

## Research



**Cite this article:** Jochum M, Thouvenot L, Ferlian O, Zeiss R, Klarner B, Pruschitzki U, Johnson EA, Eisenhauer N. 2022 Aboveground impacts of a belowground invader: how invasive earthworms alter aboveground arthropod communities in a northern North American forest. *Biol. Lett.* **18**: 20210636. <https://doi.org/10.1098/rsbl.2021.0636>

Received: 1 December 2021

Accepted: 9 March 2022

### Subject Areas:

ecology

### Keywords:

belowground, aboveground, earthworm invasion, insect decline, forest, Canada

### Author for correspondence:

Malte Jochum

e-mail: [malte.jochum@idiv.de](mailto:malte.jochum@idiv.de)

†Current address: Technical University of Munich, Chair for Terrestrial Ecology, Hans-Carl-von-Carlowitz-Platz 2, D-85354 Freising, Germany.

A contribution to the special feature 'Insect Decline' organised by Martin Gossner, Florian Menzel and Nadja Simons.

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.5896147>.

# Aboveground impacts of a belowground invader: how invasive earthworms alter aboveground arthropod communities in a northern North American forest

Malte Jochum<sup>1,2</sup>, Lise Thouvenot<sup>1,2</sup>, Olga Ferlian<sup>1,2</sup>, Romy Zeiss<sup>1,2</sup>, Bernhard Klarner<sup>3</sup>, Ulrich Pruschitzki<sup>1,2,†</sup>, Edward A. Johnson<sup>4</sup> and Nico Eisenhauer<sup>1,2</sup>

<sup>1</sup>German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstrasse 4, 04103 Leipzig, Germany

<sup>2</sup>Leipzig University, Institute of Biology, Puschstrasse 4, 04103 Leipzig, Germany

<sup>3</sup>J.F. Blumenbach Institute of Zoology and Anthropology, University of Goettingen, Untere Karspuele 2, Goettingen 37073, Germany

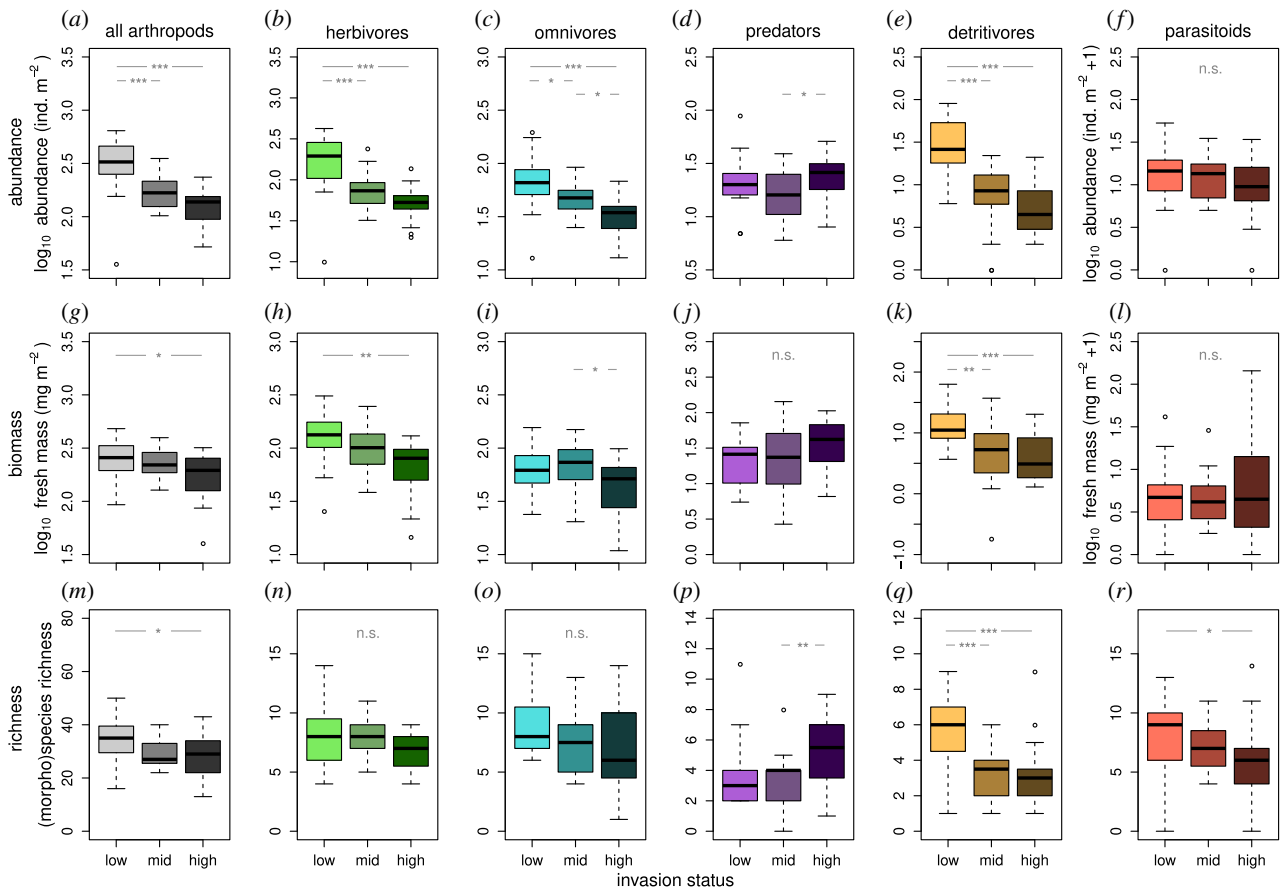
<sup>4</sup>Department Biological Sciences, University of Calgary, Calgary, Alberta, Canada T2N 1N4

MJ, 0000-0002-8728-1145; LT, 0000-0002-8719-6979; OF, 0000-0002-2536-7592; RZ, 0000-0001-8862-9185; BK, 0000-0003-1867-4911; EAJ, 0000-0002-4710-9295; NE, 0000-0002-0371-6720

Declining arthropod communities have recently gained a lot of attention, with climate and land-use change among the most frequently discussed drivers. Here, we focus on a seemingly underrepresented driver of arthropod community decline: biological invasions. For approximately 12 000 years, earthworms have been absent from wide parts of northern North America, but they have been re-introduced with dramatic consequences. Most studies investigating earthworm-invasion impacts focus on the belowground world, resulting in limited knowledge on aboveground-community changes. We present observational data on earthworm, plant and aboveground arthropod communities in 60 plots, distributed across areas with increasing invasion status (low, medium and high) in a Canadian forest. We analysed how earthworm-invasion status and biomass impact aboveground arthropod community abundance, biomass and species richness, and how earthworm impacts cascade across trophic levels. We sampled approximately 13 000 arthropods, dominated by Hemiptera, Diptera, Araneae, Thysanoptera and Hymenoptera. Total arthropod abundance, biomass and species richness declined significantly from areas of low to those with high invasion status, with reductions of 61, 27 and 18%, respectively. Structural equation models suggest that earthworms directly and indirectly impact arthropods across trophic levels. We show that earthworm invasion can alter aboveground multi-trophic arthropod communities and suggest that belowground invasions might be underappreciated drivers of aboveground arthropod decline.

## 1. Introduction

Recent reports on arthropod species richness, abundance and biomass declines [1–3] have triggered concern about 'the little things that run our world' [4] and the consequences of their loss. Even though the situation might not be equally bad for all taxa and ecosystem types [5], the extent of the reported negative trends, together with the lack of sufficient long-term datasets to establish such trends across all taxa and ecosystems [6–8], are worrying. With arthropods



**Figure 1.** Effects of earthworm-invasion status (low, mid, high; lighter to darker colour shades) on the abundance (a–f), biomass (g–l) and (morpho)species richness (m–r) of total aboveground arthropods (grey), herbivores (green), omnivores (turquoise), predators (purple), detritivores (brown) and parasitoids (red). Asterisks and ‘n.s.’ illustrate significance levels for differences between invasion status categories (‘n.s.’ not significant,  $***p \leq 0.001$ ;  $**p \leq 0.01$ ;  $*p \leq 0.05$ ;  $p > 0.05$ ).  $p$ -values are from simple linear models and GLMs with Poisson-distributed response variables (richness models), respectively.  $N = 60$ . For model results, see table 1.

contributing to central ecosystem processes and services [9], their loss will have unprecedented consequences for ecosystems and human societies.

In order to halt or reverse arthropod decline, we need to understand the underlying drivers. Given their importance as broad global change drivers [10], it is unsurprising that climate and land-use change are prominent examples [1,5,11,12]. However, though underrepresented in research on arthropod declines, other drivers might still play an important role. Here, we focus on one potentially underappreciated driver of arthropod decline: the invasion of a belowground ecosystem engineer, earthworms [13].

Although commonly perceived as having mostly positive impacts on their environment [14,15], earthworms can transform invaded ecosystems [16] that are not able to deal with their impacts on the ecosystems’ physical, chemical and biological properties [17–20]. Earthworm invasion is a globally occurring problem [21]. One region with both particularly severe impacts and a lot of research on the consequences is northern North America. Here, most earthworm species present today have been absent since the last glaciation (maximum approximately 20 000, end of cover approximately 12 000 years ago) and have only been re-introduced a few hundred years ago [17,22].

Earthworm invasion alters soil abiotic conditions [17,19], plant communities [23–25] and soil fauna [26–29]. Moreover, there are reports of consequences for aboveground vertebrates, such as salamanders, birds and deer [18,30]. There

also are some aboveground invertebrate studies, but these mostly focus on litter-dwelling fauna [28,31]. With invasive earthworms impacting soil abiotic conditions, soil fauna, plants and litter-dwelling arthropods, the open question is whether and how their invasion impacts aboveground, vegetation-dwelling arthropods, and if these changes cascade across trophic levels. For example, earthworms could directly serve aboveground arthropods as a food resource [32] or indirectly affect them via altered habitat structure, resource availability (leaf litter) or plant communities [25,33]. We used observational data on earthworm, plant and aboveground arthropod communities from a Canadian forest to investigate (i) whether belowground invasion by earthworms changes aboveground arthropod communities and, using structural equation models (SEMs), (ii) how earthworms directly and indirectly impact higher trophic levels mediated by plants, herbivores and detritivores. We expected invasive earthworms to decrease the abundance, biomass and diversity of aboveground arthropod communities via cascading effects across trophic levels [18,34].

## 2. Material and methods

We studied a south-facing forest slope above the Northwestern shore of Barrier Lake, Kananaskis Valley, Alberta, Canada (51°02’6’’ N, 115°03’54’’ W, approximately 1450 m.a.s.l.). The forest is dominated by trembling aspen (*Populus tremuloides*) interspersed

**Table 1.** Results of models relating aboveground arthropod abundance, biomass and (morpho)species richness to invasion status (figure 1). For each model, the table shows the response variable, arthropod group, sample size ( $n$ ), model type, response transformation and  $p$ -values for Tukey *post hoc* and general linear hypotheses tests (see S2 and electronic supplementary material, SuppInfo paragraph 4).  $p$ -values significant to an alpha level of 0.05 are italicized. Values are rounded.

response	group	$n$	model type	resp. transf.	$p$ low-high	$p$ low-mid	$p$ mid-high
abundance	all	60	aov	$\log_{10}$	<0.001	<0.001	0.184
abundance	herbivores	60	aov	$\log_{10}$	<0.001	<0.001	0.137
abundance	omnivores	60	aov	$\log_{10}$	<0.001	0.040	0.030
abundance	predators	60	aov	$\log_{10}$	0.682	0.238	0.043
abundance	detritivores	60	aov	$\log_{10}$	<0.001	<0.001	0.424
abundance	parasitoids	60	aov	$\log_{10}(+1)$	0.405	0.991	0.480
biomass	all	60	aov	$\log_{10}$	0.042	0.800	0.166
biomass	herbivores	60	aov	$\log_{10}$	0.002	0.295	0.113
biomass	omnivores	60	aov	$\log_{10}$	0.060	0.845	0.015
biomass	predators	60	aov	$\log_{10}$	0.135	0.988	0.179
biomass	detritivores	60	aov	$\log_{10}$	<0.001	0.002	0.894
biomass	parasitoids	60	aov	$\log_{10}(+1)$	0.859	0.981	0.758
richness	all	60	glm.nb	none	0.025	0.058	0.942
richness	herbivores	60	glm	none	0.405	0.998	0.438
richness	omnivores	60	glm	none	0.074	0.199	0.884
richness	predators	60	glm	none	0.067	0.675	0.007
richness	detritivores	60	glm	none	<0.001	<0.001	0.963
richness	parasitoids	60	glm	none	0.033	0.519	0.329

with balsam poplar (*Populus balsamifera*), with a dense understorey vegetation and a grey luvisol soil. It has a long history of earthworm-invasion research, including investigations on soil abiotic (soil chemistry and physics) and biotic (micro, meso and macrofauna) aspects [29,30,35–37]. Land-use intensity is low and homogeneous across invasion status areas and the forest last burned in 1909 [29]. We combine community data on earthworms, plants and aboveground arthropods sampled in June and July 2019 on observational plots of the ‘EcoWorm’ project (described in Eisenhauer *et al.* [30]). After verifying earthworm-invasion status along the slope, we established 20 plots of 1 m  $\times$  2 m in each of three invasion status areas: low, mid and high invasion ( $n = 60$  plots, electronic supplementary material, SuppInfo S1 and figure S1). These categories differed significantly in earthworm abundance, biomass, species richness and functional group richness (electronic supplementary material, SuppInfo S1, figures S2 and S3). Thus, we focused on invasion status as the main predictor and show responses to earthworm biomass in the electronic supplementary material, SuppInfo. We used 1 m<sup>2</sup> for plant community assessments and the other half plot for arthropod (1 m<sup>2</sup>) and earthworm sampling (0.25 m<sup>2</sup>; electronic supplementary material, SuppInfo, figure S4). We identified every plant species and estimated total plant cover using a modified decimal scale [38], and we estimated plot-level canopy openness (for details, see electronic supplementary material, SuppInfo S1, figure S5).

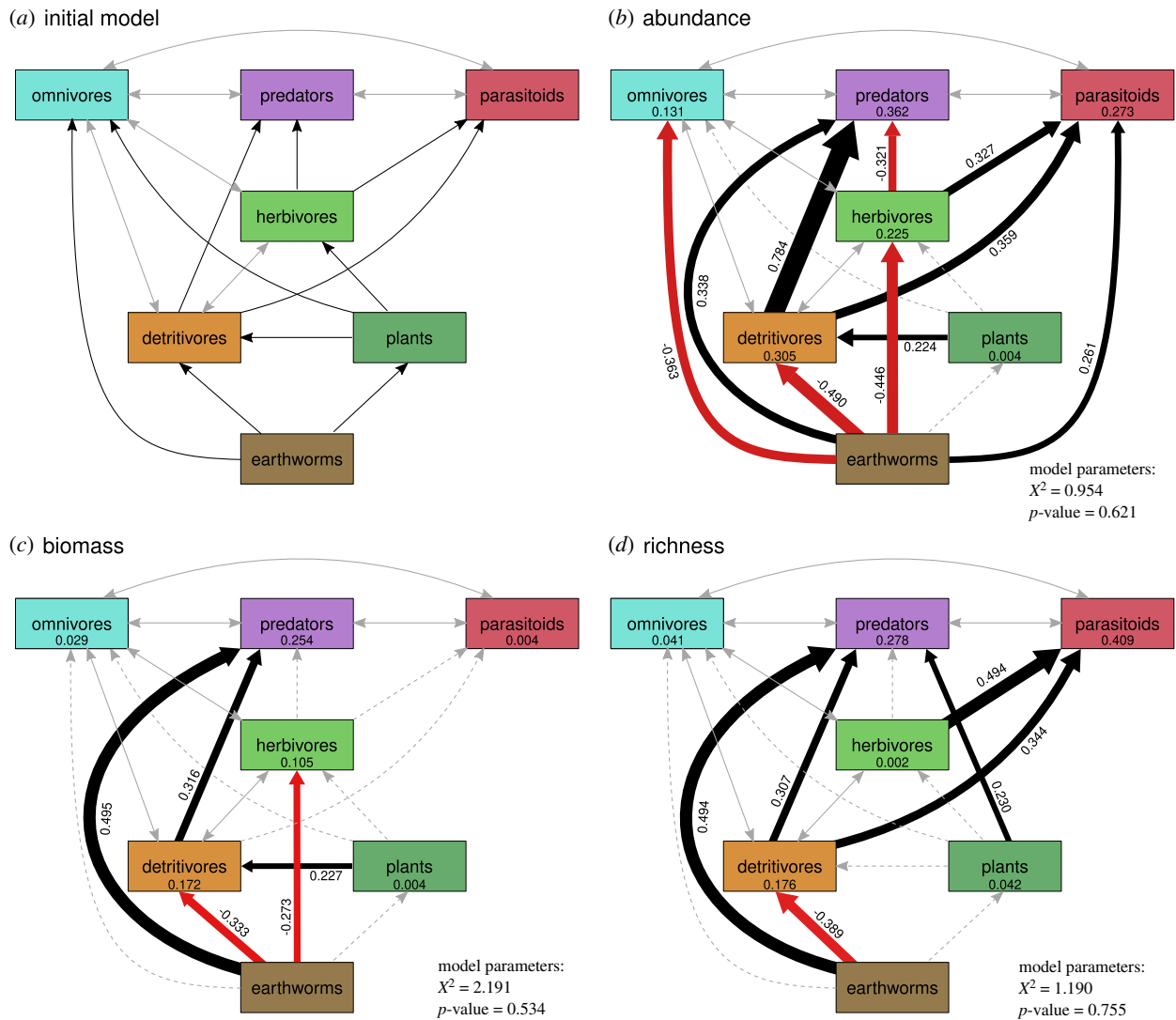
Earthworms were extracted using a combination of hand sorting and mustard extraction. Individuals were identified to species level, assigned to a functional group, and their fresh mass was assessed (electronic supplementary material, SuppInfo S1). We sampled aboveground arthropods using a vacuum suction sampler. All collected animals were hand-sorted, identified to (morpho-)species, assigned to a trophic feeding guild (see electronic supplementary material, SuppInfo S2 for details, figures S6 and S7, and table S1), and their fresh biomass was

estimated (electronic supplementary material, SuppInfo S3; [39–41]). We calculated abundance, biomass and species richness of all arthropods, and, separately, for herbivores, omnivores (combining all mixed-diet feeding guilds), predators, detritivores and parasitoids. While abundance and biomass were calculated based on all individuals (excluding mites and springtails), species richness was calculated based on adults only.

Data analysis was done in R v. 3.6.3 [42]. We assessed arthropod community responses to invasion using earthworm-invasion status (categorical: low, mid and high) and biomass (continuous,  $\log_{10}$ -transformed) as predictors in separate models for each predictor-response variable combination. For details on these analyses, please see electronic supplementary material, SuppInfo S4. We used the R lavaan 0.6-9 [43] package to construct SEMs testing direct and indirect effects of earthworm invasion on aboveground arthropod abundance, biomass and richness, separately (see electronic supplementary material, SuppInfo S6).

### 3. Results

We collected 13 037 aboveground invertebrates (230 Pulmonata individuals included; for brevity, hereafter: arthropods), 4814 of which were adults (for R-code and data, please see [44]). For taxonomic and trophic details, see electronic supplementary material, SuppInfo figures S6 and S7, and table S1. Arthropod communities differed between invasion status categories (figure 1) and along the observational earthworm biomass gradient (electronic supplementary material, SuppInfo, figure S8). Out of 18 models testing arthropod responses to earthworm-invasion status, 11 found significant negative relationships, while two relationships were positive



**Figure 2.** SEMs illustrating direct and indirect effects of earthworm invasion on plants and aboveground arthropod communities. (a) Initial model. Final models (b–d, abundance, biomass, and richness) were obtained following the steps outlined in the electronic supplementary material, SupplInfo S6. Brown boxes represent earthworm biomass. Dark green boxes represent plant total cover (b,c), or plant species richness (d). All other boxes represent trophic-group abundance (b), biomass (c) or species richness (d). Black and red arrows show positive and negative paths, respectively. Grey, double-headed arrows show covariances. Grey dashed arrows show non-significant paths. Numbers next to significant paths are standardized path coefficients. Numbers inside boxes show  $R^2$  values.  $N = 60$ . For detailed model outputs, see electronic supplementary material, tables S3–S5.

(figure 1 and table 1). All three total arthropod properties responded negatively to earthworm invasion (at least from 'low' to 'high' invasion). Predator abundance and richness increased with earthworm-invasion status (mid to high). Out of 18 models testing arthropod responses to increasing earthworm biomass, there were seven significant negative relationships and one significant positive relationship (electronic supplementary material, SupplInfo, figure S8 and table S2). Notably, total arthropod abundance declined, as well as herbivore abundance and biomass, omnivore abundance and detritivore abundance, biomass and richness; only predator biomass increased significantly.

The three SEMs showed direct and indirect effects of invasive earthworms on aboveground arthropod communities (figure 2; electronic supplementary material, tables S3–S5). Earthworm biomass directly increased predator and parasitoid abundance and directly decreased detritivore, herbivore and omnivore abundance (figure 2b). It indirectly increased predator abundance via herbivore abundance and indirectly decreased predator and parasitoid abundance via detritivore abundance. Earthworm biomass directly increased predator

biomass and directly decreased detritivore and herbivore biomass (figure 2c). It indirectly decreased predator biomass via detritivore biomass and parasitoid biomass via herbivore biomass. Earthworm biomass directly increased predator richness and directly decreased detritivore richness (figure 2d). It indirectly decreased predator and parasitoid richness via detritivore richness. There were no significant effects of earthworm biomass on plant cover or richness. However, higher plant cover facilitated detritivore abundance and biomass, while plant richness, which was positively correlated to canopy openness (electronic supplementary material, figure S8), facilitated predator richness.

## 4. Discussion

Our observational study highlights belowground invasions as a relevant, yet underrepresented driver of aboveground arthropod decline, with impacts cascading across trophic levels. All feeding types and community properties showed significant responses, with only predator communities



directly profiting from earthworm invasion in simple models. Our SEMs illustrate how these net positive effects can be decomposed into direct and indirect effects across trophic levels.

In contrast with our expectations, but in line with some previous work (e.g. [17,23]), earthworms had non-significant negative effects on the plant community. The lack of significance might be caused by earthworms changing plant functional diversity and composition instead of total cover and richness [24,45] or by high variability. Plant cover and species richness supported higher detritivore abundance and biomass, as well as predator richness—presumably by providing more resources and increased habitat heterogeneity [46,47]. Local microclimatic conditions (higher canopy openness) had an additional, indirect effect on aboveground arthropods, via increased plant species richness. This effect was independent of earthworm-invasion effects. Ubiquitous negative effects of earthworm biomass on detritivores, and omnivore abundance, were likely caused by exploitation competition for litter as a resource strongly diminished by earthworm invasion [17,25] and in this forest particularly [35]. Negative effects of earthworm biomass on herbivores might, for example, be caused by earthworm-induced changes in plant secondary metabolites [48], or alternatively via impacts on soil-dwelling herbivore life stages [27,29].

Across community properties, there were consistent and strong, direct positive effects of earthworm biomass on predators, and on parasitoid abundance, that were not mediated by plant richness or cover, or by intermediate trophic levels. Such effects might be mediated by altered habitat structure, such as reduced litter layers [35], or plant community properties [24], but we need further analyses to better understand the underlying mechanisms. It is likely that these seemingly direct effects are mediated by parameters not included in our models. Detritivores facilitated predators and parasitoids, the former as prey, the latter potentially as a host species, or indirectly via cascading positive effects on plants and herbivores (which we did not test; [49]). Herbivores facilitated parasitoids, most prominently in the richness SEM. As herbivore richness was not driven by plant richness, it might respond to plant functional diversity [50], which could also mediate the direct positive effect of earthworms on parasitoids. Finally, the negative relationship between herbivore and predator abundance might indicate that predators have reduced herbivores (top-down effect) instead of herbivores increasing predators (bottom-up effect; [51]).

As one of the first studies reporting effects of invasive earthworms on aboveground arthropod communities (see [28,31]), our paper highlights several topics for future research. First, we need studies investigating the effects of

earthworm invasion on vegetation structure, functional diversity and plant metabolites, as well as their impact on arthropod communities [45,48,52]. Furthermore, we need to assess the consequences of belowground invasions and the subsequent aboveground arthropod community changes for consumers of arthropods [12], above-belowground energy flux, ecosystem functions and services [8,53,54]. Future studies should also investigate if earthworm invasion facilitates secondary invasions in aboveground arthropod communities, potentially facilitated by non-native plants [23]. Also, they should assess how earthworm invasion might relate to and interact with other global-change drivers such as climate and land-use change to alter aboveground arthropod communities [55,56]. Finally, given the varying responses of abundance, biomass and richness, our results suggest that including multiple community parameters is key when comprehensively assessing the mechanisms of arthropod community declines under global change.

**Data accessibility.** R-code, data, and a README file are provided in the electronic supplementary material [44]. The methods section, SupplInfo and README files provide all necessary information about the dataset.

**Authors' contributions.** M.J.: conceptualization, data curation, formal analysis, investigation, methodology, software, validation, visualization, writing—original draft and writing—review and editing; L.T.: conceptualization, data curation, investigation, methodology, writing—review and editing; O.F.: conceptualization, data curation, investigation, methodology, writing—review and editing; R.Z.: investigation, methodology and writing—review and editing; B.K.: investigation, methodology and writing—review and editing; U.P.: investigation and writing—review and editing; E.A.J.: project administration and writing—review and editing; N.E.: conceptualization, funding acquisition, methodology, project administration, resources, supervision and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

**Competing interests.** We declare we have no competing interests.

**Funding.** European Research Council (European Union's Horizon 2020 research and innovation program): grant no. 677232 to N.E. German Centre for Integrative Biodiversity Research Halle-Jena-Leipzig, funded by the German Research Foundation: FZT 118, 202548816. German Research Foundation: DFG Ei 862/18-1 to L.T. and N.E. The authors acknowledge support from the iDiv Open Science Publication Fund.

**Acknowledgements.** Svenja Haenzel: coordination. Lotte Horn, Michelle Ives, Morgan Blieske and Sophia Findeisen: field- and laboratory-work, data management. Barrier Lake Field Station, Adrienne Cunnings (University of Calgary): accommodation and support. Julius Quosh: canopy-openness processing. Ian Macdonald: help with identification of plant species.

**Disclaimer.** We thank the Government of Alberta, Canada, for granting access and permits (Alberta Environment and Parks, permit no. 19-260) to do research in the forest at Barrier Lake.

## References

- Habel JC, Segerer A, Ulrich W, Torchyk O, Weisser WW, Schmitt T. 2016 Butterfly community shifts over two centuries. *Conserv. Biol.* **30**, 754–762. (doi:10.1111/cobi.12656)
- Hallmann CA *et al.* 2017 More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE* **12**, e0185809. (doi:10.1371/journal.pone.0185809)
- Seibold S *et al.* 2019 Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* **574**, 671–674. (doi:10.1038/s41586-019-1684-3)
- Wilson EO. 1987 The little things that run the world (The importance and conservation of invertebrates). *Conserv. Biol.* **1**, 344–346. (doi:10.1111/j.1523-1739.1987.tb00055.x)
- van Klink R, Bowler DE, Gongalsky KB, Swengel AB, Gentile A, Chase JM. 2020 Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science* **368**, 417–420. (doi:10.1126/science.aax9931)
- Stuart SN, Wilson EO, McNeely JA, Mittermeier RA, Rodríguez JP. 2010 The barometer of life. *Science* **328**, 177. (doi:10.1126/science.1188606)

7. Eisenhauer N, Bonn A, Guerra C. 2019 Recognizing the quiet extinction of invertebrates. *Nat. Commun.* **10**, 1–3. (doi:10.1038/s41467-018-07916-1)
8. Eisenhauer N, Hines J. 2021 Invertebrate biodiversity and conservation. *Curr. Biol.* **31**, 1214–1218. (doi:10.1016/j.cub.2021.06.058)
9. Noriega JA *et al.* 2018 Research trends in ecosystem services provided by insects. *Basic Appl. Ecol.* **26**, 8–23. (doi:10.1016/j.baae.2017.09.006)
10. Díaz S *et al.* (eds). 2019 *Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. Bonn, Germany: IPBES secretariat.
11. Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR. 2008 Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl Acad. Sci. USA* **105**, 6668–6672. (doi:10.1073/pnas.0709472105)
12. Lister BC, Garcia A. 2018 Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proc. Natl Acad. Sci. USA* **115**, E10397–E10406. (doi:10.1073/pnas.1722477115)
13. Jones C, Lawton JH, Shachak M. 1994 Organisms as ecosystem engineers. *Oikos* **69**, 373–386. (doi:10.2307/3545850)
14. Blouin M *et al.* 2013 A review of earthworm impact on soil function and ecosystem services. *Eur. J. Soil Sci.* **64**, 161–182. (doi:10.1111/ejss.12025)
15. Van Groenigen JW, Lubbers IM, Vos HM, Brown GG, De Deyn GB, Van Groenigen KJ. 2014 Earthworms increase plant production: a meta-analysis. *Sci. Rep.* **4**, 1–7. (doi:10.1038/srep06365)
16. Hendrix PF, Bohlen PJ. 2002 Exotic earthworm invasions in North America: ecological and policy implications. *Bioscience* **52**, 801. (doi:10.1641/0006-3568(2002)052[0801:EEIINA]2.0.CO;2)
17. Bohlen PJ, Scheu S, Hale CM, Mclean MA, Migge S, Groffman PM, Parkinson D. 2004 Non-native invasive earthworms as agents of change in northern temperate forests. *Front. Ecol. Environ.* **2**, 427–435. (doi:10.1890/1540-9295(2004)002[0427:NIEAAO]2.0.CO;2)
18. Frelich LE *et al.* 2019 Side-swiped: ecological cascades emanating from earthworm invasions. *Front. Ecol. Environ.* **17**, 502–510. (doi:10.1002/fee.2099)
19. Ferlian O, Thakur MP, Castañeda González A, San Emeterio LM, Marr S, da Silva Rocha B, Eisenhauer N. 2020 Soil chemistry turned upside down: a meta-analysis of invasive earthworm effects on soil chemical properties. *Ecology* **101**, 1–12. (doi:10.1002/ecy.2936)
20. Chang CH *et al.* 2021 The second wave of earthworm invasions in North America: biology, environmental impacts, management and control of invasive jumping worms. *Biol. Invasions* **23**, 3291–3322. (doi:10.1007/s10530-021-02598-1)
21. Hendrix PF, Callahan MA, Drake JM, Huang CY, James SW, Snyder BA, Zhang W. 2008 Pandora's box contained bait: the global problem of introduced earthworms. *Annu. Rev. Ecol. Evol. Syst.* **39**, 593–613. (doi:10.1146/annurev.ecolsys.39.110707.173426)
22. James SW, Hendrix PF. 2004 Invasion of exotic earthworms into North America and other regions. In *Earthworm ecology* (ed. CA Edwards), pp. 75–88. Boca Raton, FL: CRC Press.
23. Craven D *et al.* 2017 The unseen invaders: introduced earthworms as drivers of change in plant communities in North American forests (a meta-analysis). *Glob. Chang. Biol.* **23**, 1065–1074. (doi:10.1111/gcb.13446)
24. Fleri JR, Martin TG, Rodewald AD, Arcese P. 2021 Non-native earthworms alter the assembly of a meadow plant community. *Biol. Invasions* **23**, 2407–2415. (doi:10.1007/s10530-021-02513-8)
25. Nuzzo VA, Maerz J, Blossey B. 2009 Earthworm invasion as the driving force behind plant invasion and community change in northeastern North American forests. *Conserv. Biol.* **23**, 966–974. (doi:10.1111/j.1523-1739.2009.01168.x)
26. Shao Y, Zhang W, Eisenhauer N, Liu T, Xiong Y, Liang C, Fu S. 2017 Nitrogen deposition cancels out exotic earthworm effects on plant-feeding nematode communities. *J. Anim. Ecol.* **86**, 708–717. (doi:10.1111/1365-2656.12660)
27. Ferlian O, Eisenhauer N, Aguirrebengoa M, Camara M, Ramirez-Rojas I, Santos F, Tanalogo K, Thakur MP. 2018 Invasive earthworms erode soil biodiversity: a meta-analysis. *J. Anim. Ecol.* **87**, 162–172. (doi:10.1111/1365-2656.12746)
28. McCay TS, Scull P. 2019 Invasive lumbricid earthworms in northeastern North American forests and consequences for leaf-litter fauna. *Biol. Invasions* **21**, 2081–2093. (doi:10.1007/s10530-019-01959-1)
29. Jochum M, Ferlian O, Thakur MP, Ciobanu M, Klarner B, Salamon J, Frelich LE, Johnson EA, Eisenhauer N. 2021 Earthworm invasion causes declines across soil fauna size classes and biodiversity facets in northern North American forests. *Oikos* **130**, 766–780. (doi:10.1111/oik.07867)
30. Eisenhauer N, Ferlian O, Craven D, Hines J, Jochum M. 2019 Ecosystem responses to exotic earthworm invasion in northern North American forests. *Res. Ideas Outcomes* **5**, e34564. (doi:10.3897/rio.5.e34564)
31. Burtis JC, Fahey TJ, Yavitt JB. 2014 Impact of invasive earthworms on *Ixodes scapularis* and other litter-dwelling arthropods in hardwood forests, central New York state, USA. *Appl. Soil Ecol.* **84**, 148–157. (doi:10.1016/j.apsoil.2014.07.005)
32. King RA, Vaughan I, Bell J, Bohan D, Symondson W. 2010 Prey choice by carabid beetles feeding on an earthworm community analysed using species- and lineage-specific PCR primers. *Mol. Ecol.* **19**, 1721–1732. (doi:10.1111/j.1365-294X.2010.04602.x)
33. Suárez ER, Fahey TJ, Yavitt JB, Groffman PM, Bohlen PJ. 2006 Patterns of litter disappearance in a northern hardwood forest invaded by exotic earthworms. *Ecol. Appl.* **16**, 154–165. (doi:10.1890/04-0788)
34. Scherber C *et al.* 2010 Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* **468**, 553–556. (doi:10.1038/nature09492)
35. Eisenhauer N, Partsch S, Parkinson D, Scheu S. 2007 Invasion of a deciduous forest by earthworms: changes in soil chemistry, microflora, microarthropods and vegetation. *Soil Biol. Biochem.* **39**, 1099–1110. (doi:10.1016/j.soilbio.2006.12.019)
36. Scheu S, Parkinson D. 1994 Effects of earthworms on nutrient dynamics, carbon turnover and microorganisms in soils from cool temperate forests of the Canadian Rocky Mountains—laboratory studies. *Appl. Soil Ecol.* **1**, 113–125. (doi:10.1016/0929-1393(94)90031-0)
37. Straube D, Johnson EA, Parkinson D, Scheu S, Eisenhauer N. 2009 Nonlinearity of effects of invasive ecosystem engineers on abiotic soil properties and soil biota. *Oikos* **118**, 885–896. (doi:10.1111/j.1600-0706.2009.17405.x)
38. Londo G. 1976 The decimal scale for relevés of permanent quadrats. *Vegetatio* **33**, 61–64. (doi:10.1007/BF00055300)
39. Mercer RD, Gabriel AGA, Barendse J, Marshall DJ, Chown SL. 2001 Invertebrate body sizes from Marion Island. *Antarct. Sci.* **13**, 135–143. (doi:10.1017/S0954102001000219)
40. Sohlström EH, Marian L, Barnes AD, Haneda NF, Scheu S, Rall BC, Brose U, Jochum M. 2018 Applying generalized allometric regressions to predict live body mass of tropical and temperate arthropods. *Ecol. Evol.* **8**, 12 737–12 749. (doi:10.1002/ece3.4702)
41. Wardhaugh CW. 2013 Estimation of biomass from body length and width for tropical rainforest canopy invertebrates. *Aust. J. Entomol.* **52**, 291–298. (doi:10.1111/aen.12032)
42. R Core Team. 2020 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. (<https://www.r-project.org/>)
43. Rosseel Y. 2012 Lavaan: an R package for structural equation modeling. *J. Stat. Softw.* **48**, 1–36. (doi:10.18637/jss.v048.i02)
44. Jochum M, Thouvenot L, Ferlian O, Zeiss R, Klarner B, Pruschitzki U, Johnson EA, Eisenhauer N. 2022 'Aboveground impacts of a belowground invader: how invasive earthworms alter aboveground arthropod communities in a northern North American forest.' FigShare.
45. Thouvenot L, Ferlian O, Beugnon R, Künne T, Lochner A, Thakur MP, Türke M, Eisenhauer N. 2021 Do invasive earthworms affect the functional traits of native plants? *Front. Plant Sci.* **12**, 1–17. (doi:10.3389/fpls.2021.627573)
46. Gonzalez-Megias A, Maria Gomez J, Sánchez-Piñero F. 2007 Diversity-habitat heterogeneity relationship

- at different spatial and temporal scales. *Ecography (Cop.)* **30**, 31–41. (doi:10.1111/j.0906-7590.2007.04867.x)
47. MacArthur RH. 1972 *Geographical ecology: patterns in the distribution of species*. New York, NY: Harper & Row.
  48. Thakur MP, Künne T, Unsicker SB, Biere A, Ferlian O, Pruschitzki U, Thouvenot L, Türke M. 2021 Invasive earthworms reduce chemical defense and increase herbivory and pathogen infection in native trees. *J. Ecol.* **109**, 763–775. (doi:10.1111/1365-2745.13504)
  49. Megias AG, Müller C. 2010 Root herbivores and detritivores shape above-ground multitrophic assemblage through plant-mediated effects. *J. Anim. Ecol.* **79**, 923–931. (doi:10.1111/j.1365-2656.2010.01681.x)
  50. Siemann E, Tilman D, Haarstad J, Ritchie M. 1998 Experimental tests of the dependence of arthropod diversity on plant diversity. *Am. Nat.* **152**, 738–750. (doi:10.1086/286204)
  51. Letourneau DK, Jedlicka JA, Bothwell SG, Moreno CR. 2009 Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. *Annu. Rev. Ecol. Evol. Syst.* **40**, 573–592. (doi:10.1146/annurev.ecolsys.110308.120320)
  52. Schuldt A *et al.* 2019 Multiple plant diversity components drive consumer communities across ecosystems. *Nat. Commun.* **10**, 1–11. (doi:10.1038/s41467-019-09448-8)
  53. Barnes AD *et al.* 2020 Biodiversity enhances the multitrophic control of arthropod herbivory. *Sci. Adv.* **6**, eabb6603. (doi:10.1126/sciadv.abb6603)
  54. Jochum M, Eisenhauer N. 2021 Out of the dark: using energy flux to connect above- and belowground communities and ecosystem functioning. *Eur. J. Soil Sci.* **73**, 1–11. (doi:10.1111/ejss.13154)
  55. Cameron EK, Shaw CH, Bayne EM, Kurz WA, Kull SJ. 2015 Modelling interacting effects of invasive earthworms and wildfire on forest floor carbon storage in the boreal forest. *Soil Biol. Biochem.* **88**, 189–196. (doi:10.1016/j.soilbio.2015.05.020)
  56. Fisichelli NA, Frelich LE, Reich PB, Eisenhauer N. 2013 Linking direct and indirect pathways mediating earthworms, deer, and understory composition in Great Lakes forests. *Biol. Invasions* **15**, 1057–1066. (doi:10.1007/s10530-012-0350-6)