

Invasive earthworms modulate native plant trait expression and competition

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Abstract

Biological invasions have major impacts on a variety of ecosystems and threaten native biodiversity. Earthworms have been absent from northern parts of North America since the last ice age, but non-native earthworms were recently introduced there and are now being spread by human activities. While past work has shown that plant communities in earthworm-invaded areas change towards a lower diversity mainly dominated by grasses, the underlying mechanisms related to changes in the biotic interactions of the plants are not well understood. Here, we used a trait-based approach to study the effect of earthworms on interspecific plant competition and aboveground herbivory. We conducted a microcosm experiment in a growth chamber with a full-factorial design using three plant species native to northern North American deciduous forests, *Poa palustris* (grass), *Symphytotrichum laeve* (herb), and *Vicia americana* (legume), either growing in monoculture or in a mixture of three. These plant community treatments were crossed with earthworm (presence or absence) and herbivore (presence or absence) treatments. Eight out of the eleven above- and belowground plant functional traits studied were significantly affected by earthworms, either by a general effect or in interaction with plant species identity, plant diversity level, and/or herbivore. Earthworms increased the aboveground productivity and the number of inflorescences of the grass *P. palustris*. Further, earthworms countervailed the increasing effect of herbivores on root tissue density of all species, and earthworms and herbivores individually increased the average root diameter of *S. laeve* in monoculture, but decreased it in mixture. In this study, earthworm presence gave a competitive advantage to the grass species *P. palustris* by inducing changes in plant functional traits. Our results suggest that invasive earthworms can alter competitive and multitrophic interactions of plants, shedding light on some of the mechanisms behind invasive earthworm-induced plant community changes in northern North America forests.

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25 **Keywords:** biological invasion, competition, detritivore, herbivory, plant functional traits

26

27 **Introduction**

28 Biological invasions occur globally and are among the most significant direct causes of native
29 biodiversity loss worldwide (Díaz et al., 2019; Ehrenfeld, 2010; Murphy & Romanuk, 2014).
30 Dramatic changes in biodiversity can be due to invasive species acting as ecosystem
31 engineers, such as European earthworms in northern North America (Blouin et al., 2013;
32 Bohlen et al., 2004a; Ehrenfeld, 2010; Ferlian et al., 2018). Much of the native flora and fauna
33 was eradicated in this region during the last ice age, including earthworms (Gates, 1982),
34 which have been reintroduced by European settlers within the last centuries (Hendrix & Bohlen,
35 2002).

36 In areas where invasive earthworms are abundant, they alter the physico-chemical properties
37 of the soil (Bohlen et al., 2004a; Ferlian et al., 2020; Hale et al., 2005). The litter coverage is
38 reduced, soil horizons partly homogenized, nutrients redistributed, and soil pH increased while
39 soil water content decreased (Blouin et al., 2013; Eisenhauer et al., 2007; Ferlian et al., 2020;
40 Hale et al., 2005). These modifications of abiotic conditions alter the habitat for soil-living
41 organisms (Eisenhauer et al., 2007; McLean & Parkinson, 2000). As a consequence, the
42 community composition of soil microbes and invertebrates is significantly altered, while soil
43 fauna diversity and density decrease with earthworm invasion (Eisenhauer et al., 2007; Ferlian
44 et al., 2018).

45 Further, earthworms can act as an ecological filter on seeds, seedlings, and plants (Eisenhauer
46 & Scheu, 2008b; Forey et al., 2011; Frelich et al., 2012) impacting plant species establishment.
47 The diversity of understory plants was reported to decrease, and the species and functional
48 community composition change significantly in response to the invasion of earthworms (Bohlen
49 et al., 2004b; Craven et al., 2017; Hale et al., 2006). However, it was also shown that there are
50 winners and losers: while some grass and non-native plant species benefit from earthworm
51 invasion (Craven et al., 2017), the richness and abundance of herbs (Hale et al., 2006) and
52 legumes (Eisenhauer et al., 2007) decrease in invaded forests, leading in some cases to
53 sparse vegetation with only few herbaceous plant species left (Bohlen et al., 2004b).

54 Nevertheless, the total plant cover was overall shown to increase and be dominated by
55 graminoids (Craven et al., 2017), indicating that earthworms may change competitive
56 interactions by benefitting certain plant species (Eisenhauer & Scheu, 2008a; Nuzzo et al.,
57 2009; Wurst et al., 2005). In this context, our study aims to disentangle the mechanisms
58 underlying plant community changes due to earthworm invasion, by focusing on biotic
59 interactions and changes in plant functional traits (*i.e.* “morpho-physio-phenological traits
60 which impact fitness indirectly via their effects on growth, reproduction and survival” (Violle et
61 al., 2007)). Plant functional traits related to development and resource uptake can be affected
62 by earthworm presence (Thouvenot et al., 2021). Previous studies mostly focusing on native
63 plant and earthworm species have shown among others that earthworm activity enhanced
64 shoot biomass (Groenigen et al., 2014; Scheu, 2003), plant growth (Poveda et al., 2005; Wurst
65 et al., 2003; Xiao et al., 2018), seed quantity (Poveda et al., 2005), and fine-root growth
66 (Blume-Werry et al., 2020), with some variation across plant species and functional groups.

67 The provision of available nitrogen is considered as the main pathway of earthworms to affect
68 plants (van Groenigen et al., 2014). Earthworms enhance the nitrogen uptake of grasses,
69 herbs, and legumes from organic litter and soil (Eisenhauer & Scheu, 2008a; Wurst et al.,
70 2003). Furthermore, their effects on soil structure, microbiota, and water availability can also
71 influence plant growth (Blouin et al., 2013; Cameron et al., 2014; Eisenhauer et al., 2012,
72 Scheu, 2003), and thus earthworms might select for plant species that tolerate drought, can
73 germinate on bare soil, and spread vegetatively (Eisenhauer et al., 2012). By having dissimilar
74 effects on plant functional traits of different species, invasive earthworms can affect biotic
75 interactions of plants, *e.g.* competition and herbivory (Blouin et al., 2013; Eisenhauer et al.,
76 2009) and thus promote certain plant species. For example, species with a more flexible
77 rooting strategy were able to better adapt to the presence of invasive earthworms and forage
78 in their nutrient-rich burrows (Cameron et al., 2014). According to the plant economics
79 spectrum (Reich, 2014), grasses are considered as fast-growing plants that efficiently exploit
80 nutrient patches in contrast to slow growing herbs (Lavorel et al., 2007; Linder et al., 2018).
81 Therefore, grasses competitiveness could be increased by earthworm invasion (Craven et al.,

82 2017), as grasses potentially build more root biomass and take up more nitrogen when
83 earthworms are present (Eisenhauer & Scheu, 2008a; Wurst et al., 2005). Indeed, it was
84 shown that legumes had less biomass when growing with grasses in the presence of
85 earthworms (Eisenhauer & Scheu, 2008a), which indicates an elevated competitive
86 disadvantage that might explain the lower legume cover and biomass in earthworm-invaded
87 aspen forests (Eisenhauer et al., 2007).

88 In addition to plant competition, invasive earthworms may alter multitrophic interactions of
89 plants. Earthworms can affect aboveground herbivory through plant-mediated effects (Wurst
90 et al., 2003; Wurst, 2010; Xiao et al., 2018), positively (Newington et al., 2004; Thakur et al.,
91 2020), or negatively (Zaller et al., 2013). Loranger et al. (2012) reported that the nutrient
92 content and toughness of leaves are the most important plant traits linked to herbivory in
93 grassland: high plant tissue nitrogen content increases while high leaves' toughness
94 decreases leaves' palatability to herbivores. Leaf nitrogen content was shown to be enhanced
95 by earthworm activity (Newington et al., 2004; Wurst et al., 2004, Xiao et al., 2015, Blume-
96 Werry et al., 2020), while inconsistent effects were shown on leaf dry matter content, a trait that
97 could be used as proxy for leaf toughness (Elger & Willby, 2003; Thakur et al., 2020; Thouvenot
98 et al., 2021).

99 To improve the mechanistic understanding of recorded effects of invasive earthworms on
100 native understory plant communities in northern North American forests (e.g. Craven et al.,
101 2017), we set up a microcosm experiment in a growth chamber with plants belonging to three
102 functional groups (grasses, herbs, and legumes), either in monoculture or mixture. Each plant
103 community was subjected to the presence and absence of earthworms and aboveground
104 herbivores, respectively, resulting in a full-factorial design. To shed light on potential treatment
105 effects, we assessed a set of plant functional traits that are likely to play critical roles in plant
106 resource use, competition, and responses to herbivores. As earthworms were expected to
107 increase nutrient availability for plants, we hypothesized that (1) invasive earthworms increase
108 overall productivity of native plant species. Given that grasses can exploit soil nutrients rapidly

109 (Linder et al., 2018) and their response to invasive earthworms is more pronounced than that
110 of herbs (Thouvenot et al., 2021), we hypothesized that (2) grasses become stronger
111 competitors and show increased growth, while herbs and legumes show decreased growth
112 due to high competition from grasses in the presence of earthworms. Moreover, as herbivory
113 can affect plant traits (Heinze, 2020), we expected (3) potential short-term effects of
114 aboveground herbivory on plant traits (Poveda et al., 2003), while (4) invasive earthworms may
115 modulate herbivory effects due to changes in soil nutrient availability (Eisenhauer & Scheu,
116 2008a). Further, we (5) expected that the effects of invasive earthworms and aboveground
117 herbivory depend on plant community composition, e.g. with grasses benefiting most from the
118 presence of earthworms and herbivores in plant mixtures (Eisenhauer & Scheu, 2008a).

119 **Methods**

120 **Experimental set-up**

121 Earthworm effects on biotic interactions (e.g. competition and herbivory) were studied in a
122 microcosm experiment under controlled conditions using a full-factorial design with four types
123 of plant communities and four earthworms/herbivore treatments. Three species of the native
124 plant community from Canadian forest understories (Hallworth & Chinnappa, 1997; Royer &
125 Dickinson, 2007), namely *Poa palustris* (grass, purchased at Sheffield's Seed Co. Inc, USA),
126 *Vicia americana* (legume, purchased at ALCLA Native Plants, Canada), and *Symphytichum*
127 *laeve* (herb, purchased at Wild About Flowers, Canada), were each grown in monoculture and
128 in mixture (*i.e.* all three together); resulting in four plant community treatments. We manipulated
129 the presence of earthworms (*Lumbricus terrestris*, anecic species from Europe, but invasive
130 across northern North America; Hendrix et al., 2006, 2008) and aboveground herbivores
131 (larvae of *Spodoptera exigua*, chewing generalists) in a full-factorial design: (1) control (no
132 earthworms, no herbivores), (2) with earthworms only, (3) with herbivores only, and (4) with
133 both earthworms and herbivores. Each of the 16 different treatment combinations (4x plant
134 communities, 2x earthworms, 2x herbivores) was replicated 6 times, resulting in 96
135 microcosms. The experiment was conducted for 82 days. Microcosms were randomly

136 distributed on four tables in an air temperature-controlled climate chamber with 60% humidity,
137 at a day/night cycle of 16/8h and $23/15 \pm 0.9^{\circ}\text{C}$ (mean \pm sd), with a light intensity of around
138 $400\text{-}450 \mu\text{mol m}^{-2} \text{s}^{-1}$ of photosynthetically active radiation. Each microcosm was watered with
139 20-100 ml of water every 2-3 days during the experiment. Microcosms were randomly
140 redistributed between the tables every two weeks, but always at least one replicate of each
141 treatment was placed on each table.

142 Microcosms consisted of PVC tubes (inner diameter 10 cm, height 24 cm) with a 700 μm mesh
143 glued to the bottom to allow drainage of water. At the top of the tube, a barrier of transparent
144 plastic film (height 15 cm) was attached to prevent earthworms from escaping (Eisenhauer et
145 al., 2012). Soil (sandy-clay soil, pH= 7.38; N= 0.06%; C= 1.20%; C:N= 20.98) was ordered
146 from a commercial supplier (Kies Direkt, Germany), and each microcosm was filled with 3 kg
147 of sterile (*i.e.* autoclaved at 120° ; 90 min) soil. To leach nutrients and compounds released
148 during the sterilization procedure, 1 l of water was added to each microcosm.

149 Then, a soil microbial inoculation, using native soil that was sampled in September 2020 in an
150 uninvaded Aspen forest of the Kananaskis Valley (Alberta, Canada), was performed by directly
151 mixing soil and by using a microbial wash. Native soil was shipped frozen, stored at -20°C until
152 usage, and, after defrosting, sieved through a 4 mm mesh. For each microcosm, we
153 homogenized the 3 kg of sterilized soil with around 137 g of the Canadian soil in a sterilized
154 (70% ethanol) bucket, before filling it back to the microcosm. To perform the microbial wash,
155 we mixed 46 g of Canadian soil with 100 ml of water and poured it into each microcosm,
156 followed by another 100 ml of water to dissolve the remains of the Canadian soil from the
157 vessel. To ensure microbial community development, we stored the microcosms for ten days
158 at room temperature ($20\text{-}25^{\circ}\text{C}$) and held their soil water content at 40-60% of their maximum
159 water holding capacity.

160 **Plant material**

161 Seeds were sown in soil from the Bad Lauchstädt Experimental Research Station of the
162 Helmholtz Centre for Environmental Research- UFZ ($11^{\circ}53'\text{E}$ $51^{\circ}24'\text{N}$). Prior to sowing, the

163 soil was autoclaved (120°C; 90 min), washed with tap water, and inoculated using both
164 approaches described above. Seeds of *V. americana* were scarified using sandpaper (grit size
165 150) and sown at 3-6 mm soil depth, *S. laeve* at 2 mm soil depth, and *P. palustris* at the soil
166 surface. Seeds then germinated in a reach-in climate chamber (night temperature: 18°C, day
167 temperature: 22°C, duration day/night: 16 h/8 h; light intensity day: 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (partial light
168 at 85%), humidity: 70%). After six weeks, the seedlings were transplanted into microcosms,
169 and their vegetative height was measured (mean \pm sd: *P. palustris*: 11.5 \pm 3.1 cm; *S. laeve*:
170 0.7 \pm 0.3 cm; *V. americana*: 8.8 \pm 2.3 cm; the reader should note the initial height differences
171 among plant species due to the specificity of each plant functional group; the plant individuals
172 were randomly distributed for the treatments, but we observed a significant initial difference of
173 0.11 cm between *S. laeve* individuals that received no herbivores (0.70 \pm 0.25 cm) and *S.*
174 *laeve* individuals that received herbivores (0.59 \pm 0.27 cm) (Supplementary material, Table
175 A1)). Further, *V. americana* individuals growing in mixture not receiving herbivores (9.58 \pm 2.47
176 cm) were initially 2.58 cm taller by chance than *V. americana* individuals in mixture that
177 received herbivores (7.00 \pm 2.08 cm) (Supplementary material, Table A1). We accounted for
178 these initial height differences in the statistical analyses. In each microcosm, the respective
179 three plants were planted in a triangle of about 5 cm from each other.

180 **Earthworm treatment**

181 Earthworms were ordered at a commercial supplier (easyzoo.de) and handled according to
182 Fründ et al. (2010). We sorted them into juveniles and adults, according to the presence or
183 absence of a clitellum and weighed them (after starving for 24 h at 12°C). The body mass of
184 adults ranged from 2.8 g to 4.6 g (fresh weight of alive earthworms; mean \pm sd: 3.6 \pm 0.5 g),
185 while the weight of juveniles ranged from 1.8 g to 3.5 g (2.6 \pm 0.4 g). Pairs of adults and
186 juveniles were formed to add a similar total body mass of earthworms per microcosm (mean \pm
187 sd: 6.2 \pm 0.12 g). Earthworms were added to half of the microcosms (with earthworm
188 treatment). Four grams of autoclaved (120°C; 90 min) and cut (\sim 1 cm²) litter of poplar species

189 (*Populus sp.*; C:N= 22.6) sampled in a forest close to Leipzig, was added to each microcosm
190 to feed earthworms and simulate litter conditions in uninvaded Aspen forests.

191 **Herbivore treatment**

192 Herbivores were added in the last week of the experiment and left on the plants for five days
193 in clip cages to prevent them from escaping. Prior to their addition, herbivores were starved
194 for one day and weighed. One clip cage was added to the second (or third if needed) green
195 and healthy leaf per plant, fixing ~50% of it in the cage, and receiving one herbivore each. In
196 total, 141 herbivores were added (three plant individuals were dead at this point in time) to half
197 of the microcosms (with herbivore treatment), and plants without herbivore treatment also
198 received an empty clip cage to control for potential side effects. Clip cages consisted of two
199 foam rings of pipe insulation (inner diameter: ~3 cm, thickness: ~1.5 cm) with mesh of 250 µm
200 closing it on both sides, held together by three hair clips, and fixed by a wire to a wooden stick
201 next to the plant. After herbivore removal, the area consumed by the larvae was visually
202 estimated according to predefined classes (0%, <1%, 1-5%, 6-15%, 16-25%, 26-50%, 51-75%,
203 >76%). The median values of these classes (0, 0.5, 3, 10, 20, 38, 63, 88) were used for further
204 analyses.

205 **Plant trait measurements**

206 Aboveground plant traits were measured for each plant individual. After herbivory rate
207 estimation, ramets were counted, and the height was measured (for *S. laeve* and *P. palustris*,
208 we measured the vegetative height; for *V. americana*, we measured the stretched height due
209 to its growth form). Further analyses were conducted with the height growth values to exclude
210 initial height differences among plant individuals and treatments. To calculate height growth of
211 plants in monoculture, we subtracted the mean initial height per microcosm from the final height
212 of each plant individual. For mixtures, the respective initial height was subtracted from the final
213 height of each individual plant. In microcosms with plant mixtures, inflorescences (only *P.*
214 *palustris* developed inflorescences) were documented per plant individual, while in

215 monocultures, they were counted per microcosm, divided by three, and this average value was
216 then used once per (grass) monoculture microcosm for further analysis. Three green and
217 healthy leaves including the petiole (preferably the 3rd, 4th, and 5th youngest) were cut off the
218 plant, weighed, and scanned fresh using a CanoScan LIDE220 Scanner (Canon Inc., Vietnam)
219 at 600 dpi in grayscale. The leaf that was secured in the clip cage (irrespective of herbivore
220 treatment) was previously taken for metabolomic measurements, which are not part of this
221 manuscript. The aboveground biomass was then cut off and stored in paper bags.

222 To measure belowground plant traits, the soil was removed from the microcosms. Earthworms
223 were collected, starved again, and reweighed after 24 h. Soil samples for pH and water content
224 (each 30 g) analyses were taken and stored at -20°C until further processing. Roots from each
225 plant individual were disentangled and thoroughly washed with water. Debris and black/dead
226 parts of roots were picked out using a tweezer. Roots were sorted into fine roots (<2 mm
227 diameter) and coarse roots (>2 mm diameter). Detached roots were grouped as community
228 roots (including small root pieces from the soil), and the water used for cleaning the roots was
229 sieved (250 µm) to not lose any root material. Further analysis of belowground traits was done
230 on one random individual from plant monocultures and all individuals from plant mixtures.
231 Depending on the mass of the fine roots, either the whole sample or a representative fraction
232 (mean ± sd: 0.6 ± 0.6 g) of it was weighed and scanned using an Epson Perfection 11000XL
233 Scanner (Epson America, Inc., CA, USA) at 600 dpi in grayscale. All samples (aboveground
234 biomass, scanned leaves, and all root samples) were oven-dried at 60°C for 72 h and weighed
235 again to assess their dry mass. Above- and belowground community (microcosm) biomasses
236 were determined by adding the respective dry weights, and community shoot:root ratio was
237 calculated.

238 Leaf scans were analyzed using the software WinFOLIA (Version: 2014a Pro; Regent
239 Instruments Inc., Canada). Leaf area (cm²) was provided by the software, and we calculated
240 specific leaf area (SLA; leaf area divided by its dry mass (mm² mg⁻¹)), and leaf dry matter
241 content (LDMC; dry mass divided by fresh mass (mg g⁻¹)) using standardized protocols (Pérez-

242 Harguindeguy et al., 2016). For SLA and LDMC, an average per individual was determined.
243 Root scans were analyzed using the software WinRhizo (Version 2013e Pro, Regent
244 Instruments Inc., Canada), removing objects with an area smaller than 0.001 cm². Larger
245 debris pieces, air bubbles, and scratches were manually excluded. Root average diameter
246 (mm) was provided by the software, and we calculated specific root length (SRL; root length
247 divided by dry mass (m g⁻¹)), root tissue density (RTD; dry mass divided by volume (g cm⁻³)),
248 and root dry matter content (RDMC; dry mass divided by fresh mass (mg g⁻¹)) (Pérez-
249 Harguindeguy et al., 2016; Roumet et al., 2016). For carbon (C) and nitrogen (N) content
250 measurement, leaves of the same plant individual were pooled, and 30 g of soil of each
251 microcosm were analyzed. All samples were dried (60°C for 72 h), ground, and transferred
252 into tin capsules (30 mg, respectively). Analysis was performed using dry combustion with an
253 elemental analyzer (Vario EL cube IR, Elementar Analysensysteme GmbH, Langenselbold,
254 Germany). C and N content were provided as the relative mass proportion of the element (%)
255 per sample mass, and C:N ratio was calculated from these.

256 **Measurements of soil abiotic properties**

257 For the first four weeks of the experiment, one plastic strip with respectively one ion-exchange
258 membrane glued to each side (IEMs, 2.5 cm x 2.5 cm; AMI-7001S and CMI-7000S,
259 Membranes International Inc., Ringwood, NJ, USA) was added to each microcosm at 10 cm
260 depth to assess soil inorganic N availability (Durán et al., 2013). Prior to addition, the
261 membranes were immersed in 5% NaCl solution for 2 h at 37°C to allow for membrane
262 hydration and expansion. After 29 days, anion and cation membrane from IEMs were removed
263 from the soil, air dried, brushed to remove soil particles, and carefully removed from plastic
264 strips. The extraction was performed with 2 M KCL by orbital spinning (1 h at 200 rpm). The
265 extracts were analyzed for ammonium (NH₄⁺), nitrate (NO₃⁻) by the indophenol blue method
266 (Sims et al., 1995) and phosphate (PO₄³⁻) by the molybdenum blue method (Allen et al., 1986),
267 with a microplate reader (Durán et al., 2008). One sample was excluded from statistical
268 analysis, as we only found the plastic strip at the end of the experiment and not after 29 days

269 (Grass-Control-2). For pH measurements, 10 g of air-dried soil was solved in 25 ml of 0.01 M
270 CaCl₂ solution, shaken, and left for 1 h. Measurements were conducted with a pH-meter (Orion
271 Star A211, Thermo scientific, MA) according to the manual. To determine soil water content,
272 fresh soil was weighed, dried in a drying oven (75°C for at least 24 h), and reweighed.

273 **Statistical analyses**

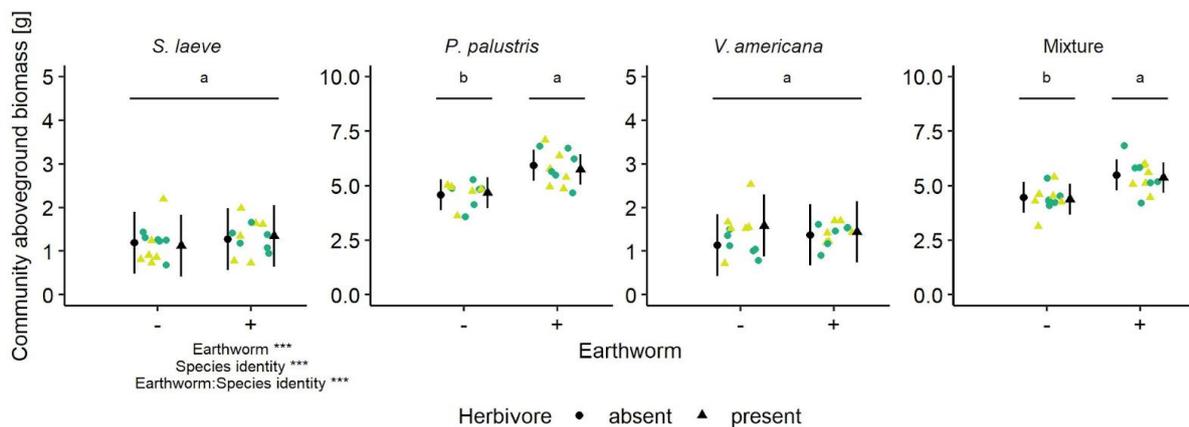
274 Statistical analyses and figures were conducted and created, respectively, using the R
275 software version 4.1.2 (R Core Team, 2021). Each trait was analyzed using a linear model,
276 followed by a Type II ANOVA from the package 'car' (Fox & Weisberg, 2019) after removing
277 missing data (NAs). Plant species identity, plant diversity level, earthworm treatment, and
278 herbivore treatment were analyzed as factors in a four-way interaction, respectively.
279 Assumptions of the models were visually checked using the R packages 'performance'
280 (Lüdecke et al., 2021a) and 'see' (Lüdecke et al., 2021b). When needed, variables were log
281 transformed, such as aboveground biomass, leaf area, LDMC, SLA, SRL, RTD, nitrogen
282 content of leaves, soil water content, herbivory rate, PO₄³⁻, and NH₄⁺ of soil. To analyze height
283 growth and aboveground biomass, the averaged initial height was added to the model as a
284 covariate, but not in interaction with the other factors. For count (ramets) and proportion
285 (survival data) data, generalized linear models (Poisson and binomial, respectively) were
286 performed using the package 'stats' (R Core Team, 2021). As only *P. palustris* developed
287 inflorescences, species identity was not considered for the analysis. When analyzing herbivore
288 survival/rate or earthworm survival the respective treatments (*i.e.* herbivore and/or earthworm
289 presence) were excluded as an explanatory variable. For community traits and soil abiotic
290 measurements the species column included the necessary information (*S. laeve*, *P. palustris*,
291 *V. americana*, or mixture) and the plant diversity level was therefore excluded as an
292 explanatory variable. Post-hoc tests of the significant interactions were conducted using the
293 function 'emmeans' from the correspondent R package (Lenth, 2021) with Holm correction.
294 Compact letter displays were created using the R package 'multcomp' (Hothorn et al., 2008).
295 Data were plotted per trait using 'ggplot2' (Wickham, 2016) and the letters correspond to the

296 significant interaction with the highest number of factors. For calculating the change of traits in
 297 percentage the estimated marginal means from the post-hoc tests were used. All results are
 298 in SI and the following abbreviations are used for the statistical effects in the results: earthworm
 299 treatment= EW; herbivore treatment= Hrb; plant species identity= Spc; Plant diversity level=
 300 Clt.

301 Results

302 Plant community productivity responses

303 Only five out of the 288 plant individuals died during the experiment (1.7%), four of which
 304 were *V. americana* individuals growing in mixture and one *S. laeve* from a monoculture
 305 (Supplementary material, Table A2). In the presence of earthworms, *P. palustris* and mixed
 306 communities produced significantly more aboveground biomass than when earthworms were
 307 absent (*P. palustris*: +26%, mixed community: +23%; EW:Spc interaction effect: $p=0.0006$;
 308 Figure 1; Supplementary material, Table A3). Root community biomass and community
 309 shoot:root ratio were not significantly affected by earthworm presence (Supplementary
 310 material, Table A3, Figure A1 and A2).



311

312 Figure 1: Community aboveground biomass (per microcosm) (estimated marginal mean \pm CI_{95%}) of different plant
 313 communities (monocultures of *Symphyotrichum laeve*, *Poa palustris*, and *Vicia americana*, or mixture of all three
 314 species) with (+) and without (-) earthworm as well as herbivore treatment (presence (yellow triangles) vs. absent
 315 (green circles)). A linear model was applied to analyze these data after excluding NA's. The letters were derived
 316 from a post-hoc test (pairwise comparison of estimated marginal means using the "holm" correction) investigating

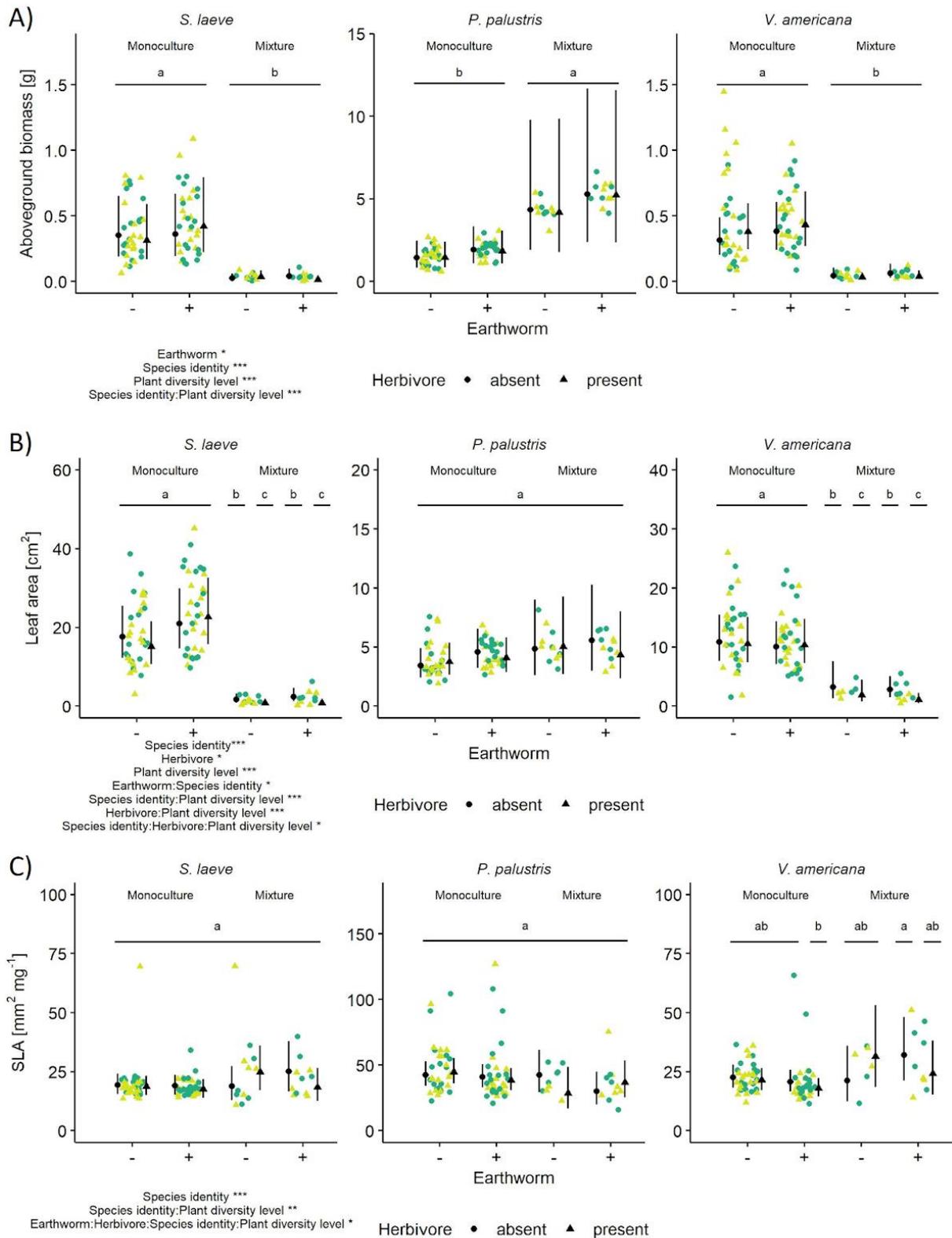
317 the effect of earthworm treatment for each plant community. Different letters represent a significant difference (p-
318 value < 0.05) and can be interpreted only within each community. In total, 96 observations were analyzed (each
319 community type: 24; earthworm and herbivore absence/presence: 48 each). Significant factors are displayed in the
320 bottom left corner (**** 0.001; *** 0.01; ** 0.05).

321 **Plant functional trait responses**

322 All studied plant functional traits differed significantly among plant species. Eight out of eleven
323 plant functional traits were significantly affected by earthworm presence; either by a general
324 effect across all treatments or the effect differed significantly among plant species, with plant
325 diversity level, and/or herbivore presence.

326 *Aboveground trait responses*

327 Among the aboveground traits measured, earthworm treatment overall affected aboveground
328 biomass, leaf area, specific leaf area, and leaf dry matter content, but not the height growth
329 (Supplementary material, Table A4). Earthworm presence increased aboveground biomass
330 across all plant species (+15%), irrespective of other treatments (EW effect: p=0.017). Overall,
331 *V. americana* and *P. palustris* individuals had the largest height difference between initial and
332 final height (*V. americana*: 22.10 ± 11.39 cm, *P. palustris*: 16.55 ± 5.60 cm), while *S. laeve*
333 individuals grew the least (3.80 ± 2.73 cm; Supplementary material, Figure A3). Earthworm
334 and herbivore treatments did not significantly affect the height growth of any plant species.
335 *Symphyotrichum laeve* and *P. palustris* individuals had a higher leaf area when earthworms
336 were present (*S. laeve*: +22%, *P. palustris*: +9%), while it was the opposite for *V. americana*
337 individuals (-18%; EW:Spc interaction effect: p=0.043). Despite leaf area changes, the SLA of
338 *S. laeve* and *P. palustris* were not significantly affected by the experimental treatments.
339 However, in the presence of earthworms, the SLA of *V. americana* was higher in the absence
340 of herbivores in mixture in comparison to the treatment with herbivores in monoculture (-44%),
341 while the other treatment combinations had a similar SLA (EW:Hrb:Clt:Spc interaction effect:
342 p=0.013; Figure 2; Supplementary material, Table A4). The LDMC was generally higher (+9%)
343 when earthworms were present (EW effect: p=0.006; Supplementary material, Figure A4).



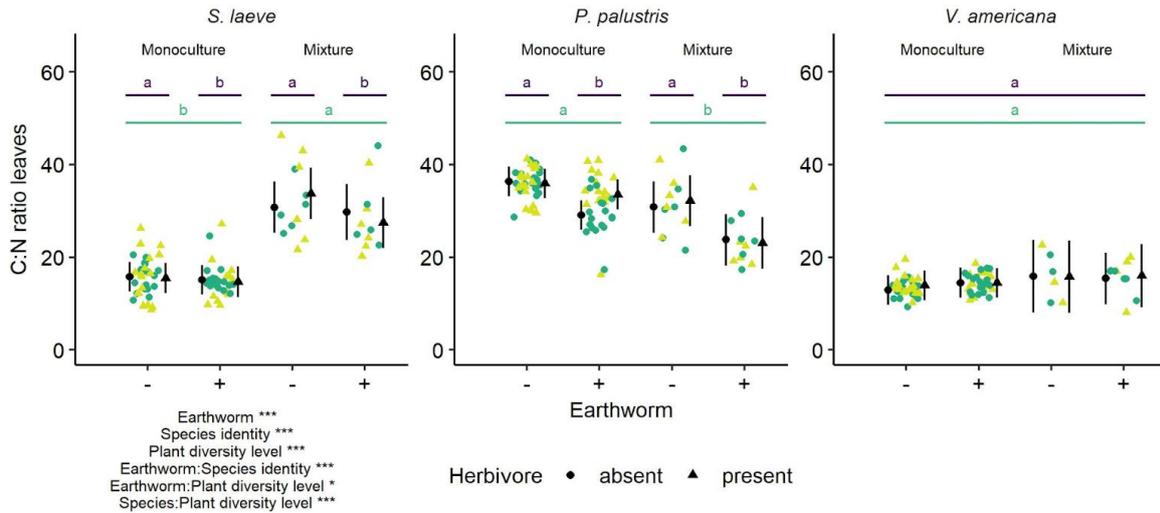
344

345 Figure 2: Aboveground biomass (A), leaf area (B), and specific leaf area (C) (estimated marginal mean \pm CI_{95%}) of
 346 the three plant species studied (*Symphyotrichum laeve*, *Poa palustris*, and *Vicia americana*) growing in different
 347 plant diversity levels(monoculture vs. mixture) with (+) and without (-) earthworm as well as herbivore treatment
 348 (presence (yellow triangles) vs. absent (green circles)). A linear model with a log transformation was applied to

349 analyze these data after excluding NA's. Data were back-transformed before plotting. The letters were all derived
350 from post-hoc tests (pairwise comparison of estimated marginal means using the "holm" correction). Different letters
351 represent a significant difference (p -value < 0.05) and can be interpreted only within each species. Significant
352 factors are displayed in the bottom left corners (**** 0.001; *** 0.01; ** 0.05). A) Post hoc tests investigated the
353 effect of plant diversity level for each species. In total, 286 observations were analyzed (*S. laeve*: 95; *V. americana*:
354 95; *P. palustris*: 96; monoculture: 215; mixture: 71; earthworm and herbivore absence/presence: each 143). B) Post
355 hoc tests investigated the interaction between herbivore treatment and plant diversity level for each species. In total,
356 277 observations were analyzed (*S. laeve*: 93; *P. palustris*: 96; *V. americana*: 88; monoculture: 214; mixture: 63;
357 earthworm absence: 137; earthworm presence: 140, herbivore absence: 139; herbivore presence: 138). C) Post
358 hoc tests investigated the interaction of plant diversity level, earthworm, and herbivore treatment for each species.
359 In total, 272 observations were analyzed (*S. laeve*: 93; *V. americana*: 87; *P. palustris*: 92; monoculture: 214; mixture:
360 58; earthworm absence: 138, earthworm presence: 134, herbivore absence: 137; herbivore presence: 135).

361

362 Earthworms affected the C, N, and C:N ratio of the leaves (Supplementary material, Table A4).
363 The C content of *S. laeve* leaves growing in mixture without earthworms was higher compared
364 to individuals growing in monoculture irrespective of earthworm presence (+6%; EW:Clt:Spc
365 interaction effect: $p=0.006$). The leaf N content of *P. palustris* was increased in the presence
366 of earthworms (+27%), while no significant difference was found for the other two species
367 (EW:Spc interaction effect: $p=0.0004$). *Symphyotrichum laeve* and *P. palustris* both had a
368 lower C:N ratio when earthworms were present (*S. laeve*: -9%; *P. palustris*: -19%; EW:Spc
369 interaction effect: $p<0.0001$; Figure 3). Across all species, plant individuals growing in mixture
370 without earthworms had the highest C:N ratio, and plant individuals growing in monoculture
371 with earthworms present the lowest (EW:Clt interaction effect: $p=0.040$). The C:N ratio of plant
372 individuals growing in mixture with earthworms did not differ significantly from plant individuals
373 growing in monoculture without earthworms, and their C:N ratios were between the other two
374 plant diversity level/ earthworm treatment combinations (Figure 3). Overall, plant individuals
375 growing in monocultures with earthworms had a lower C:N ratio (-7%) than the ones without
376 earthworms. Plant individuals growing without earthworms had a higher C:N ratio in mixtures
377 (+18%) than in monocultures.



378

379 Figure 3: C:N ratio of leaves (estimated marginal mean \pm CI_{0.95%}) of the three plant species studied (*Symphytotrichum*
 380 *laeve*, *Poa palustris*, and *Vicia americana*) growing in different plant diversity levels (monoculture vs. mixture) with
 381 (+) and without (-) earthworm as well as herbivore treatment (presence (yellow triangles) vs. absent (green circles)).
 382 A linear model was applied to analyze these data after excluding NA's. The letters were derived from post-hoc tests
 383 (pairwise comparison of estimated marginal means using the "holm" correction). The purple letters (upper) come
 384 from a post-hoc investigating the effect of earthworm treatment for each species. The green letters (lower) were
 385 derived from a post-hoc test investigating the effect of plant diversity level for each species. Different letters
 386 represent a significant difference (p-value < 0.05) and can be interpreted only within each species. In total, 278
 387 observations were analyzed (*S. laeve*: 94; *V. americana*: 88; *P. palustris*: 96; monoculture: 215; mixture: 63;
 388 earthworm absence: 138; earthworm presence: 140; herbivore absence: 140; herbivore presence: 138). Significant
 389 factors are displayed in the bottom left corner (**** 0.001; *** 0.01; ** 0.05).

390 *Reproductive trait responses*

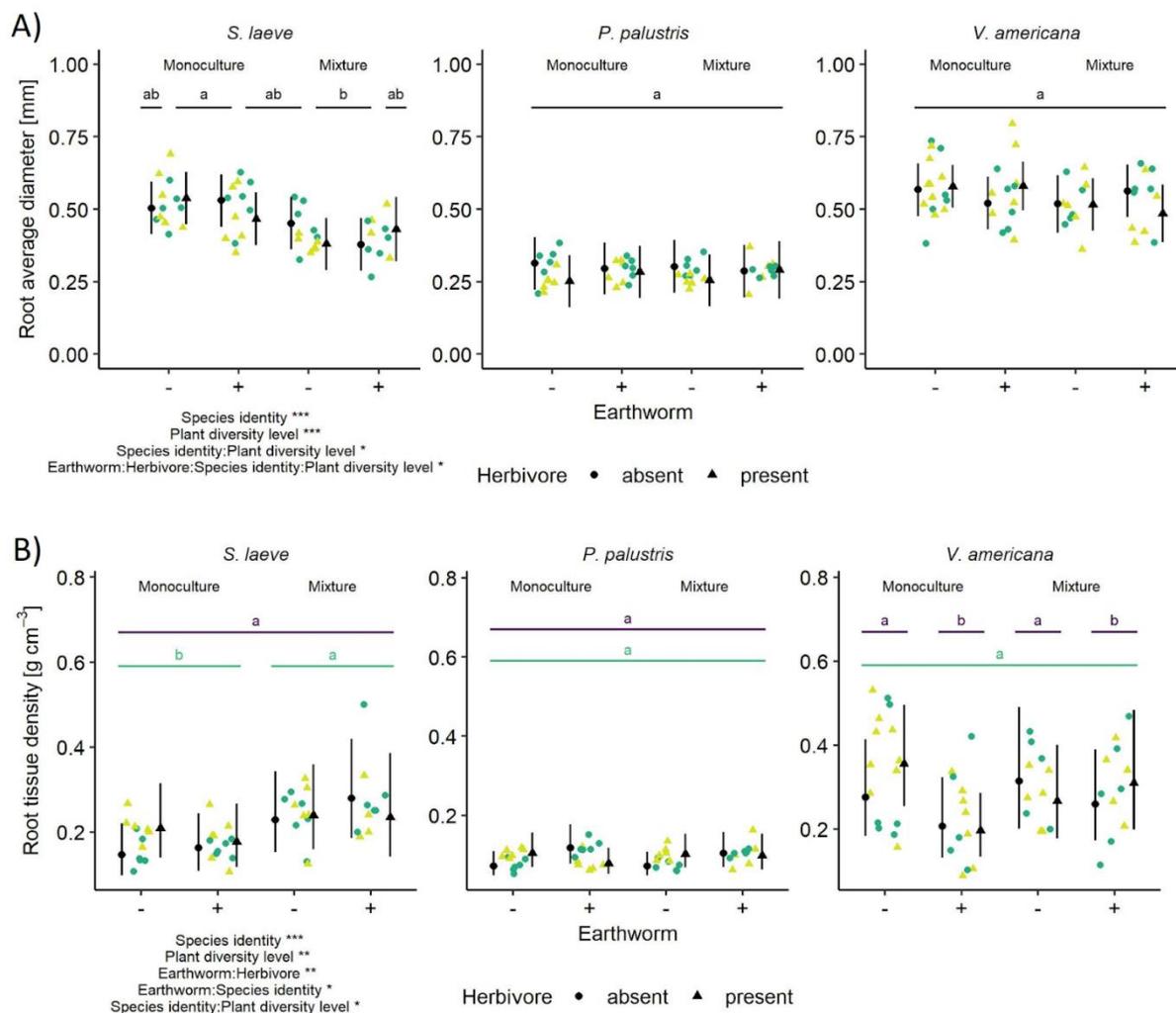
391 While only *P. palustris* individuals developed inflorescences that were produced in higher
 392 number in mixtures (+172%; Clt effect: p<0.0001) and when earthworms were present (+17%;
 393 EW effect: p=0.011; Supplementary material, Figure A7, Table A5), vegetative reproductive
 394 abilities (*i.e.* number of ramets) were overall increased for all species in the presence of
 395 earthworms (+12%; EW effect: p<0.0001; Supplementary material, Figure A8, Table A5).
 396 Moreover, *Poa palustris* produced more ramets in plant mixtures (+124%), while *V. americana*
 397 had a lower number of ramets in mixtures (-36%; Spc:Clt interaction effect: p<0.0001).

398

399 *Belowground trait responses*

400 We found coarse roots for *V. americana* (46 samples) and *S. laeve* (four samples), while *P.*
401 *palustris* only had fine roots. Only root average diameter and root tissue density measured on
402 the fine roots samples varied in response to the earthworm treatment, the herbivore treatment,
403 and the plant species (Figure 4; Supplementary material, Table A6). Root dry matter content
404 (RDMC) was higher in mixture compared to monoculture (+54%; Clt effect: $p=0.018$), but was
405 not affected by earthworm presence nor another treatment (Table 3; Supplementary material,
406 Figure A9). In the same way, plant diversity level, earthworm presence, and herbivore
407 presence did not significantly affect specific root length (Supplementary material, Table A6).
408 However, root average diameter of *S. laeve* individuals growing in mixture with either
409 earthworms present and herbivore absent, or earthworms absent and herbivore present was
410 lower (-30%) than that of the same species in monoculture with the same treatment
411 combinations (EW:Hrb:Clc:Spc interaction effect: $p=0.033$; Figure 4), while the other plant
412 species were not significantly affected by this interaction of the experimental treatments. The
413 roots of *V. americana* individuals had a lower root tissue density (RTD) when earthworms were
414 present compared to the treatment without earthworms (-21%; Spc:EW: $p=0.015$; purple letters
415 in Figure 4). In the absence of earthworms, all three studied plant species had higher RTD
416 when herbivores were present (+23%) compared to the treatment without herbivores (EW:Hrb
417 interaction effect: $p=0.009$).

418



419

420 Figure 4: Root average diameter (A) and root tissue density (B) (estimated marginal mean \pm CI_{95%}) of the three plant
 421 species studied (*Symphyotrichum laeve*, *Poa palustris*, and *Vicia americana*) growing in different plant diversity
 422 levels (monoculture vs. mixture) with (+) and without (-) earthworm as well as herbivore treatment (presence (yellow
 423 triangles) vs. absent (green circles)). After excluding NA's, a linear model was applied to analyze data. The letters
 424 were all derived from post-hoc tests (pairwise comparison of estimated marginal means using the "holm" correction).
 425 Different letters represent a significant difference (p-value < 0.05) and can be interpreted only within each species.
 426 Significant factors are displayed in the bottom left corner (**** 0.001; *** 0.01; * 0.05), respectively. A) Post hoc
 427 tests investigated the interaction of plant diversity level and earthworm and herbivore treatment for each species. In
 428 total, 143 observations were analyzed (*S. laeve*: 46; *V. americana*: 47; *P. palustris*: 50; monoculture: 76; mixture:
 429 67; earthworm absence: 69; earthworm presence: 67; herbivore absence: 71; herbivore presence: 72). B) Data
 430 was log transformed before analysis and back- transformed before plotting The purple letters (upper) come from a
 431 post-hoc investigating the effect of earthworm treatment for each species. The green letters (lower) were derived
 432 from a post-hoc test investigating the effect of plant diversity level for each species. In total, 142 observations were

433 analyzed (*S. laeve*: 46; *V. americana*: 49; *P. palustris*: 47; monoculture: 75; mixture: 67; earthworm absence: 74;
434 earthworm presence: 68; herbivore absence: 70; herbivore presence: 72).

435

436 **Earthworm / herbivore survival and herbivory rate**

437 Out of the 96 earthworms added to experimental microcosms, 68 were found alive at the end
438 of the experiment (70%), and no experimental treatment influenced their survival significantly
439 (Supplementary material, Table A2). We also found that 118 herbivores died or escaped (84%)
440 after five days, while 23 were still alive and present (16%), and 97 out of 141 leaves (64%) had
441 marks of herbivory on them. Most herbivores survived on *S. laeve* growing in monoculture
442 (44%) followed by *V. americana* monoculture (17%), while no herbivores survived on these
443 plant species growing in mixture. One herbivore survived on *P. palustris* growing in mixture,
444 none when growing in monoculture (Supplementary material, Table A2). Overall, the *S. exigua*
445 larvae fed most on *S. laeve*, secondly on *V. americana*, and the least on *P. palustris* (Spc
446 effect: $p=0.017$; Supplementary material, Table A7, Figure A11). Earthworm presence had no
447 significant effect on the herbivory rate.

448 **Soil abiotic properties**

449 Soil pH (7.41 ± 0.05) and soil C:N ratio (17.65 ± 3.67) were not significantly affected by the
450 experimental treatments (Supplementary material, Table A8, Figure A12 and A13). Soil water
451 content was significantly lower (-9%) in the presence of earthworms (EW effect: $p=0.027$;
452 Supplementary material, Table A8, Figure A14). Soil C content did not differ among plant
453 species, but soil of *P. palustris* communities contained less C when earthworms were present
454 (-19%; EW:Spc interaction effect: $p=0.013$; Supplementary material, Table A8, Figure A15),
455 and soil of *Vicia americana* communities had an increased soil C content in the presence of
456 herbivores (+17%; Hrb:Spc interaction effect: $p=0.012$). Soil of *P. palustris* communities
457 contained significantly more N without earthworms and herbivores present (+48%) compared
458 to other treatment combinations (EW:Spc:Hrb interaction effect: $p=0.041$). Within the first four
459 weeks of the experiment, no other factor apart from plant species identity had a significant

460 effect on PO_4^{3-} (Spc effect: $p=0.0003$; Supplementary material, Table A8, Figure A17). In
461 presence of earthworms, soil NO_3^- increased significantly (+54%; EW effect: $p=0.0003$;
462 Supplementary material, Table A8, Figure A18). NH_4^+ did not change significantly in response
463 to any treatment, including plant species identity and earthworm treatments (Supplementary
464 material, Table A8, Figure A19).

465 **Discussion**

466 **Earthworms change plant trait expression**

467 Given that earthworm invasion is changing plant communities in North American forests
468 towards lower diversity and grass dominance (Craven et al., 2017), we investigated the
469 underlying mechanisms by examining how earthworms affect the functional traits of plant
470 species belonging to three different plant functional groups (*i.e.* grasses, herbs, and legumes)
471 in different plant communities (*i.e.* different levels of competition) and in the presence and
472 absence of aboveground herbivores. Our study confirms that invasive earthworms can affect
473 plant functional traits of native plants in a significant way, which is in line with the recent findings
474 of Thouvenot et al. (2021) and Blume-Werry et al. (2020). We observed that eight out of eleven
475 measured plant functional traits were affected either by the main effect of earthworms, or
476 earthworm effects in combination with those of plant species identity, plant diversity level,
477 and/or herbivore presence. Only height growth, root dry matter content, and specific root length
478 did not respond significantly to earthworm presence. Across all plant species, earthworm
479 treatment (alone) increased the number of ramets, the LDMC, and induced a modification in
480 the leaf area. For example, we found that *V. americana* developed a smaller leaf area, while
481 *S. leave* and *P. palustris* developed a larger leaf area when growing in earthworm presence.
482 These changes might be based on higher nutrient availability due to the activities of
483 earthworms (van Groenigen et al., 2014). Indeed, it was shown that LDMC is a predictor for
484 soil fertility (Hodgson et al., 2011), and Zaller & Arnone (1999) explained increased ramet
485 production close to earthworm casts mainly by enhanced nutrient availability. This is in line

486 with increased concentrations of nitrate in soil and higher leaf nutritional value in *S. laeve*
487 (lower C:N) and *P. palustris* (lower C:N; higher N) in the presence of earthworms. The
488 observed increase of soil nitrate in the presence of earthworms supports the assumption that
489 earthworms enhance soil nitrogen availability and uptake by plants (van Groenigen et al.,
490 2014).

491 **Grass aboveground productivity and reproduction benefits from interspecific** 492 **competition and earthworms**

493 Aboveground productivity of *P. palustris* monocultures and the mixed community were
494 significantly increased in the presence of earthworms, while productivity of *S. laeve* and *V.*
495 *americana* communities did not show any general short-term responses to the earthworm
496 treatment. These results support the findings that slow-growing species cannot exploit
497 additional nutrients as rapidly as fast-growing species (Reich, 2014), and provide only partial
498 support for our hypothesis (1), expecting that plant productivity is generally increased by
499 earthworm presence. Grass community productivity may be more responsive to earthworm
500 activity due to their high resource competitiveness and rapid growth (Eisenhauer & Scheu,
501 2008a; Linder et al., 2018; Thouvenot et al., 2021).

502 When growing in interspecific competition, several traits of *P. palustris* (lower C:N, more
503 aboveground biomass, ramets, and inflorescences) indicate an elevated nutrient uptake,
504 growth, and reproduction. Reduced SLA points to decreased photosynthetic rate (Violle et al.,
505 2007), probably due to less competition for light. Moreover, *P. palustris* developed more
506 inflorescences when growing in earthworm presence. Inflorescences are an indicator for
507 individual plant performance (Roscher et al., 2011), and an increased sexual reproduction may
508 represent a competitive advantage (E-Vojtkó et al., 2020) rarely reported in previous studies
509 on the consequences of earthworm invasion (Blume-Werry et al., 2020). As earthworms can
510 change nutrient and water availability (Ferlian et al., 2020), they might act as a filter on plant
511 reproduction (Eisenhauer et al., 2012; E-Vojtkó et al., 2020). Even though we found that *P.*
512 *palustris* individuals benefit from earthworm presence and from interspecific competition (or

513 missing intraspecific competition), we did not find an interaction effect of these two factors.
514 Besides several functional traits of the legume species *V. americana* and the herb species *S.*
515 *laeve* changing in interspecific competition (e.g. lower aboveground biomass, lower height
516 growth, less ramets), four out of 24 *V. americana* individuals died that grew in mixed
517 communities. The legume individuals developed a higher SLA in interspecific competition,
518 which is a strategy to cope with lower light availability by raising their photosynthetic rate
519 (Roscher et al., 2011; Violle et al., 2007). Nevertheless, we did not find an interaction effect of
520 plant diversity level and earthworm presence for any of the studied traits for these two species,
521 providing little support for our hypothesis (2).
522 The finding that neither earthworm presence, nor a change of plant diversity level had a
523 significant effect on the C:N ratio of *V. americana* leaves, supports results of former studies
524 that state that legumes are rather independent of soil nutrient changes, e.g. caused by plant
525 competition or the presence of earthworms (van Groenigen et al., 2014; Wurst et al., 2003).
526 Since *S. laeve* and *V. americana* did not develop inflorescences in any of the treatments, it
527 seems that the experiment was too short for this to happen. As seed production is often
528 referred to as “the fitness currency” of plants (Schwachtje et al., 2006) and flowering is a critical
529 prerequisite, the effects of earthworms on flowering and seed production deserve more
530 attention, and experiments carried out over a longer period of time are needed. Moreover, such
531 studies would help finding out whether the grasses only developed inflorescences earlier or
532 more overall when earthworms were present.

533 **Earthworm presence does not affect herbivory rate or herbivore survival**

534 Neither herbivory rate, nor herbivore survival, of any of the plant species was affected by
535 earthworm presence (Hypothesis (4)). As the initial C:N ratio of the soil used (20.98) was higher
536 and the N% (0.06%) lower than in comparable studies (Eisenhauer et al., 2007; Thouvenot et
537 al., 2021; Wurst et al., 2005), we do not expect the lack of earthworm effects on herbivory and
538 herbivore survival to be due to a too high initial soil nutrient status (van Groenigen et al., 2014).
539 Contrary to the expectations that slow-growing species have a better defense than fast-

540 growing species (Reich, 2014), the grass species studied was not only the least palatable, but
541 also the least suitable for the survival of herbivores. A possible explanation is that grass leaves
542 contain silica, which enhances the tissues abrasiveness and reduces its digestibility (Luyckx
543 et al., 2017; Vicari & Bazely, 1993) by changing leaf surface morphology (Hall et al., 2020).
544 The increase of LDMC (higher defense; all plant species) and the decrease of C:N ratio (higher
545 nutritious value; *P. palustris* and *S. laeve*) caused by earthworms could also have balanced
546 each other out and, thus, prevented a change of herbivory rate. Furthermore, multiple aspects
547 that have an impact on the outcome of earthworm effects on herbivory have been identified,
548 which may also differ with the environmental context. For example, it was shown that the
549 density and diversity (species and ecological groups) of earthworms, the herbivore feeding
550 guilds (chewing, phloem-feeding, cell-feeding), and plant functional group identity may play a
551 role (Xiao et al., 2018).

552 **Earthworm presence and competitive environment modulate herbivore effects on** 553 **specific traits**

554 We found effects of short-term aboveground herbivory on plant traits (*i.e.* LDMC, leaf area,
555 RTD; hypothesis (3)). However, the effects were modulated by interspecific competition and
556 earthworm presence, supporting our hypothesis (5) (*i.e.* effects of invasive earthworms and
557 aboveground herbivory depend on plant community composition). Leaf traits (LDMC and leaf
558 area) of plants growing in interspecific competition changed in the presence of herbivores,
559 which indicates that interspecific competition led to the leaf development being more sensitive
560 to herbivory, and plants invested more into mechanical defense (tougher leaves) (Loranger et
561 al., 2012).

562 In the absence of earthworms, herbivore presence led to a higher RTD across plant species,
563 which is associated with higher resistance to pathogens and drought (Pérez-Harguindeguy et
564 al., 2016). This might offer an advantage in tolerating herbivore attack by reducing the risk of
565 other influences that may harm the herbivory-weakened plant (e.g. drought and pathogens).
566 Further, a higher RTD might indicate translocation of resources after herbivore attack (Babst

567 et al., 2008; Gómez et al., 2010; Schwachtje et al., 2006) or a more conservative use of, for
568 example, carbon through lower root exudation (Wen et al., 2021). Vice versa, our data shows
569 that the RTD of plants that grew with earthworms did not change in response to herbivory,
570 indicating that earthworms suppressed an herbivory-induced increase of RTD. Herbivory rate
571 was not lower when earthworms were present. Possibly, firmer leaf tissue (measured as higher
572 LDMC) might have reduced the effect of herbivory on the plants' condition and thus did not
573 cause any significant change of RTD.

574 The effects of earthworm presence on the root average diameter of *S. laeve* and to a lesser
575 extent on the SLA of *V. americana* were also dependent on the biotic context. The similar effect
576 of earthworms and herbivores, respectively, in the absence of the other leading to the highest
577 and lowest values of root average diameter within the plant diversity level is surprising, since
578 they have fundamentally different effects on plants. Presumably, herbivory led to a
579 redistribution of resources towards roots (e.g. Schwachtje et al., 2006), while earthworms are
580 known to improve nutrient availability for plants (Scheu, 2003; van Groenigen et al., 2014).
581 Changed resource availability due to competition (Aschehoug et al., 2016) modulated these
582 effects, but when earthworms and herbivores were both present, root average diameter
583 changes were not observed, regardless of plant diversity levels. These complex interactions
584 for the first time indicate that earthworms interact with interspecific competition and herbivory.
585 We recommend for future studies to investigate the mechanisms behind these interactions on
586 belowground traits for different plant species to be able to predict the consequences for plant
587 community structure. Further, we suggest studying additional root resource-acquisition
588 strategies, such as mycorrhizal symbiosis and root exudation, since these may also play critical
589 roles in plant resource use and competition (Wen et al., 2021). To relate all our results more
590 broadly to the functional groups of plants, we recommend testing more and different plant
591 species per plant functional group in future studies.

592

593

594 **Conclusions**

595 Our study provides experimental evidence that invasive earthworms affect plant resource
596 acquisition and competitive abilities by inducing changes in above- and belowground plant
597 functional traits. These effects were partly modulated by competition and herbivory, and may
598 reveal some of the mechanisms behind plant community changes in northern North American
599 forests after earthworm invasion. Earthworms did not only enhance the aboveground biomass
600 of the grass *P. palustris* but also improved its competitive advantage, such as reflected by a
601 higher number of inflorescences, enhanced leaf area, and elevated tissue N content. Our
602 findings thus confirm that the grass species *P. palustris* is a strong competitor and benefits
603 from earthworm presence at least in the short term. The herb and legume species did not
604 benefit to a similar extent by earthworm presence, which is why we assume that earthworms
605 increased the competitive strength of the grass species at the expense of the other plant
606 functional groups. Earthworms did not affect herbivory rate and herbivore survival, but
607 suppressed an effect of herbivores on the root tissue density. Our study shows that changed
608 plant trait expression by earthworms is partly depending on the biotic context of the plants; *i.e.*
609 competition and herbivory. Taken together, the results of the present study thus shed light on
610 trait-based mechanisms potentially underlying observed shifts in plant community composition
611 in northern North American forests to the benefit of grasses and the expense of legumes.

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