel *et al.*, 2016). Furthermore, introduced earthworms have been found to have positive, direct effects on non-native plant species (Roth *et al.*, 2015) by burying seeds in their burrows, which have high nutrient concentrations and may attenuate drought stress (Migge-Kleian *et al.*, 2006; Eisenhauer & Scheu, 2008). There is also growing evidence of a synergistic effect of introduced earthworms and deer herbivory on non-native plant species (Dávalos *et al.*, 2015). Particularly in newly invaded North American forests, introduced earthworms – in combination with deer herbivory – may be increasing disturbance frequency relative to historical norms (Frelich *et al.*, 2012), which is an important factor in explaining increases in the abundance of non-native species (Moles *et al.*, 2012).

Our analysis showed that cover of native plant species did not change consistently in earthworm-invaded forests. While the trend of decreasing native species cover with increasing introduced earthworm biomass supports the idea that earthworm invasion may lead to declines in native plant species diversity (Nuzzo *et al.*, 2009), high across-study variation reduced the overall strength of this signal. This result suggests that physical disturbance of the forest floor by introduced

earthworms may increase the heterogeneity of regeneration sites, creating a greater diversity of favorable microhabitats for seed germination of both native and non-native plant species (Asshoff *et al.*, 2010; Nuzzo *et al.*, 2015). In addition, we found that total plant cover increased significantly with earthworm biomass (Fig. S2 and Table S4), possibly indicating that earthworm invasion enhances germination of many plant species (Nuzzo *et al.*, 2015). Results from previous studies have shown both positive and negative effects of introduced earthworms on seedling survival of native plant species. Dobson & Blossey (2015) found that twelve of fifteen native species were negatively affected by earthworm invasion, while other microcosm and field studies have reported both types of responses to the presence of introduced earthworms (Holdsworth *et al.*, 2007a; Corio *et al.*, 2009; Drouin *et al.*, 2014). Native species’ responses to earthworms could be driven by tolerance to drought and frost upheaval (Dobson & Blossey, 2015), mycorrhizal associations (Lawrence *et al.*, 2003; Paudel *et al.*, 2016), or tolerance to root herbivory (Cameron *et al.*, 2014).

Changes in plant community composition: graminoids

We predicted and found a positive relationship between graminoid cover and all measures of earthworm invasion. This finding suggests that earthworm invasion acts as a significant ecological filter that appears to drive strong changes in plant community composition. The long-term effects of earthworm invasion on abiotic conditions in the forest understory, for example, rapid soil nutrient release and subsequent depletion, decreased soil water content, and increased surface runoff (Hale *et al.*, 2005; Eisenhauer *et al.*, 2012; Resner *et al.*, 2015), may confer a competitive advantage to graminoids, particularly those with greater drought tolerance (Craine *et al.*, 2013) and persistent bud banks (Bond, 2008; VanderWeide & Hartnett, 2015). Certain graminoids, such as those with greater tolerance of root herbivory (Cameron *et al.*, 2014; Gilbert *et al.*, 2014) or those without obligate mycorrhizal associations (e.g., *Carex pensylvanica*; Holdsworth *et al.*, 2007a), also may respond positively to earthworm invasion. However, positive responses of graminoids to earthworms might be restricted to a subset of species within this functional group (Corio *et al.*, 2009; Dobson & Blossey, 2015). Increasing graminoid cover in North American forests also may be attributable to positive, synergistic interactions with co-occurring disturbances, such as deer browsing, fire history, forest management, and land-use history (Powers & Nagel, 2008; Fisichelli *et al.*, 2013). Given the prevalence of disturbances in northern North American forests that may influence biodiversity

(Murphy & Romanuk, 2014), future studies should account for co-occurring disturbances to add greater precision to estimates of the impacts of earthworm invasion on biodiversity of above- and belowground communities (Cameron *et al.*, 2016).

Variation across studies

Across studies, impacts of earthworm invasion were significantly heterogeneous, likely due to variation in biophysical factors (Hale *et al.*, 2005; Resner *et al.*, 2015), invasion history (Hale *et al.*, 2006), and co-occurring disturbances (Fisichelli *et al.*, 2013; Dávalos *et al.*, 2015). Variation and error associated with measurement of earthworm and plant communities also may contribute to this heterogeneity. Estimates of earthworm density or biomass may be imprecise or inconsistent because of the scale of sampling, time of year, and year to year fluctuations in abundance (Callaham & Hendrix, 1997). In contrast, measures of plant communities likely reflect the history of earthworm invasion at a given site (Larson *et al.*, 2010), which may also vary within studies (e.g., Hale *et al.*, 2006; Holdsworth *et al.*, 2007b). However, one-time plant inventories along earthworm invasion fronts have a limited capacity to capture taxonomic and functional turnover of plant communities in response to earthworm invasion; repeated inventories, including those of uninvaded forests to establish pre-invasion baselines, are vital for improving current estimates of biodiversity change (Eisenhauer *et al.*, 2016; Gonzalez *et al.*, 2016). Disentangling the impacts of earthworm invasion from biophysical and other co-occurring disturbances on plant communities may be best addressed by combining field experiments (e.g., Dobson & Blossey, 2015) with quantitative trait and phylogenetic information (e.g., Cassin & Kotanen, 2016; Lemoine *et al.*, 2016). Accounting for such factors in future studies, particularly in regions where plant communities have interacted with native earthworm fauna, would help to clarify the mechanisms through which earthworm invasion affects biodiversity.

Overall, our results show that earthworm invasion is associated with significant changes in the diversity of plant communities in North American forests. By changing the functional composition and facilitating the invasion of non-native plant species, earthworm invasion may have long-lasting impacts on ecosystem functioning and services in these forests. Furthermore, there is growing evidence that terrestrial, invertebrate invaders likely have strong impacts on other trophic levels and associated ecosystem functions (Wardle *et al.*, 2011; Cameron *et al.*, 2016), which may be accentuated with climate change (Eisenhauer *et al.*, 2012). A more holistic approach to assessing the impacts of

earthworm invasion, therefore, will be vital for developing management and conservation strategies that enhance the resilience of North American forests (Nimmo *et al.*, 2015).

Acknowledgments

This project received support from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (grant agreement no 677232), the German Research Foundation (DFG FZT 118), and the German Academic Exchange Service (DAAD).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1.

Appendix S1. PRISMA diagram

Appendix S2. References of studies included in meta-analysis

Appendix S3. Metadata of 'Cravenetal_Earthworms_PlantDiversity.csv'

Appendix S4. Metadata of 'Cravenetal_EffectSizes_Earthworms_PlantFuncGroups.csv'

Table S1. Studies included in meta-analysis and additional information about each study

Table S2. Introduced earthworm species and their corresponding ecological groups

Table S3. Summary of mixed-effects model testing associations between introduced earthworm biomass, density, and ecological group richness.

Table S4. Summary of mixed-effects model testing the relationships between introduced earthworm biomass, density, and ecological group richness and total plant cover.

Fig. S1. Frequency of earthworm ecological group richness and correlations among measures of introduced earthworm abundance.

Fig. S2. Effect sizes of relationships between introduced earthworm communities and total plant cover.

Data S2. Cravenetal_Earthworms_PlantDiversity.csv

Data file containing effect sizes of relationships between introduced earthworm communities and plant species diversity, evenness, and richness of forest understory communities in North America.

Data S3. Cravenetal_Earthworms_PlantFunctionalGroups.csv

Data file containing effect sizes of relationships between introduced earthworm communities and cover of plant functional groups of forest understory communities in North America.