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

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Running headline: Belowground invasion – aboveground impact

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30 **Abstract**

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

47

48 **Keywords:** belowground, aboveground, earthworm invasion, insect decline, arthropod, forest, Canada

49

50 **Introduction**

51 Recent reports on arthropod species richness, abundance, and biomass declines (Habel et al. 2016,
52 Hallmann et al. 2017, Seibold et al. 2019) have triggered concern about “the little things that run our
53 world” (Wilson 1987) and the consequences of their loss. Even though the situation might not be
54 equally bad for all taxa and ecosystem types (van Klink et al. 2020), the sheer number and extent of the
55 reported negative trends, together with the fact that we simply do not have enough long-term datasets
56 to establish such trends across all taxa and ecosystems (Stuart et al. 2010, Eisenhauer et al. 2019a,
57 Eisenhauer and Hines 2021), is worrying. With arthropods contributing to central ecosystem processes
58 and services (Noriega et al. 2018), their loss will have unprecedented consequences for ecosystems and
59 human societies.

60 In order to halt or reverse arthropod decline, we need to understand the underlying drivers.
61 Given their importance as broad global-change drivers (Díaz et al. 2019), it is unsurprising that climate
62 and land-use change are prominent examples (Deutsch et al. 2008, Habel et al. 2016, Lister and Garcia
63 2018, van Klink et al. 2020). However, though underrepresented in research on arthropod declines,
64 other drivers might still play an important role depending on the focal ecosystem and community. Here,
65 we focus on one potentially underappreciated driver of arthropod decline: the invasion of a
66 belowground ecosystem engineer, earthworms (Jones et al. 1994).

67 Although commonly perceived as having mostly positive impacts on their environment (Blouin
68 et al. 2013, Van Groenigen et al. 2014), earthworms can transform invaded ecosystems (Hendrix and
69 Bohlen 2002) that are not able to deal with their impacts on the ecosystem’s physical, chemical, and
70 biological properties (Bohlen et al. 2004, Ferlian et al. 2020, Jochum et al. 2021). Earthworm invasion
71 is a global problem (Hendrix et al. 2008). One region with both, particularly severe impacts and a lot of
72 research on the consequences, is northern North America. Here, most earthworm species present today

have been absent since the last glaciation and have only been re-introduced a few hundred years ago (Bohlen et al. 2004, James and Hendrix 2004).

Earthworm invasion alters soil abiotic conditions (Bohlen et al. 2004, Ferlian et al. 2020), plant communities (Nuzzo et al. 2009, Craven et al. 2017, Fleri et al. 2021), and soil fauna (Shao et al. 2017, Ferlian et al. 2018, McCay and Scull 2019, Jochum et al. 2021). Moreover, there are reports of consequences for aboveground vertebrates, such as salamanders, birds, and deer (Eisenhauer et al. 2019b, Frelich et al. 2019). There also are some aboveground-invertebrate studies, but these mostly focus on litter-dwelling fauna (Burtis et al. 2014, McCay and Scull 2019). 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 (King et al. 2010), or indirectly affect them via altered habitat structure, resource availability (leaf litter), or plant communities (Suárez et al. 2006, Nuzzo et al. 2009). We used earthworm, plant, and aboveground-arthropod community data 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 (Scherber et al. 2010, Frelich et al. 2019).

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, ~1450 m a.s.l.). The forest is dominated by trembling aspen (*Populus tremuloides*) interspersed with balsam poplar (*Populus balsamifera*), with a dense

understorey vegetation and a grey luvisol soil. It has a long history of earthworm-invasion research (Scheu and Parkinson 1994, Eisenhauer et al. 2007, Jochum et al. 2021). 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. (2019)). After verifying earthworm-invasion status along the slope, we established 20 1x2m plots in each of three invasion-status areas: low, mid, high invasion (n=60 plots, **Appendix Fig. S1**). These categories differed significantly in earthworm abundance, biomass, species richness, and functional-group richness (**Appendix Fig. S2 and S3**). Thus, we focused on invasion status as the main predictor and show responses to earthworm biomass in the appendix. We used 1 m² for plant-community assessments and the other half plot for arthropod (1 m²) and earthworm sampling (0.25 m², **Appendix Fig. S4**). We identified every plant species and estimated total plant cover using a modified decimal scale (Londo 1976 ; details in **Appendix section 1**).

Earthworms were extracted using a combination of hand sorting and mustard extraction. All individuals were identified to species level, assigned to a functional group, and their fresh mass was assessed (**Appendix section 1**). 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 **Appendix section 2** for details, **Figures S5 and S6, and Table S1**), and their fresh biomass was estimated (**Appendix section 3**; Mercer et al. 2001, Wardhaugh 2013, Sohlström et al. 2018). We calculated abundance, biomass, and species richness of the total arthropod community, 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 version 3.6.3 (R Core Team 2020). We assessed arthropod community responses to invasion using earthworm invasion status (categorical: low, mid, 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 **Appendix Section 4**. We used the R lavaan 0.6-9 (Rosseel 2012) package to construct SEMs testing direct and indirect effects of earthworm invasion on aboveground-arthropod abundance, biomass, and richness, separately (see **Appendix Section 6**).

Results

We collected 13,037 aboveground invertebrates (230 Pulmonata individuals included; for brevity, hereafter: arthropods), 4,814 of which were adults. For taxonomic and trophic details, see **Appendix Figures S5 and S6, Table S1**. Arthropod communities differed between invasion-status categories (**Fig. 1**) and along the earthworm-biomass gradient (**Appendix Figure S7**). Out of 18 models testing arthropod responses to earthworm-invasion status, eleven found significant negative relationships, while two relationships were positive (**Fig 1, 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 (**Appendix Figure S7, 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 SEM’s showed direct and indirect effects of invasive earthworms on aboveground-arthropod communities (**Fig. 2, Tables S3-5**). Earthworm biomass directly increased predator and parasitoid abundance and directly decreased detritivore, herbivore, and omnivore abundance (**Fig. 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 (**Fig. 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 (**Fig. 2d**). It indirectly decreased predator and parasitoid richness via detritivore richness. There were no significant effects of earthworm biomass on plant cover or richness.

Discussion

Our 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 to our expectations but in line with some previous work (e.g. Bohlen et al. 2004, Craven et al. 2017), 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 (Fleri et al. 2021, Thouvenot et al. 2021) or by high variability in plant communities. Plant cover and species richness supported higher detritivore abundance and biomass, as well as predator richness – supposedly by providing more resources and increased habitat heterogeneity (MacArthur 1972, Gonzalez-Megias et al. 2007). 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 (Bohlen et al. 2004, Nuzzo et al. 2009) and in this forest particularly (Eisenhauer et al. 2007). Negative effects of earthworm biomass on herbivores might, for example, be caused by earthworm-induced changes in plant secondary metabolites (Thakur et al. 2021), or alternatively via impacts on herbivore life stages in

the soil (Ferlian et al. 2018, Jochum et al. 2021).

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 intermediate trophic levels. Such effects might be mediated by altered habitat structure, such as reduced litter layers (Eisenhauer et al. 2007), or plant-community properties (Fleri et al. 2021), 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; Megías and Müller (2010)). 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 (Siemann et al. 1998), 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; Letourneau et al. 2009).

As one of the first studies reporting effects of invasive earthworms on aboveground-arthropod communities, 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 multifaceted impact on arthropod communities (Schuldt et al. 2019, Thakur et al. 2021, Thouvenot et al. 2021). Furthermore, we need to assess the consequences of belowground invasions and the subsequent aboveground arthropod community changes for consumers of arthropods (Lister and Garcia 2018), above-belowground energy flux, ecosystem functions, and services (Barnes et al. 2020, Eisenhauer and Hines 2021, Jochum and Eisenhauer 2021). Future studies should also investigate if earthworm invasion facilitates secondary invasions in aboveground-arthropod

communities, potentially facilitated by non-native plants (Craven et al. 2017), and how earthworm invasion might interact with other global-change drivers (Fisichelli et al. 2013, Cameron et al. 2015). 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.

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Author contributions

MJ, LT, OF, and NE conceived and designed the study. MJ, LT, OF, RZ, and UP did the field work. BK identified arthropod fauna and assessed their trophic identity. MJ analyzed the data and drafted the manuscript. All authors discussed the results and contributed to writing the manuscript.

Permits

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Code and data accessibility

R-code, data, and a README file are being made available upon submission and will be made publicly-available upon acceptance of the paper.

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324

Figures

Fig. 1. Effects of earthworm invasion status (low, mid, high - lighter to darker color shades) on the abundance (upper row), biomass (middle row) and (morpho)species richness (lower row) of total aboveground arthropods (gray), 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, $p > 0.05$; * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$). P-values are from simple linear models and glm’s with Poisson-distributed response variables (richness models), respectively. N=60. For model results, please see Table 1.

Fig. 2. Structural equation models illustrating direct and indirect effects of earthworm invasion on plants and aboveground-arthropod communities. a) Represents the initial model. Final models b-d) were obtained following the steps outlined in **Appendix Section 6**. Brown boxes represent earthworm biomass. Dark green boxes represent plant total cover (b and c), or plant species richness (d). All other boxes represent trophic group abundance (b), biomass (c), or species richness (d). Gray, double-headed arrows show covariances. Black, red, and dashed lines show positive, negative, and non-significant paths, respectively. Numbers next to significant paths are standardized path coefficients. Numbers inside boxes show R^2 values. $N=60$. For detailed model outputs, see **Tables S3-S5**.

Tables

Table 1: Results of models relating aboveground-arthropod abundance, biomass, and (morpho)species richness to invasion status (Fig. 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 Methods). p-values significant to an alpha level of 0.05 are set in bold. Values are rounded.

Response	Group	n	Model type	Resp. transf.	p low-high	p low-mid	p mid-high
Abundance	all	60	aov	log10	< 0.001	< 0.001	0.184
Abundance	herbivores	60	aov	log10	< 0.001	< 0.001	0.137
Abundance	omnivores	60	aov	log10	< 0.001	0.040	0.030
Abundance	predators	60	aov	log10	0.682	0.238	0.043
Abundance	detritivores	60	aov	log10	< 0.001	< 0.001	0.424
Abundance	parasitoids	60	aov	log10(+1)	0.405	0.991	0.480
Biomass	all	60	aov	log10	0.042	0.800	0.166
Biomass	herbivores	60	aov	log10	0.002	0.295	0.113
Biomass	omnivores	60	aov	log10	0.060	0.845	0.015
Biomass	predators	60	aov	log10	0.135	0.988	0.179
Biomass	detritivores	60	aov	log10	< 0.001	0.002	0.894
Biomass	parasitoids	60	aov	log10(+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

Supplementary Information

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

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1. Study design, earthworm, and plant communities

Figure S1. Distribution of 60 study plots on the forest slope above Barrier Lake, Kananaskis Valley, Alberta, Canada. Colors show low (orange), mid (light brown), and high (dark brown) invasion-status.

Earthworm communities

Earthworms were extracted on 0.25 m² per plot using a combination of digging and hand-sorting (upper 10 cm), and mustard extraction as described in Jochum et al. (2021). Subsequently, the obtained

15 earthworms were stored in 70% ethanol, taken to the lab, counted, weighed for fresh weight, identified
16 to species, and assigned to one of three ecological groups (epigeic, endogeic, anecic).

17 We collected 761 earthworms of five species, across all three ecological groups (anecic,
18 endogeic, epigeic; all European earthworm species). Across earthworm-community properties (i.e.,
19 abundance, biomass, richness, and ecological group richness), we found significant differences between
20 the three invasion-status categories, all increasing from low, over medium, to high invasion status

21 (Figure S2).

23 **Figure S2.** Earthworm community abundance, biomass, richness, and ecological group richness for the
24 three invasion-status categories. Asterisks show significant differences between categories tested with
25 R base function TukeyHSD() on aov() models of community properties against invasion status.
26

Figure S3. Earthworm biomass for all 60 study plots in increasing order. As can be assumed from the biomass results in Fig. S2, the mid and high invasion status plots are closer to each other and mixed than any of these two groups is with the low status plots.

Figure S4. Plot design of the 60 1x2 m plots. We used 1 m² for aboveground fauna sampling and afterwards a quarter m² of the same area for earthworm sampling, and the other 1 m² for plant community assessments.

Plant communities

Plant cover was estimated using 13 cover categories (<1%, 1-3%, 3-5%, 5-15%, eight subsequent 10% steps, and >95%). The median values of these categories were used in all analyses. Missing total plant

cover for one plot was inferred by averaging over the 19 other plots in this invasion status (high).

2. Aboveground-arthropod communities

We sampled aboveground arthropods using an ecoTech (Bonn, Germany) ecoVac insect suction sampler and a 2x1x1 m (lxbxh) insect rearing cage (BugDorm-6E1020, 150x150 µm Nylon mesh, bottom mesh removed) between June 5th and 10th 2019 (covering all three categories on each day). We placed the mesh cage on the ground when approaching the plot. Then, we collected vegetation- and ground-dwelling arthropods by operating the suction sampler across all vegetation and ground with full throttle for 2 min (90° turning the cage after 1 min to better reach all areas) and afterwards emptying out the cage. Suction samples were kept cool and dark in the field, put in a -20 °C freezer overnight, hand-sorted to separate animals from debris, and stored in 70% ethanol. After removing springtails and mites, all remaining animals were then identified to (morpho)species, assigned to a trophic feeding guild. Communities were numerically dominated by Hemiptera, Diptera, Araneae, Thysanoptera, and Hymenoptera, with pure herbivores dominating, followed by predatory-herbivorous arthropods, pure predators, pure detritivores, and parasitoids (**Figures S5 and S6, Table S1**). Subsequently, up to five individuals per morphospecies-plot combination were measured for body length. Afterwards, we used length-mass regressions to estimate fresh body masses (**Appendix section 3**; Mercer et al. (2001), Wardhaugh (2013), Sohlström et al. (2018)).

58 **Figure S5.** Proportional distribution of taxa among the 13,037 individuals (only groups with >20 ind.
59 shown).
60

61 **Figure S6.** Proportional distribution of trophic feeding guilds among the 13,037 individuals (only
62 groups with >20 ind. shown).
63

Table S1: Distribution of the 13,037 individuals across taxonomic family and order (or lower and higher taxonomic levels) for each of the ten trophic feeding guilds. “NA” means that a taxon level was unknown.

Trophic feeding guild	Order/higher taxon	Family/lower taxon	Individuals
detri.	Chordeumatida	Conotylidae	2
detri.	Coleoptera	Corylophidae	41
detri.	Coleoptera	Cryptophagidae	5
detri.	Coleoptera	Latridiidae	72
detri.	Coleoptera	Nitidulidae	1
detri.	Coleoptera	Ptiliidae	4
detri.	Coleoptera	Scirtidae	1
detri.	Diptera	Canthyloscelidae	1
detri.	Diptera	Cecidomyiidae	111
detri.	Diptera	Chironomidae	1
detri.	Diptera	Fanniidae	4
detri.	Diptera	Muscidae	12
detri.	Diptera	Mycetophilidae	13
detri.	Diptera	Sciaridae	677
detri.	Diptera	Simuliidae	2
detri.	Diptera	Sphaeroceridae	84
detri.	Psocoptera	NA	6
detri.herb.	Archaeognatha	Machilidae	33
detri.herb.	Coleoptera	Brentidae	6
detri.herb.	Diptera	Anthomyiidae	24
detri.herb.	Diptera	Chloropidae	18
detri.herb.	Diptera	Clusiidae	1
detri.herb.	Diptera	Drosophilidae	3
detri.herb.	Diptera	Stratiomyiidae	2
detri.herb.	Pulmonata	Discidae	34
detri.herb.	Pulmonata	Gastrocoptidae	6
detri.herb.	Pulmonata	Oxychilidae	8
detri.herb.	Pulmonata	Truncatellinidae	37
detri.herb.	Pulmonata	Vitrinidae	49
detri.herb.	Pulmonata	NA	96
detri.herb.pred.	Coleoptera	NA	15

detri.herb.pred.	Diptera	NA	115
detri.para.	Diptera	Calliphoridae	1
detri.pred.	Coleoptera	Staphylinidae	85
detri.pred.	Diptera	Ceratopogonidae	200
detri.pred.	Diptera	Culicidae	14
detri.pred.	Diptera	Empididae	21
detri.pred.	Diptera	Phoridae	231
herb.	Coleoptera	Chrysomelidae	46
herb.	Coleoptera	Curculionidae	23
herb.	Diptera	Agromyzidae	12
herb.	Diptera	Otitidae	5
herb.	Hemiptera	Acanthosomatidae	1
herb.	Hemiptera	Aphididae	84
herb.	Hemiptera	Aphrophoridae	1
herb.	Hemiptera	Cicadellidae	4587
herb.	Hemiptera	Coccidae	55
herb.	Hemiptera	Delphacidae	574
herb.	Hemiptera	Ortheziidae	11
herb.	Hemiptera	Psyllidae	6
herb.	Hemiptera	NA	2
herb.	Hymenoptera	Tenthredinidae	21
herb.	Lepidoptera	Gelechiidae	16
herb.	Lepidoptera	Geometridae	20
herb.	Lepidoptera	Noctuidae	6
herb.	Lepidoptera	Nymphalidae	1
herb.	Lepidoptera	Pterophoridae	23
herb.	Lepidoptera	Pyrilidae	3
herb.	Lepidoptera	NA	35
herb.	Orthoptera	Acrididae	15
herb.	Thysanoptera	Aeolothripidae	629
herb.	Thysanoptera	Phlaeothripidae	163
herb.	Thysanoptera	Thripidae	104
herb.	Thysanoptera	NA	261
herb.pred.	Diptera	Syrphidae	5

herb.pred.	Hemiptera	Miridae	971
herb.pred.	Hemiptera	NA	799
omni.	Coleoptera	Cantharidae	21
omni.	Coleoptera	Elateridae	1
omni.	Diplura	Campodeidae	2
omni.	Hymenoptera	Formicidae	367
para.	Diptera	Scatophagidae	3
para.	Diptera	Tachinidae	1
para.	Hymenoptera	Aphelinidae	6
para.	Hymenoptera	Bethylidae	3
para.	Hymenoptera	Braconidae	86
para.	Hymenoptera	Ceraphronidae	41
para.	Hymenoptera	Charipidae	7
para.	Hymenoptera	Diapriidae	2
para.	Hymenoptera	Encyrtidae	5
para.	Hymenoptera	Eulophidae	9
para.	Hymenoptera	Eupelmidae	4
para.	Hymenoptera	Eurytomidae	153
para.	Hymenoptera	Ichneumonidae	33
para.	Hymenoptera	Megaspilidae	15
para.	Hymenoptera	Mymaridae	90
para.	Hymenoptera	Platygastridae	146
para.	Hymenoptera	Pteromalidae	25
para.	Hymenoptera	Scelionidae	100
para.	Hymenoptera	Torymidae	3
para.	Hymenoptera	Trichogrammatidae	35
pred.	Araneae	Agelenidae	2
pred.	Araneae	Araneidae	7
pred.	Araneae	Clubionidae	80
pred.	Araneae	Corinnidae	3
pred.	Araneae	Dictynidae	2
pred.	Araneae	Gnaphosidae	6
pred.	Araneae	Linyphiidae	995
pred.	Araneae	Liocranidae	5

pred.	Araneae	Lycosidae	64
pred.	Araneae	Philodromidae	6
pred.	Araneae	Salticidae	11
pred.	Araneae	Sparassidae	1
pred.	Araneae	Theridiidae	93
pred.	Araneae	Thomisidae	13
pred.	Araneae	NA	3
pred.	Coleoptera	Carabidae	15
pred.	Coleoptera	Coccinellidae	1
pred.	Coleoptera	Staphylinidae	7
pred.	Diptera	Chamaemyiidae	10
pred.	Diptera	Pipunculidae	3
pred.	Diptera	Scatophagidae	1
pred.	Hemiptera	Anthocoridae	2
pred.	Hemiptera	Nabidae	8
pred.	Neuroptera	Hemerobiidae	4
pred.	Opiliones	NA	14
pred.	Pseudoscorpiones	Neobisiidae	8

68

69 3. Length-mass regressions

70 We used body length-fresh body mass regressions from Sohlström et al. (2018) for all taxa except for
71 Pulmonata as follows: LTR model, temperate (Araneae, Chordeumatidae-Polydesmida, Coleoptera,
72 Diptera adults, Hemiptera, Hymenoptera, Lepidoptera adults, Neuroptera, Opiliones, Orthoptera) and
73 tropical (Diptera larvae, Lepidoptera larvae, Pseudoscorpiones, Psocoptera), LR model, temperate
74 (Archaeognatha, Diplura, Thysanoptera). Models with code including “L”, “T”, and “R” use body
75 length (L), taxonomic information (T), and geographical region (R, temperate or tropical). For taxa
76 where specific taxonomic regressions were not available, we used the LR models. For those without
77 temperate models, we used tropical, but taxonomically-specific regressions. Body masses of Pulmonata
78 were calculated using a combination of a length-dry mass regression for gastropods (Wardhaugh

2013) and a general dry-fresh mass conversion (Mercer et al. 2001). For 63 out of 13,037 individuals, there was no length measurement available. These lengths were replaced either a) by averaging over the other individuals measured in the same plot or b), if no other lengths were available in the same plot, by averaging over all individuals of that species from all plots.

4. Statistical analysis

We used simple linear models with `lm()` for earthworm biomass and anova's with `aov()` for invasion-status models. For richness models, we used generalized linear models with `glm()` with “family=poisson” and, if overdispersed (tested using the performance package; Lüdtke et al. 2020; only the case for total richness), we used negative binomial generalized linear models with `glm.nb()` (MASS package; Venables and Ripley 2002)). We $\log_{10}$ -transformed abundances and biomasses ($\log_{10}(x+1)$ for parasitoids because of zero-abundance cases). We used Tukey post hoc tests with `TukeyHSD()` in base R for `lm()` and `aov()` models, and general linear hypotheses tests with `glht()` in `multcomp` (Hothorn et al. 2008) for richness `glm`'s to detect differences between invasion-status categories.

5. Models of arthropod community properties versus earthworm biomass

Fig. S7: Effects of invasive earthworm biomass on the abundance (upper row), biomass (middle row) and (morpho)species richness (lower row) of aboveground arthropods (all, gray), herbivores (green), omnivores (turquoise), predators (purple), detritivores (brown), and parasitoids (red). Solid and dashed lines show significant and non-significant relationships, respectively. P-values are from simple linear models and glm's with Poisson-distributed response variables (richness models), respectively. Model predictions in richness models are curved because of the model type. Earthworm biomass, all abundances, and all biomasses have been $\log_{10}$ transformed to meet model assumptions. Point colors show low, mid, and high invasion from light to darker shades for each color family. N=60. For model results, please see Table S2.

Table S2: Results of models relating aboveground arthropod abundance, biomass, and (morpho)species richness to earthworm biomass (Fig. S7). For each model, the table shows the response variable, arthropod group, sample size (n), model type, response transformation, slope estimates, approximated lower and upper 95% confidence intervals, F- and p-value. P-values are from simple linear models and glm's with Poisson distributed response variables (richness models), respectively. Predictor variable is earthworm biomass (log₁₀-transformed) for all models. p-values significant to an alpha level of 0.05 are set in bold. Values are rounded.

Response	Group	n	Model type	Resp. transf.	Slope	low	upp	F-value	p-value
Abundance	all	60	lm	log10	-0.18	-0.26	-0.10	22.12	< 0.001
Abundance	herbivores	60	lm	log10	-0.24	-0.34	-0.13	21.55	< 0.001
Abundance	omnivores	60	lm	log10	-0.13	-0.21	-0.06	12.75	< 0.001
Abundance	predators	60	lm	log10	0.02	-0.06	0.10	0.31	0.578
Abundance	detritivores	60	lm	log10	-0.41	-0.53	-0.29	45.95	< 0.001
Abundance	parasitoids	60	lm	log10(+1)	-0.02	-0.13	0.10	0.09	0.770
Biomass	all	60	lm	log10	-0.03	-0.1	0.04	0.93	0.339
Biomass	herbivores	60	lm	log10	-0.11	-0.19	-0.02	5.93	0.018
Biomass	omnivores	60	lm	log10	-0.02	-0.11	0.07	0.24	0.626
Biomass	predators	60	lm	log10	0.16	0.03	0.29	5.74	0.020
Biomass	detritivores	60	lm	log10	-0.31	-0.45	-0.16	17.84	< 0.001
Biomass	parasitoids	60	lm	log10(+1)	0.05	-0.09	0.20	0.54	0.464
Richness	all	60	glm.nb	none	-0.09	-0.17	0.00	64.81	0.055
Richness	herbivores	60	glm	none	-0.05	-0.17	0.08	31.55	0.459
Richness	omnivores	60	glm	none	-0.09	-0.21	0.04	70.57	0.170
Richness	predators	60	glm	none	0.15	-0.03	0.32	76.68	0.098
Richness	detritivores	60	glm	none	-0.36	-0.52	-0.19	71.10	< 0.001
Richness	parasitoids	60	glm	none	-0.10	-0.23	0.03	85.52	0.128

6. SEM approach

All three SEMs used earthworm biomass as the basal exogenous variable. Plants are represented by total cover for abundance and biomass SEMs, and plant species richness for the richness SEM. All other groups are represented by their abundance, biomass, and richness in the respective models.

a) Initial model

The initial model (see Fig. 1a) was based on assumed trophic relationships, covariance for groups sharing resources or sharing a joint feeding type (omnivores with most others). Earthworms were additionally allowed to impact plants directly (Scheu 2001, Van Groenigen et al. 2014). Assumed trophic relationships: Detritivores consume dead plant material. Herbivores consume plants. Omnivores feed on plants. Predators consume detritivores and herbivores. Parasitoids feed on herbivores and detritivores. Groups sharing resources: Omnivores and earthworms. Detritivores and earthworms. Predators and Parasitoids. Parasitoids and Omnivores. Omnivores and Predators. Herbivores and detritivores. Groups with partly overlapping feeding type: Omnivores and detritivores, herbivores, predators, parasitoids.

b) Adding paths

We used modification indices (parameter *mi*) as indicated by the lavaan R package to look for paths that should be added and included those showing values larger than 3.84 as suggested by James Grace in his lavaan tutorials (https://www.usgs.gov/centers/wetland-and-aquatic-research-center/science/quantitative-analysis-using-structural-equation?qt-science_center_objects=0#qt-science_center_objects).

c) Selection of final model

Once paths were added, we checked the validity of the model (chi-square statistic and value). If paths were borderline, in our case only for the abundance model, adding the path from earthworm biomass to parasitoid abundance, we compared the models without and with this path using R functions `anova()` and `aictab.lavaan()` downloaded from http://jarrettbyrnes.info/ubc_sem/lavaan_materials/ looking at the significance of chisquare tests and

AICc differences. In this case, the model with the path added was significantly better than the one without it, so we included it in the final abundance SEM (Fig. 2 b).

We did not deliberately strip down models to improve fit by removing non-significant paths from valid models, because the initially-selected paths are ecologically meaningful, e.g. predators depend on herbivores as a resource even if this is not significant in a given model.

d) lavaan output tables for final models

Table S3: lavaan standardizedSolution() output for abundance SEM, Fig. 2b. Lhs and rhs denote the left-hand and right-hand side of regression (op ~) or covariance relationships (op ~~). est.std are standardized parameter estimates. se is the corresponding standard error. z is the z-value. P-values of significant paths in bold. Finally, ci.lower and ci.upper show lower and upper 95% confidence intervals for standardized parameters.

lhs	op	rhs	est.std	se	z	p-value	ci.lower	ci.upper
plant_cover	~	worm_biomass	-0.0658	0.1284	-0.5127	0.6082	-0.3175	0.1858
detri_abund	~	plant_cover	0.2242	0.106	2.1157	0.0344	0.0165	0.4318
detri_abund	~	worm_biomass	-0.4901	0.0891	-5.5002	< 0.0001	-0.6648	-0.3155
herb_abund	~	worm_biomass	-0.4458	0.0971	-4.5919	< 0.0001	-0.6361	-0.2555
herb_abund	~	plant_cover	0.1346	0.1131	1.1897	0.2342	-0.0871	0.3563
pred_abund	~	worm_biomass	0.3385	0.1163	2.9113	0.0036	0.1106	0.5664
pred_abund	~	herb_abund	-0.3208	0.13	-2.4679	0.0136	-0.5756	-0.066
pred_abund	~	detri_abund	0.7841	0.1165	6.7306	< 0.0001	0.5558	1.0125
omni_abund	~	plant_cover	-0.0287	0.1107	-0.2596	0.7952	-0.2456	0.1882
omni_abund	~	worm_biomass	-0.3626	0.1087	-3.3355	0.0009	-0.5756	-0.1495
para_abund	~	worm_biomass	0.2607	0.1266	2.0596	0.0394	0.0126	0.5087
para_abund	~	herb_abund	0.3273	0.1367	2.3949	0.0166	0.0594	0.5951
para_abund	~	detri_abund	0.3593	0.1403	2.5605	0.0105	0.0843	0.6344
detri_abund	~~	omni_abund	0.6229	0.0786	7.9278	< 0.0001	0.4689	0.7769
herb_abund	~~	omni_abund	0.4543	0.1024	4.4372	< 0.0001	0.2536	0.655
pred_abund	~~	omni_abund	0.3979	0.0835	4.7661	< 0.0001	0.2343	0.5616
omni_abund	~~	para_abund	0.186	0.0947	1.9647	0.0495	0.0004	0.3715
pred_abund	~~	para_abund	0.1935	0.1243	1.5572	0.1194	-0.05	0.4371
detri_abund	~~	herb_abund	0.4613	0.1016	4.5399	< 0.0001	0.2622	0.6605

Table S4: lavaan standardizedSolution() output for biomass SEM, Fig. 2c. Lhs and rhs denote the left-hand and right-hand side of regression (op ~) or covariance relationships (op ~~). est.std are standardized parameter estimates. se is the corresponding standard error. z is the z-value. P-values of significant paths in bold. Finally, ci.lower and ci.upper show lower and upper 95% confidence intervals for standardized parameters.

lhs	op	rhs	est.std	se	z	p-value	ci.lower	ci.upper
plant_cover	~	worm_biomass	-0.0658	0.1284	-0.5127	0.6082	-0.3175	0.1858
detri_biomass	~	plant_cover	0.2267	0.115	1.9704	0.0488	0.0012	0.4522
detri_biomass	~	worm_biomass	-0.3332	0.1082	-3.0795	0.0021	-0.5452	-0.1211
herb_biomass	~	worm_biomass	-0.2727	0.1157	-2.3576	0.0184	-0.4995	-0.046
herb_biomass	~	plant_cover	0.1574	0.121	1.3005	0.1934	-0.0798	0.3946
pred_biomass	~	worm_biomass	0.4953	0.102	4.8556	< 0.0001	0.2954	0.6952
pred_biomass	~	herb_biomass	-0.126	0.1238	-1.0184	0.3085	-0.3686	0.1165
pred_biomass	~	detri_biomass	0.3164	0.1238	2.5548	0.0106	0.0737	0.5591
omni_biomass	~	plant_cover	-0.1551	0.1236	-1.2547	0.2096	-0.3973	0.0872
omni_biomass	~	worm_biomass	-0.084	0.1268	-0.6623	0.5077	-0.3325	0.1645
para_biomass	~	herb_biomass	0.0367	0.1417	0.259	0.7956	-0.241	0.3144
para_biomass	~	detri_biomass	-0.0709	0.1415	-0.5013	0.6161	-0.3482	0.2063
detri_biomass	~~	omni_biomass	0.1971	0.1239	1.5901	0.1118	-0.0458	0.44
herb_biomass	~~	omni_biomass	0.2995	0.1175	2.5497	0.0108	0.0693	0.5297
pred_biomass	~~	omni_biomass	0.2027	0.1174	1.7266	0.0842	-0.0274	0.4329
omni_biomass	~~	para_biomass	-0.0133	0.1224	-0.1089	0.9132	-0.2533	0.2266
pred_biomass	~~	para_biomass	-0.0052	0.1291	-0.0404	0.9678	-0.2582	0.2478
detri_biomass	~~	herb_biomass	0.3289	0.1151	2.8566	0.0043	0.1032	0.5546

Table S5: lavaan standardizedSolution() output for richness SEM, Fig. 2d. Lhs and rhs denote the left-hand and right-hand side of regression (op ~) or covariance relationships (op ~~). est.std are standardized parameter estimates. se is the corresponding standard error. z is the z-value. P-values of significant paths in bold. Finally, ci.lower and ci.upper show lower and upper 95% confidence intervals for standardized parameters.

lhs	op	rhs	est.std	se	z	p-value	ci.lower	ci.upper
plant_richness	~	worm_biomass	-0.2055	0.1223	-1.6802	0.0929	-0.4453	0.0342
detri_richness	~	plant_richness	0.0941	0.1193	0.789	0.4301	-0.1397	0.3279
detri_richness	~	worm_biomass	-0.3894	0.1058	-3.6809	0.0002	-0.5968	-0.1821
herb_richness	~	plant_richness	0.0455	0.1288	0.3531	0.724	-0.207	0.298
pred_richness	~	worm_biomass	0.4944	0.1045	4.7302	< 0.0001	0.2896	0.6993
pred_richness	~	plant_richness	0.2299	0.1107	2.0758	0.0379	0.0128	0.4469

pred_richness	~	herb_richness	0.1391	0.1102	1.2613	0.2072	-0.077	0.3551
pred_richness	~	detri_richness	0.3068	0.1189	2.5805	0.0099	0.0738	0.5399
omni_richness	~	plant_richness	0.2069	0.1264	1.6376	0.1015	-0.0407	0.4546
omni_richness	~	worm_biomass	0.0342	0.1257	0.272	0.7857	-0.2121	0.2805
para_richness	~	herb_richness	0.4935	0.09	5.4846	< 0.0001	0.3171	0.6699
para_richness	~	detri_richness	0.344	0.0966	3.5613	0.0004	0.1547	0.5333
detri_richness	~~	omni_richness	0.2935	0.118	2.4876	0.0129	0.0622	0.5247
herb_richness	~~	omni_richness	0.2284	0.1224	1.8667	0.0619	-0.0114	0.4682
pred_richness	~~	omni_richness	0.1746	0.1173	1.4884	0.1367	-0.0553	0.4045
omni_richness	~~	para_richness	-0.0099	0.121	-0.0821	0.9346	-0.2471	0.2272
pred_richness	~~	para_richness	0.0383	0.1289	0.2973	0.7662	-0.2143	0.291
detri_richness	~~	herb_richness	0.1433	0.1264	1.1332	0.2571	-0.1045	0.3911

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