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

Malte Jochum1,2, Lise Thouvenot1,2, Olga Ferlian1,2, Romy Zeiss1,2, Bernhard Klarner3, Ulrich Pruschitzki1,2,†, Edward A. Johnson4 and Nico Eisenhauer1,2

1German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstrasse 4, 04103 Leipzig, Germany
2Leipzig University, Institute of Biology, Puschstrasse 4, 04103 Leipzig, Germany
3J.F. Blumenbach Institute of Zoology and Anthropology, University of Goettingen, Untere Karspule 2, Goettingen 37073, Germany
4Department Biological Sciences, University of Calgary, Calgary, Alberta, Canada T2N 1N4

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

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

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...
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 detrivores. 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′26″ 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 §2 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-vegetation research, including investigations on soil abiotic (soil chemistry and physics) and biotic (micro, meso and macro-fauna) 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 x 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 §1, 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 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 §6).

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...
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, SuppInfo, 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 above-ground 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 below-ground invasions and the subsequent above-ground arthropod community changes for consumers of arthropods [12], above—below-ground energy flux, ecosystem functions and services [8,53,54]. Future studies should also investigate if earthworm invasion facilitates secondary invasions in above-ground 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 above-ground 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, SuppInfo 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; A.B.: 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, 20548816, 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 Findseis: 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

1. Habel JC, Segerer A, Ulrich W, Torchky O, Weisser WW, Schmitt T. 2016 Butterfly community shifts over two centuries. Conserv. Biol. 30, 754–762. (doi:10.1111/cobi.12656)
2. 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)
3. Seibold S et al. 2019 Anthropic decline in grasslands and forests is associated with landscape-level drivers. Nature 574, 671–674. (doi:10.1038/s41586-019-1684-3)
4. 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)
5. 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.aax931)
6. Stuart SN, Wilson EO, McNeilly JA, Mittermeier RA, Rodriguez JP. 2010 The parameter of life. Science 328, 177. (doi:10.1126/science.1188606)
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, Praschitzki 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. Megías 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:10.1111/1365-2745.13154)

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. Fischelli 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)