

1 **Earthworms affect plant growth and resistance against herbivores: a**

2 **meta-analysis**

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22 Running headline: Earthworm effects on plant resistance

23 **Summary**

24 **1.** Subterranean detritivores such as earthworms can increase soil nutrient availability
25 through their burrowing and casting activities. A number of recent studies have
26 explored whether these changes caused by earthworms may in turn affect plant
27 performance and resistance to herbivores, but no formal synthesis of this literature has
28 been conducted to date.

29 **2.** We here formally tested for the effects of earthworms on plant growth, resistance
30 and chemical defence against insect herbivores by performing a meta-analysis of the
31 existing literature up to 2016. We also explored ecological factors that might explain
32 among-studies variation in the magnitude of the earthworm effects on plant growth
33 and resistance.

34 **3.** We found that earthworm presence increases plant growth (by 20 %) and nitrogen
35 content (by 11 %). Overall, earthworms did not affect plant resistance against
36 chewing herbivores (caterpillars, slugs and rootworms), and even led to a 22 %
37 decrease in plant resistance against phloem-feeding herbivores (aphids). However,
38 earthworm presence increased production of chemical defences by 31% when plants
39 where attacked by cell-feeders (thrips), and resulted in an 81 % increase in resistance
40 against thrips. The magnitude of earthworm effects was stronger when earthworm
41 inoculations consisted of a mix of species and ecological types, and when densities of
42 earthworms were high.

43 **4.** These results suggest that earthworm presence is an important factor underlying
44 natural variation in plant defences against herbivores, and call for a better integration

45 of the soil fauna in the studies of plant-herbivore interaction, both for applied and

46 fundamental research.

47

48 **Key-words:** Endogeic earthworms, detritivore diversity, herbivore-feeding guilds,

49 plant nutrients, plant resistance, chemical defences, plant growth-defence trade-off,

50 meta-analysis.

51

52 **Introduction**

53 In response to the constant threat imposed by herbivores, plants have evolved a broad
54 range of defensive strategies, including mechanical and chemical barriers that reduce
55 herbivore performance (Schoonhoven, Van Loon & Dicke 2005; Agrawal 2007;
56 Johnson 2011). The effect of defensive traits on herbivore performance and fitness is
57 termed plant resistance (Karban & Baldwin 2007), while the ability of the plants to
58 recover from tissue loss is termed tolerance (Strauss & Agrawal 1999; Tiffin 2000;
59 Núñez-Farfán, Fornoni & Valverde 2007). Understanding the factors driving variation
60 in plant anti-herbivore strategies remains a core question in ecology (Walling 2000),
61 and advances in this area could be used to inform crop protection (Lyon, Newton &
62 Walters 2014).

63 It is generally assumed that plant ability to defend itself is costly, and thus it
64 should trade off with other life history traits such as growth and reproduction (Coley,
65 Bryant & Chapin 1985; Herms & Mattson 1992; Koricheva 2002). Nonetheless, the
66 consequences of differences in allocation between growth and defences against
67 herbivores vary depending on environmental conditions, such as variation in soil
68 nutrients (Coley, Bryant & Chapin 1985; Fine et al. 2006).

69 For optimal plant growth, soil nutrients must be available in sufficient and
70 balanced amounts (Aerts & Chapin 1999). While soils generally contain a relatively
71 large stock of nutrients, these reserves are usually present in the forms of complexed
72 organic compounds, rendering nutrients inaccessible for plants. The turnover and
73 release of nutrients from soil organic matter (SOM) depend on the rate of

74 decomposition and mineralization of elements through biogeochemical processes
75 (Seastedt 1984; Prescott 2005). Therefore, the efficiency of SOM decomposition and
76 mineralization will influence the magnitude of soil nutrient availability, in turn
77 affecting plant growth and performance (Ladha et al. 2004; Yoshitake, Soutome &
78 Koizumi 2014). Among the highly diverse soil fauna, the invertebrates of the meso-
79 and macrofauna are the key organisms participating in SOM turnover and nutrient
80 release (Bardgett & Chan 1999; Edwards 2004; Bhadauria & Saxena 2010), owing to
81 their critical role in breaking down detrital inputs and priming detritus for microbial
82 decomposition (Seastedt 1984; Prescott 2005).

83 Earthworms are among the most important detritivores within soil food webs and
84 are commonly considered as ecosystem engineers (Edwards 2004; Blouin et al. 2013;
85 Cunha et al. 2016). Through their burrowing and casting activities, earthworms
86 improve soil nutrient availability via greater mineralization and/or humification of soil
87 organic matter, modifications of soil porosity and aggregation, and the stimulation of
88 soil microflora (Scheu 2003; Brown, Edwards & Brussaard 2004; van Groenigen et al.
89 2014; Bertrand et al. 2015; Cunha et al. 2016). In addition to these proven
90 growth-promoting effects (e.g. van Groenigen et al. 2014), recent studies have
91 highlighted that earthworms can also benefit plants by increasing their ability to resist
92 herbivore attacks (Wurst et al. 2008; Lohmann, Scheu & Muller 2009; Wurst 2013;
93 Trouve et al. 2014).

94 The mechanisms of earthworm-mediated plant resistance include, for example, an
95 increase in plant tolerance to herbivores by stimulating plant biomass production

96 during herbivore attack (Blouin et al. 2005; Wurst et al. 2008). Additionally,
97 earthworms can alter plant resistance by influencing the expression of
98 stress-responsive genes, and subsequently, the production of toxic secondary
99 metabolites (Blouin et al. 2005; Lohmann, Scheu & Muller 2009; Jana et al. 2010).
100 Nonetheless, earthworm effects on plant resistance against herbivores range from
101 negative to positive (e.g. Scheu, Theenhaus & Jones 1999; Johnson et al. 2011;
102 Loranger-Merciris et al. 2012). For instance, the endogeic earthworm *Aporrectodea*
103 *caliginosa* had a negative effect on the aphid *Rhopalosiphum padi* (Ke & Scheu 2008),
104 while the anecic earthworm *Lumbricus terrestris* had a positive effect on the same
105 aphid species (Eisenhauer & Scheu 2008). Moreover, the positive impact of
106 earthworms on plant growth could interact with defence allocation (Coley, Bryant &
107 Chapin 1985; Herms & Mattson 1992; Koricheva 2002). Therefore, earthworm effects
108 on plant resistance against herbivores seem to be highly context dependent (Wurst
109 2010; 2013), but are there general trends that emerge from the literature?

110 We here performed a meta-analysis to formally quantify the effects of earthworms
111 on plant growth and resistance against herbivores, and to identify ecological factors,
112 such as earthworm ecological types and diversity in the soil and herbivore feeding
113 guilds, driving variation in the magnitude of earthworm effects among studies.

114 Earthworm species are classified into three major ecological types (anecic, epigeic
115 and endogeic), which have distinct burrowing patterns. Epigeic earthworms live in
116 litter or topsoil layers where they forage primarily on plant residues. Anecic
117 earthworms live in permanent deep vertical burrows, and endogeic earthworms live in

118 the soil and forage on soil organic matter (Bouché 1977). Distinct burrowing patterns
119 and food preferences, as well as variation in earthworm density and species richness
120 have been shown to differentially affect soil nutrient mobilization and plant nutrient
121 uptake (Bossuyt, Six & Hendrix 2006; Curry & Schmidt 2007; Spurgeon et al. 2013;
122 Andriuzzi et al. 2016). We therefore hypothesized that the combination of different
123 earthworm ecological types should result in better resource acquisition via niche
124 partitioning, and therefore favour plant growth and nutrient content more than a single
125 earthworm type (Newington et al 2004).

126 In addition, earthworms could modify plant eco-physiological status, in turn
127 affecting the ability of plants to respond to herbivore attack. For instance, *Arabidopsis*
128 *thaliana* plants growing in the presence of *A. caliginosa* showed that enhanced
129 expression of genes involved in phytohormone signalling (e.g. auxin, ethylene,
130 jasmonic acids or salicylic acid), known to respond to biotic and abiotic stresses
131 (Puga-Freitas et al. 2012; Puga-Freitas et al. 2016). Generally, plants activate the
132 jasmonic acid (JA)-dependent signalling pathways in response to tissue-chewing
133 herbivores such as caterpillars and cell-content-feeding herbivores such as thrips
134 (Howe & Jander 2008), whereas salicylic acid (SA)-dependent defences are activated
135 in response to phloem-feeders such as aphids (Stam et al. 2014; Onkokesung et al.
136 2016). We therefore hypothesized that earthworms could enhance plant resistance
137 against a variety of herbivore types by simultaneously activating several
138 phytohormonal pathways.

139 Finally, given that selection for increased yield in domesticated crops often leads
140 to reduced levels of resistance to herbivores as compared to wild relatives (Rosenthal
141 & Welter 1995; Rosenthal & Dirzo 1997; Whitehead, Turcotte & Poveda 2017), we
142 postulated that the magnitude of earthworm effects on plant growth would be stronger
143 for wild plants, whereas the effects of earthworms on resistance to herbivores would
144 be stronger for crop plants.

145 We specifically asked the four following questions: 1) Do earthworms increase
146 plant growth and nutrient content? 2) Do earthworms increase plant resistance and
147 defences against herbivores? 3) Which ecological factors (plant type; herbivore
148 feeding guild; earthworm ecological type, earthworm density and species richness)
149 lead to variation in earthworm-mediated plant resistance/defence? 4) Is there a
150 trade-off between earthworm-mediated plant growth and resistance/ defence under
151 herbivore attack? We predicted that: 1) earthworm presence increases plant growth
152 and nutrient content, 2) earthworm presence reduces plant resistance due to increased
153 plant nutritional quality, 3) earthworm effects on plant defences are context dependent,
154 and 4) earthworms have opposing effects on plant growth and resistance.

155

156 **Materials and methods**

157 *DATA COLLECTION*

158 The data set was compiled by conducting keyword searches in the ISI Web of
159 Science up to December 2016 using combinations of relevant terms (“earthworm”,
160 “decomposer invertebrate”, “ecosystem engineers”, “plant growth or tolerance”,

161 “herbivore or herbivory or insect or nematode”, “defence or defense or resistance”).

162 Additional searches using the same keywords were conducted in the Google Scholar

163 and reference lists of individual papers were screened to finally obtain a list of studies

164 that met all the following inclusion criteria: 1) plants were subjected to at least two

165 treatments: an earthworm inoculation treatment and control treatment without

166 earthworm; 2) plants in both treatments were under herbivore attack; 3) Concerning

167 plant growth, the study included at least one parameter of plant growth (e.g.

168 aboveground biomass, belowground biomass or total biomass) was measured;

169 concerning plant resistance, the study included at least one measured parameter of

170 plant resistance (i.e. herbivore performance parameters such as growth rate, mass,

171 fecundity, development time, consumption, oviposition preference, density, or the

172 degree of plant damage), and/or plant chemical defences (i.e. secondary metabolite

173 production); and 4) the data included means, some measure of variance, and at least

174 three independent replicates of each treatment. In total, the search yielded 20 papers

175 published between 1999 and 2016 that met our criteria (See Appendix S1 in

176 Supporting Information). However, meta-analyses exclusively based on published

177 studies may produce biased results since the probability of the study to be published

178 could depend upon the statistical significance, magnitude, and/or direction of research

179 findings (Koricheva, Gange & Jones 2009). It has been recommended, therefore,

180 whenever possible, to include unpublished studies and grey literature (e.g.

181 dissertations) in a meta-analysis (Møller & Jennions 2001). By searching in Google

182 using the same keywords as in Web of Science and by contacting individual

183 researchers, we obtained one published PhD thesis (Kadir 2014), in which the effects
184 of 18 different earthworm combinations on *Brassica rapa* growth and resistance were
185 tested. Finally, we also included two own unpublished studies (Xiao et al.,
186 unpublished data shown on Fig. S1). Overall, this grey literature based-dataset
187 includes work done on tomato and corn plants, and represents 15%, 13%, 4%, and 48%
188 of the total sample size for growth, nutrient, resistance, and defence-related effect
189 sizes, respectively (Appendix S1, Fig. S1). To test whether inclusion of our own
190 unpublished datapoints affected the results of the analysis, we performed sensitivity
191 analyses by excluding these data and reanalysing the overall effects for all major
192 variables (see Table S1). Overall, we found no significant differences in results (Table
193 S1 versus Tables S2-S5), therefore we report the results of analyses including the
194 unpublished data.

195 In total, our full searches yielded 79, 64, and 23 datapoints for plant responses in
196 terms of growth, resistance, and defence, respectively (Appendix S1). When available,
197 we also included data that measured earthworm effects on plant nutritional elemental
198 composition (i.e. total carbon, nitrogen and phosphorous concentration), as a measure
199 of how earthworms might modify plant nutrient content (n = 65 datapoints, Appendix
200 S1).

201 Finally, because of our initial search constraints, earthworm effects on plant
202 growth were assessed when plants were infested with herbivores. We thus aimed at
203 confirming that earthworm effects on plant growth we observed were not masked by
204 the presence of herbivores feeding on the plants. In addition, when available, we

205 collected a subset of datapoints on plant growth parameter when plants were left
206 herbivore-free, but only if these datapoints came from the same experiments as the
207 dataset described above (n = 25, Appendix S1, Fig. S2). This allowed a direct
208 comparison of the magnitude of earthworm effects on plant growth in the presence
209 and absence of herbivores.

210 Earthworm effects on plant growth were computed by including any
211 measurements of plant biomass, such as aboveground biomass, belowground biomass,
212 and/or total biomass. When fresh and dry mass were both reported, dry mass was
213 chosen. Earthworm effects on plant resistance against herbivores were assessed by
214 including measures of herbivore growth and development and plant damage imposed
215 by herbivores (Karban & Baldwin 2007). Earthworm effects on plant chemical
216 defences were assessed by including all data on plant secondary metabolites
217 (Appendix S1).

218 We included multiple outcomes per study when data were reported from several
219 independent experiments, tested on different plant species, or reported for treatments
220 with different ecological type, species richness and density of earthworms. However,
221 if repeated measurements of plant growth and/or resistance were available from the
222 same experiment, only the last date of the measurements was used. If the experiments
223 included additional treatments (e.g. manipulative drought and ambient rainfall
224 patterns), only data of the ambient (control) condition were used. For each
225 observation we extracted the means of the control treatment (without earthworm) and
226 the experimental treatment (with earthworms), as well as their standard deviation (SD)

227 and sample size (n). When SE was reported, we transformed it to SD by using
228 formula $SD = SE * \sqrt{n}$. If data were presented in graphical form, we extracted
229 data points using the GetData software (<http://www.getdata-graph-digitizer.com>).

230 Following van Groenigen et al. (2014), our initial dataset included five
231 categorical moderating variables that were used to explore additional sources of
232 variation across the treatments: 1) herbivore feeding guild (three levels: cell-feeding
233 herbivores including nematodes and thrips; chewing herbivores including slugs,
234 caterpillars and rootworms; and phloem-feeding herbivores including aphids), 2) plant
235 type (two levels: wild plants *versus* crops), 3) earthworm ecological type (four levels:
236 epigeic alone, endogeic alone, anecic alone, and mixtures of the three ecological
237 categories), 4) earthworm density (four levels: <100, 100-199, 200-400, >400
238 earthworms per m² of soil), and 5) earthworm species richness (two levels: single
239 species *versus* multi-species) (Appendix S1).

240

241 *META-ANALYSIS*

242 Effect sizes for earthworm effects were calculated using the natural logarithm of
243 the response ratio (lnR) (Hedges, Gurevitch & Curtis 1999) of the mean responses in
244 the presence (+E) and the absence (-E) of earthworm such that $\ln R = \ln(+E/-E)$. For
245 interpretation of the results, mean effects and confidence intervals were
246 back-transformed using the formula: $(\text{EXP}(\ln R)-1) \times 100$ and reported as the
247 percentage changes between control and earthworm additions.

248 Because higher herbivore performance (e.g. abundance, larva mass etc.) means
249 that plants are less resistant to herbivores whereas higher levels of plant secondary
250 metabolites mean that plants are better defended, the effect sizes for plant resistance
251 and plant defence had different initial signs. In order to compare resistance and
252 defence effect sizes within the same analyses, all resistance effect sizes, beside the
253 development time of herbivores, were calculated as inverse of $\ln R$ such as: $\ln R_{\text{resistance}}$
254 $= \ln (+E/-E)^{-1}$. Therefore, for all our analyses, effect sizes with positive values
255 indicate that earthworm presence increased plant growth, nutrient content, resistance
256 and defences against herbivores. The variance associated with effect size was
257 calculated from the standard deviation (SD) and sample size (n) associated with each
258 mean value of plant growth, nutrients, resistance and chemical defences, respectively
259 (Koricheva, Gurevitch & Mengersen 2013).

260 Meta-analysis was performed with the ‘metafor’ package (Viechtbauer 2010) in
261 R (R Development Core Team 2015). First, we estimated the overall effects of
262 earthworms on plant growth, nutrients, resistance, and chemical defences using a
263 random-effects model. The random-effects model was selected because of the
264 across-studies variability and in order to partition the variance into within- and
265 between-studies. In this analysis, individual effect sizes are weighted by the reciprocal
266 of the sum of the variance between-study and sampling variance within study. The
267 restricted maximum likelihood method (REML) was used to estimate between-study
268 variance. The mean effect size was considered as significantly different from zero if

269 its 95% confidence intervals (CIs) did not include zero (Koricheva, Gurevitch &
270 Mengersen 2013).

271 We assessed potential publication bias in the overall database using funnel plot
272 and the ‘trim and fill’ method (Jennions et al. 2013). In order to assess the robustness
273 of the observed overall effects of earthworm presence on plant growth, nutrients and
274 resistance/defences, fail-safe numbers (Nfs) were calculated by using Rosenberg’s
275 weighted method ($\alpha = 0.05$) (Rosenberg 2005) (See Tables S2-S5). Rosenberg’s Nfs
276 indicates how many studies reporting zero effect size would need to be added to the
277 meta-analysis to render the observed effect non-significantly different from zero
278 (Rosenberg 2005).

279 Next, we performed meta-regressions to explore how multiple moderator
280 variables could affect the earthworm-mediated effect size on plant resistance and
281 defences. Meta-regressions are more effective than standard meta-analytic techniques
282 at examining the impact of moderator variables for studying effect sizes (Benton,
283 2014). To avoid potential non-independence between moderators, their effects were
284 tested hierarchically as described in Fig. S3. Moderator analyses were performed only
285 when there were at least two levels with large enough sample size ($n > 3$, Fig. S3).
286 We used mixed-effects models to estimate the effect of each moderator (herbivore
287 type, plant type, earthworm ecological type, earthworm density, and earthworm
288 species richness) on the magnitude of earthworm presence. This model assumes that
289 differences among studies within a group are due to random variation, whereas
290 variation between groups is fixed. With this model, the between-group homogeneity

291 (Q_B) was used to estimate the significance of each categorical moderator (Koricheva,
292 Gurevitch & Mengersen 2013). If the Q_B was significant, we inferred that the mean
293 effect size differed between moderator levels, and two moderator levels were
294 considered to be significantly different from one another if their 95% CIs did not
295 overlap.

296 Finally, we computed correlations between: 1) the effect of earthworms on plant
297 growth versus plant resistance/defences, and 2) the effect of earthworms on plant
298 resistance versus plant nutritional parameters using Pearson's correlation analysis
299 (Table S6-S8). Each data point of the correlation corresponded to an $\ln R$ value as
300 calculated above. A significant positive correlation means that an increase in plant
301 resistance in the presence of earthworms is associated with an increase in plant
302 growth and/or plant nutritional parameters.

303

304 **Results**

305 *EARTHWORM EFFECTS ON PLANT GROWTH*

306 Overall, earthworm presence increased plant biomass by 20 % (Fig. 1a, Table S2).
307 Specifically, earthworm presence significantly increased plant aboveground biomass
308 by 16 %, belowground biomass by 29 % and total biomass by 22 % (Fig. 1a, Table
309 S2). The 'trim and fill' method detected three missing studies to the left of the grant
310 mean. The addition of three missing cases to the dataset produced a new grand mean
311 effect size of 19 % (95% CIs: 13 % to 26 %, $n = 82$), suggesting a robust positive
312 overall effect of earthworms on plant growth in the presence of herbivores (Table S2).

313 The Rosenberg's Nfs for the overall database is 6420, which is 15 times higher than
314 the threshold of 405 ($5 \times 79 + 10$), also indicating a robust mean effect size (Table
315 S2).

316 Additionally, by directly comparing the magnitude of earthworm effects on plant
317 growth in the presence and absence of herbivores using a balanced subset (i.e.
318 datapoints come from the same study, $n = 25$), we found that earthworm presence
319 increased overall plant biomass by 14 % and by 11% when plants grew in the
320 presence and absence of herbivores, respectively (Fig. S2).

321

322 *EARTHWORM EFFECTS ON PLANT NUTRIENT CONTENT*

323 Earthworm presence stimulated an overall 11 % increase in plant nutrient content
324 in the presence of herbivores (Rosenberg's Nfs = 19035, $n = 65$, Fig. 1b, Table S3).
325 The addition of 14 missing cases to the dataset by the 'trim and fill' method produced
326 a new grand mean effect size of 21 % (95% CIs: 12 % to 31 %, $n = 79$), suggesting a
327 robust positive overall effect of earthworms on plant nutrient content in response to
328 herbivory (Table S3). This result was mainly driven by a 21 % increase in plant
329 nitrogen content, while we detected a 20 % decrease in phosphorus and a 1% decrease
330 in carbon content when earthworms were present (Fig. 1b, Table S3).

331

332 *EARTHWORM EFFECTS ON PLANT RESISTANCE*

333 Overall, earthworm presence decreased plant resistance to herbivores by 15% (95%
334 CIs: -24 % to -4 %, $n = 64$). After 6 missing cases were added to the analysis by the

335 'trim and fill' method, the new grand mean effect size was -9 % (95% CIs: -19 % to
336 3 %, n = 70) (Table S4). Between-study variation explained 83 % of the observed
337 variation in the magnitude of the effect. While plant cultivation type did not influence
338 earthworm effects on plant resistance ($Q_B = 0.04$, $df = 1$, $p = 0.844$), we found a
339 strong effect of herbivore type ($Q_B = 12.098$, $df = 2$, $p = 0.002$). Earthworm presence
340 increased plant resistance to cell-feeders by 34 % (and by 50 % after adding two
341 missing cases with the 'trim and fill' method; Table S4). This result was mainly
342 driven by 80 % increase in plant resistance to thrips and 11% increase in resistance to
343 root-feeding nematodes (Fig. 2a, Table S4). In contrast, earthworm presence had no
344 significant effect on plant resistance to chewing herbivores (Fig. 2b, Table S4), and
345 decreased plant resistance to phloem-feeders by 22 % (Fig. 2c, Table S4). We
346 therefore proceeded to explore the possible causes of this heterogeneity using
347 moderator analyses (including earthworm ecological type, species richness and
348 density) with chewing and phloem-feeding herbivores separately (Fig. S3).

349 Earthworm ecological type and species richness did not affect earthworm effects
350 on plant resistance against chewing herbivores (Fig. 2b, Table S4). Plant resistance
351 against phloem-feeders was particularly decreased when a mixture of the three
352 earthworm ecological types or a mixture of different species of earthworms
353 (multi-species) was added in the experiments, and when earthworm densities were
354 high (i.e. above 400 individuals m^{-2}) (Fig. 2c, Table S4).

355

356 *EARTHWORM EFFECTS ON PLANT CHEMICAL DEFENCES*

357 Overall, earthworm presence did not significantly affect plant defence
358 compounds (Fig. 3). Between-study variation explained 81 % of the observed
359 variation in the magnitude of the effect. Again, while plant type did not affect
360 earthworm effects on plant chemical defences ($Q_B = 2.659$, $df = 1$, $p = 0.103$), we
361 found a strong effect of herbivore type ($Q_B = 12.139$, $df = 2$, $p = 0.002$). Specifically,
362 we found that earthworms had no effect on chemical defences in the presence of
363 chewing herbivores (Table S5). However, earthworm presence increased overall
364 chemical defences by 32 % in the presence of cell-feeding herbivores; this result was
365 driven by a 38 % increase in defensive compounds in the presence of nematodes and a
366 31% increase in the presence of thrips (Table S5). Additionally, earthworm presence
367 decreased chemical defences by 48 % in the presence of phloem-feeders (Table S5),
368 although this result was driven by one data-point only.

369 Because of lack of data for phloem-feeding and chewing herbivores (Fig. S3), we
370 proceeded to perform moderator analyses only for the cell-feeding herbivores (thrips).
371 We found that single-species earthworm inoculations significantly increased plant
372 chemical defences in the presence of cell-feeding thrips (Table S5). In addition,
373 earthworm-mediated plant chemical defences against thrips were not dependent on
374 earthworm ecological type (Table S5).

375

376 *EARTHWORM-MEDIATED RELATIONSHIPS BETWEEN PLANT GROWTH, NUTRIENTS,*
377 *RESISTANCE AND DEFENCES*

378 Effects of earthworm presence on plant resistance were negatively correlated with
379 earthworm effects on plant growth (Fig. 4a, Table S6). However, this relationship was
380 affected by herbivore type, plant type, earthworm ecological type, density, and
381 species richness (Table S7). Negative correlations between earthworm effects on plant
382 resistance and growth were strongest against phloem-feeders ($r = -0.48$, $p = 0.008$), in
383 wild plants ($r = -0.51$, $p = 0.009$), with endogeic earthworm inoculations ($r = -0.53$, p
384 $= 0.008$), with earthworm density below 100 individuals m^{-2} ($r = -0.95$, $p = 0.012$) and
385 with earthworm multi-species inoculations ($r = -0.52$, $p = 0.022$) (Table S7). On the
386 other hand, earthworm presence mediated an overall positive relationship between
387 plant growth and chemical defences ($r = 0.48$, $p = 0.021$, Fig. 4b, Table S6). This
388 positive earthworm-mediated relationship was strongest in crop plants ($r = 0.52$, $p =$
389 0.025 , Table S7), with earthworm single species treatment ($r = 0.49$, $p = 0.045$, Table
390 S7), and with earthworm multi-species treatment ($r = 0.97$ $p < 0.001$, Table S7).

391 Effects of earthworm presence on plant resistance were negatively correlated with
392 earthworm effects on plant nutrients only when earthworms were endogeic species (r
393 $= -0.42$, $p = 0.032$), and their density was less than 100 individuals m^{-2} ($r = -0.98$, $p =$
394 0.003) and 200-400 individuals m^{-2} ($r = -0.61$, $p = 0.026$) (Table S8). Effects of
395 earthworm presence on plant phosphorus content were negatively correlated with
396 earthworm effects on plant chemical defences (Table S6). Finally, effects of
397 earthworm presence on plant growth were positively correlated with earthworm
398 effects on plant nutrient content, total nitrogen and carbon in particular. (Table S6).

399

400 **Discussion**

401 We found that earthworm presence had an overall positive effect on plant growth
402 and nutritional content, and variable overall effects on plant resistance and chemical
403 defences. The results were strongly dependent on the herbivore feeding guild, as well
404 as on the ecological type, density and species richness of earthworms.

405

406 *EARTHWORM EFFECTS ON PLANT GROWTH*

407 We found an overall positive effect of earthworms on plant biomass gain against
408 herbivores (20 % more biomass on plants inoculated with earthworms) (Fig. 1a). This
409 is in line with previous results that extrapolated the positive effects of earthworms on
410 plant production (e.g. van Groenigen et al. 2014). In addition to the previous studies,
411 our subset data enabled a direct comparison of the effects of earthworms on plant
412 growth in the presence or absence of herbivores. We found that the magnitude of the
413 relative change in biomass of plants that experienced herbivores (14 %) was similar to
414 that of herbivore-free plants (11 %) (Fig. S2), indicating that herbivores did not
415 attenuate the effects of earthworms on plant growth.

416 Because herbivores are generally thought to decrease plant biomass, these results
417 might be suggestive of an earthworm-mediated tolerance in plants under herbivore
418 attack. While the meta-analysis could not tease apart the mechanisms behind plant
419 growth enhancement in the presence of earthworms, the compensatory continuum
420 hypothesis (CCH) asserts that plants have a greater potential for compensating for
421 herbivore damage under resource-rich conditions (Maschinski & Whitham 1989).

422 Therefore, earthworms could favour tolerance responses of plants by increasing soil
423 nutrient availability.

424

425 *EARTHWORM EFFECTS ON PLANT RESISTANCE*

426 Plant resistance against herbivores is generally mediated by changes in nutritional
427 quality and/or production of toxic secondary metabolites. Earthworms have been
428 shown to affect primary and secondary metabolism in plants, as well as the expression
429 of stress-responsive genes in both aboveground and belowground parts of plants, thus
430 potentially impacting herbivore performance (Blouin et al. 2005; Lohmann, Scheu &
431 Muller 2009; Jana et al. 2010). We found that earthworms increased plant
432 susceptibility to phloem feeders, but increased resistance to cell-feeding herbivores,
433 and had no effect on resistance to chewing herbivores.

434 Across the studies involving the phloem feeders (aphids), we observed an overall
435 increase in abundance of the herbivores when earthworms were present. Nonetheless,
436 these results were context-dependent. In particular, only high densities and higher
437 levels of species and functional diversity of earthworms decreased plant resistance
438 against aphid herbivores. Under aphid attack, plants activate the SA pathway for
439 stimulating chemical and physical barriers such callose deposition and the production
440 of defensive secondary metabolites, which are transported into the phloem to increase
441 toxicity (Elzinga & Jander 2013; Züst & Agrawal 2016). In turn, aphids could inject
442 effector proteins to prevent callose deposition, and deal with toxic metabolites by
443 metabolization or excretion (Kim & Jander 2007; Elzinga & Jander 2013; Züst &

444 Agrawal 2016). Earthworms, therefore, could favour plant susceptibility to aphids by
445 inhibiting the SA signalling pathway. While earthworms have been shown to affect
446 plant defence signalling pathways and gene expression (Puga-Freitas et al. 2012;
447 Puga-Freitas et al. 2016), we are not aware of studies directly linking earthworm
448 presence to plant physiological and molecular mechanisms for deterring aphid attack,
449 but this should be considered for future avenues of research.

450 In addition, accessible nutrients, such as sugars, amino acids and nitrogen are also
451 important determinants for the growth and development of herbivores including
452 aphids (Mattson 1980; Caillaud et al. 1995; Cao *et al.* 2016). Therefore, the positive
453 effects of earthworms on plant nutritional quality (e.g. higher nitrogen content), might
454 also cause increased plant susceptibility to aphids. This idea is corroborated by the
455 fact that in a more complex earthworm community, earthworm species act
456 synergistically to increase soil fertility (Curry & Schmidt 2007; Spurgeon et al. 2013;
457 Bertrand et al. 2015) and plant nutrient content (e.g. Laossi et al. 2009), in turn
458 increasing plant susceptibility to aphid attack.

459 Contrary to the aphids, earthworms mediated increased plant resistance against
460 cell-feeders. This was particularly true when measuring resistance against thrips (Fig.
461 2a), while the effects were more variable when measuring resistance against
462 soil-dwelling nematodes. While the effects of earthworms on nematodes could
463 partially be explained by direct interference (i.e. earthworms could ingest nematodes
464 while ingesting the surrounding substrate (Boyer et al. 2013)), the effects of
465 earthworms on thrips are likely to be mediated by changes in aboveground plant

466 functional traits. Our unpublished study, as described in Fig. S1, showed that
467 earthworm-inoculated plants under thrips attack had higher concentrations of total
468 carbon and nitrogen, lower concentrations of total phosphorus, and higher levels of
469 jasmonic acid and total phenolic compounds (Fig. S1 d, e). Earthworm-mediated
470 increase in resistance against thrips can thus be due to the activation of the JA
471 signalling pathway. In addition, we speculate that stimulation of the soil microbial
472 community by earthworms could have enhanced defence priming in plants (Blouin et
473 al. 2005; Jana et al. 2010; Puga-Freitas et al. 2012), and ultimately increase resistance
474 by promoting chemical defence accumulation in the plants. This however, has never
475 been specifically tested so far.

476

477 *EARTHWORM EFFECTS ON PLANT CHEMICAL DEFENCES*

478 We found that overall, earthworm presence did not significantly affect plant
479 chemical defences when chewing herbivores were on plants, but notably increased
480 chemical defences when cell-content feeders, particularly thrips were present. For
481 example, earthworm presence promoted the induction of defence compounds such as
482 jasmonic acid and phenolics in tomato leaves when under thrips attack (Fig S1e).
483 Similarly, earthworms significantly increased concentrations of total glucosinolates, a
484 nitrogen-based defence compound class, in leaves of *Sinapis alba* (Lohmann, Scheu
485 & Muller 2009). Therefore, in these cases, earthworm presence could favour plant
486 resistance by increasing plant chemical defences. On the other hand, Wurst et al.
487 (2006) showed that concentrations of two glucosinolates (glucoiberin and

488 glucoraphanin) in shoots of *Brassica oleracea* decreased when the endogeic
489 earthworm *Octolasion tyrtaeum* was added to the system. Similarly, earthworms
490 could induce a decline of root sesquiterpene (*E*)- β -caryophyllene when rootworms are
491 present (Fig. S1 j).

492 The inconsistent effects of earthworms on plant chemistry might be due to the
493 interactive effects of plant growth and nutrient uptake on plant secondary metabolism.
494 For instance, it was shown that phytosterol concentration in *Plantago lanceolata*
495 plants was not affected by earthworms directly, but increased with increasing nitrogen
496 concentration of the leaves (Wurst et al. 2004), which is mediated by earthworm
497 presence (Wurst & Jones 2003). Additionally, several studies have shown that the
498 initial soil nutrient content and the distribution of soil organic matter could influence
499 plant defensive secondary metabolites (Wurst et al. 2003; Wurst, Dugassa-Gobena &
500 Scheu 2004; Ke & Scheu 2008). For instance, earthworms favoured an increase in
501 total phytosterol content of *P. lanceolata* shoots, but only when the spatial distribution
502 of organic residues/litter was mixed homogeneously with soil (Wurst,
503 Dugassa-Gobena & Scheu 2004). Only few studies in our meta-analysis addressed the
504 effects of differences in initial soil properties such as distribution of organic litter, or
505 the changes in soil available nutrients (e.g. mineral nitrogen), driven by earthworm
506 presence. This prevented the use of soil bio-chemical properties as a moderator in this
507 study. Nonetheless, an increasing number of studies demonstrate that soil nutrients
508 and microorganisms both modify the synthesis of defensive secondary metabolites
509 (e.g. Ohkama-Ohtsu & Wasaki 2010; Badri et al. 2013), and ultimately influence

510 plant-herbivore interactions (Badri et al. 2013; Pineda et al. 2013). This indeed calls
511 for a better integration of earthworms living in different soil conditions and with
512 different ecologies into plant-herbivore interaction studies.

513

514 *EARTHWORM EFFECTS ON THE TRADE-OFFS BETWEEN PLANT PERFORMANCE,*
515 *RESISTANCE AND CHEMICAL DEFENCES*

516 We found that the effects of earthworms on growth and resistance of plants under
517 herbivory were overall negatively correlated (Fig. 4a), as would be predicted by
518 classic plant defence theory (Herms & Mattson 1992; Züst & Agrawal 2017). An
519 increasing number of studies indicate that earthworms could indirectly influence the
520 performance of herbivores such as phloem-feeders by predominantly affecting plant
521 size, vigour, and nutrient content (Scheu, Theenhaus & Jones 1999; Eisenhauer &
522 Scheu 2008; Trouve et al. 2014), and to a lesser extent by changes in plant secondary
523 chemistry (Francis et al. 2001; Wurst et al. 2004; Katsanis, Rasmann & Mooney
524 2016). For example, Cao et al. (2016) showed that the green peach aphid (*Myzus*
525 *persicae*) performed better on an enhanced amino acid: sugar ratio and enhanced
526 absolute amino acid concentration in the phloem, but also activated genes responsible
527 for glucosinolates synthesis in the leaves of Chinese cabbage. Similarly, Wurst et al.
528 (2004) showed that *A. caliginosa* earthworm presence decreased the concentration of
529 the defence compound catalpol in *P. lanceolata* leaves, but this was not positively
530 correlated with the performance in term of development time of the aphid *M.*
531 *persicae*.

532 Contrary to expectations, earthworm presence simultaneously increased both
533 plant growth and chemical defences (Fig.4b). These effects were particularly strong
534 on crop plants. Because of lack of data, we could not highlight a particular
535 combination of factors explaining these results, besides the fact that bigger plants had
536 higher level of secondary metabolites, independently of any particular plant by
537 herbivore by earthworm combination. Several studies have shown that the assumed
538 growth-defence trade-off might be modified (i.e. reduced or even reversed) by
539 different levels of nutrients in the soil (Coley, Bryant & Chapin 1985; Donaldson,
540 Kruger & Lindroth 2006; Lind et al. 2013), or not detected due to the failure to
541 address the appropriate measure of growth-related traits (Züst et al. 2011; Züst,
542 Rasmann & Agrawal 2015). Overall, these different patterns suggest that earthworm
543 effects on defence allocation in plants are in part dictated by resource allocation, and
544 are highly context dependent in terms of categories of defence compounds. However,
545 this needs to be systematically addressed in future manipulative studies.

546

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557

558 **Data accessibility**

559 All data used in the meta-analysis are present in the manuscript or online supporting
560 information and deposited in the Dryad Digital Repository:
561 <http://doi.org/10.5061/dryad.382k1> (Xiao et al. 2017).

562

563 **Authorship**

564 ZX, ML, FH and SR designed the study. ZX, XW and AK collected data and
565 performed the meta-analysis. JK assisted with the meta-analysis. ZX and SR wrote the
566 first draft of the manuscript and all authors contributed to revisions.

567

568 **References**

- 569 Aerts, R. & Chapin, F.S. (1999) The mineral nutrition of wild plants revisited: a re-evaluation of
570 processes and patterns. *Advances in Ecological Research*, **30**, 1–67.
- 571 Agrawal, A.A. (2007) Macroevolution of plant defense strategies. *Trends in Ecology & Evolution*,
572 **22**, 103–109.
- 573 Andriuzzi, W.S., Schmidt, O., Brussaard, L., Faber, J.H. & Bolger, T. (2016) Earthworm
574 functional traits and interspecific interactions affect plant nitrogen acquisition and
575 primary production. *Applied Soil Ecology*, 104, 148–156.
- 576 Badri, D.V., Zolla, G., Bakker, M.G., Manter, D.K. & Vivanco, J.M. (2013) Potential impact of
577 soil microbiomes on the leaf metabolome and on herbivore feeding behavior. *New*
578 *Phytologist*, **198**, 264–273.
- 579 Bardgett, R.D. & Chan, K.F. (1999) Experimental evidence that soil fauna enhance nutrient
580 mineralization and plant nutrient uptake in montane grassland ecosystems. *Soil Biology*
581 *and Biochemistry*, **31**, 1007–1014.
- 582 Benton, T., 2014. Using meta-regression to explore moderating effects in surveys of international
583 achievement. *Practical Assessment Research and Evaluation* **19**, 3.
- 584 Bertrand, M., Barot, S., Blouin, M., Whalen, J., de Oliveira, T. & Roger-Estrade, J. (2015)
585 Earthworm services for cropping systems. A review. *Agronomy for Sustainable*
586 *Development*, **35**, 553–567.
- 587 Bhadauria, T. & Saxena, K.G. (2010) Role of earthworms in soil fertility maintenance through the
588 production of biogenic structures. *Applied and Environmental Soil Science*, **2010**, 1–7.
- 589 Blouin, M., Zuily-Fodil, Y., Pham-Thi, A.-T., Laffray, D., Reversat, G., Pando, A., Tondoh, J. &

590 Lavelle, P. (2005) Belowground organism activities affect plant aboveground phenotype,
591 inducing plant tolerance to parasites. *Ecology letters*, **8**, 202–208.

592 Blouin, M., Hodson, M.E., Delgado, E.A., Baker, G, Brussard, L., Butt, K.R., Dai, J., Dendooven,
593 L., Peres, G., Tondoh, J.E., Cluzeau, D., Brun, J.-J. (2013). A review of earthworm impact on
594 soil function and ecosystem services. *European Journal of Soil Science*, 64, 161–182.

595 Bossuyt, H., Six, J. & Hendrix, P.F. (2006) Interactive effects of functionally different earthworm
596 species on aggregation and incorporation and decomposition of newly added residue
597 carbon. *Geoderma*, **130**, 14–25.

598 Bouché, M. B. (1977). Strategies lombriciennes. *Ecological Bulletins*, 122–132.

599 Boyer, J., Reversat, G., Lavelle, P. & Chabanne, A. (2013) Interactions between earthworms and
600 plant-parasitic nematodes. *European Journal of Soil Biology*, **59**, 43–47.

601 Brown, G.G., Edwards, C.A. & Brussaard, L. (2004) How earthworms affect plant growth:
602 burrowing into the mechanisms. *Earthworm Ecology*, **2**, 13–49.

603 Cao, H.H., Liu, H.R., Zhang, Z.F. & Liu, T.X. (2016) The green peach aphid *Myzus persicae*
604 perform better on pre-infested Chinese cabbage *Brassica pekinensis* by enhancing host
605 plant nutritional quality. *Scientific Reports*, **6**, 21954.

606 Caillaud, C.M., Pierre, J., Chaubet, B. & Pietro, J. (1995) Analysis of wheat resistance to the
607 cereal aphid *Sitobion avenae* using electrical penetration graphs and flow charts
608 combined with correspondence analysis. *Entomologia Experimentalis et Applicata*, **75**, 9–
609 18.

610 Coley, P.D., Bryant, J.P. & Chapin, F.S. (1985) Resource availability and plant antiherbivore
611 defense. *Science*, **230**, 895–899.

612 Cunha, L., Brown, G.G., Stanton, D.W.G., Da Silva, E., Hansel, F.A., Jorge, G., McKey, D.,
613 Vidal-Torrado, P., Macedo, R.S., Velasquez, E., James, S.W., Lavelle, P. & Kille, P. (2016)
614 Soil animals and pedogenesis: the role of earthworms in anthropogenic soils. *Soil Science*,
615 181, 110–125.

616 Curry, J.P. & Schmidt, O. (2007) The feeding ecology of earthworms – A review. *Pedobiologia*, **50**,
617 463–477.

618 Donaldson, J.R., Kruger, E.L. & Lindroth, R.L. (2006) Competition- and resource-mediated
619 tradeoffs between growth and defensive chemistry in trembling aspen (*Populus*
620 *tremuloides*). *New Phytologist*, **169**, 561–570.

621 Edwards, C.A. (2004) *Earthworm ecology*. CRC Press.

622 Eisenhauer, N. & Scheu, S. (2008) Earthworms as drivers of the competition between grasses and
623 legumes. *Soil Biology and Biochemistry*, **40**, 2650–2659.

624 Elzinga, D.A. & Jander, G. (2013) The role of protein effectors in plant-aphid interactions.
625 *Current Opinion in Plant Biology*, **16**, 451-456.

626 Fine, P.V., Miller, Z.J., Mesones, I., Irazuzta, S., Appel, H.M., Stevens, M.H.H., Sääksjärvi, I.,
627 Schultz, J.C. & Coley, P.D. (2006) The growth-defense trade-off and habitat
628 specialization by plants in Amazonian forests. *Ecology*, **87**, S150–S162.

629 Francis, F., Lognay, G., Wathelet, J.-P. & Haubruge, E. (2001) Effects of Allelochemicals from
630 First (*Brassicaceae*) and Second (*Myzus persicae* and *Brevicoryne brassicae*) Trophic
631 Levels on *Adalia bipunctata*. *Journal of Chemical Ecology*, **27**, 243–256.

632 Hedges, L.V., Gurevitch, J. & Curtis, P.S. (1999) The meta - analysis of response ratios in
633 experimental ecology. *Ecology*, **80**, 1150–1156.

- 634 Herms, D.A. & Mattson, W.J. (1992) The dilemma of plants: to grow or defend. *Quarterly Review*
635 *of Biology*, 283–335.
- 636 Howe, G.A. & Jander, G. (2008) Plant immunity to insect herbivores. *Annual Review of Plant*
637 *Biology*, **59**, 41–66.
- 638 Jana, U., Barot, S., Blouin, M., Lavelle, P., Laffray, D. & Repellin, A. (2010) Earthworms
639 influence the production of above- and belowground biomass and the expression of genes
640 involved in cell proliferation and stress responses in *Arabidopsis thaliana*. *Soil Biology*
641 *and Biochemistry*, **42**, 244–252.
- 642 Jennions, M.D., Lortie, C.J., Rosenberg, M.S. & Rothstein, H.R. (2013) Publication and related
643 biases. *Handbook of Meta-analysis in Ecology and Evolution*, 207–236.
- 644 Johnson, M.T.J. (2011) Evolutionary ecology of plant defences against herbivores. *Functional*
645 *Ecology*, **25**, 305–311.
- 646 Johnson, S.N., Staley, J.T., McLeod, F.A.L. & Hartley, S.E. (2011) Plant-mediated effects of soil
647 invertebrates and summer drought on above-ground multitrophic interactions. *Journal of*
648 *Ecology*, **99**, 57–65.
- 649 Kadir, N. (2014) Plant mediated effects of earthworms on aphid dynamics. Plymouth University
650 Press, Plymouth.
- 651 Karban, R., and Baldwin, I. T. (2007). Induced responses to herbivory. University of Chicago
652 Press, Chicago.
- 653 Katsanis, A., Rasmann, S. & Mooney, K.A. (2016) Herbivore diet breadth and host plant defense
654 mediate the tri-trophic effects of plant toxins on multiple coccinellid predators. *PLoS*
655 *ONE*, 11, e0155716.

- 656 Ke, X. & Scheu, S. (2008) Earthworms, Collembola and residue management change wheat
657 (*Triticum aestivum*) and herbivore pest performance (Aphidina: *Rhopalosiphum padi*).
658 *Oecologia*, **157**, 603–617.
- 659 Kim, J.H. & Jander, G. (2007) *Myzus persicae* (green peach aphid) feeding on Arabidopsis
660 induces the formation of a deterrent indole glucosinolate. *Plant Journal*, **49**, 1008-1019.
- 661 Koricheva, J. (2002) Meta - analysis of sources of variation in fitness costs of plant antiherbivore
662 defenses. *Ecology*, **83**, 176–190.
- 663 Koricheva, J., Gange, A.C. & Jones, T. (2009) Effects of mycorrhizal fungi on insect herbivores: a
664 meta - analysis. *Ecology*, **90**, 2088-2097.
- 665 Koricheva, J., Gurevitch, J. & Mengersen, K. (2013) *Handbook of meta-analysis in ecology and*
666 *evolution*. Princeton University Press.
- 667 Ladha, J., Khind, C., Khera, T. & Bueno, C. (2004) Effects of residue decomposition on
668 productivity and soil fertility in rice–wheat rotation. *Soil Science Society of America*
669 *Journal*, **68**, 854–864.
- 670 Lafont, A., Risède, J.-M., Loranger-Merciris, G., Clermont-Dauphin, C., Dorel, M., Rhino, B. &
671 Lavelle, P. (2007) Effects of the earthworm *Pontoscolex corethrurus* on banana plants
672 infected or not with the plant-parasitic nematode *Radopholus similis*. *Pedobiologia*, **51**,
673 311–318.
- 674 Laossi, K.-R., Noguera, D.C., Bartolomé-Lasa, A., Mathieu, J., Blouin, M. & Barot, S. (2009)
675 Effects of an endogeic and an anecic earthworm on the competition between four annual
676 plants and their relative fecundity. *Soil Biology and Biochemistry*, **41**, 1668–1673.
- 677 Lind, E.M., Borer, E., Seabloom, E., Adler, P., Bakker, J.D., Blumenthal, D.M., Crawley, M.,

678 Davies, K., Firm, J., Gruner, D.S., Harpole, W.S., Hautier, Y., Hillebrand, H., Knops, J.,
679 Melbourne, B., Mortensen, B., Risch, A.C., Schuetz, M., Stevens, C. & Wragg, P.D.
680 (2013) Life-history constraints in grassland plant species: a growth-defence trade-off is
681 the norm. *Ecology Letters*, **16**, 513–521.

682 Lohmann, M., Scheu, S. & Muller, C. (2009) Decomposers and root feeders interactively affect
683 plant defence in *Sinapis alba*. *Oecologia*, **160**, 289–298.

684 Loranger-Merciris, G., Cabidoche, Y.M., Deloné, B., Quénéhervé, P. & Ozier-Lafontaine, H.
685 (2012) How earthworm activities affect banana plant response to nematodes parasitism.
686 *Applied Soil Ecology*, **52**, 1–8.

687 Lyon, G.D., Newton, A.C. & Walters, D.R. (2014) Induced resistance in crop protection: the future,
688 drivers and barriers. *Induced resistance for plant defense: a sustainable approach to crop*
689 *protection*, 316-325. Oxford: Blackwell Publishing.

690 Møller, A.P. & Jennions, M.D. (2001) Testing and adjusting for publication bias. *Trends in*
691 *Ecology & Evolution*, **16**, 580–586.

692 Maschinski, J. & Whitham, T.G. (1989) The continuum of plant responses to herbivory: the
693 influence of plant association, nutrient availability, and timing. *The American Naturalist*,
694 1–19.

695 Mattson, W.J. (1980) Herbivory in relation to plant nitrogen content. *Annual Review of Ecology*
696 *and Systematics*, **11**, 119–161.

697 Núñez-Farfán, J., Fornoni, J. & Valverde, P.L. (2007) The evolution of resistance and tolerance to
698 herbivores. *Annual Review of Ecology, Evolution, and Systematics*, 541–566.

699 Newington, J., Setälä, H., Bezemer, T. & Jones, T. (2004) Potential effects of earthworms on

700 leaf - chewer performance. *Functional Ecology*, **18**, 746–751.

701 Ohkama-Ohtsu, N. & Wasaki, J. (2010) Recent progress in plant nutrition research: cross-talk
702 between nutrients, plant physiology and soil microorganisms. *Plant Cell Physiology*, **51**,
703 1255–1264.

704 Onkokesung, N., Reichelt, M., van Doorn, A., Schuurink, R.C. & Dicke, M. (2016) Differential
705 costs of two distinct resistance mechanisms induced by different herbivore species in
706 arabidopsis. *Plant Physiology*, **170**, 891–906.

707 Pieterse, C.M., Van der Does, D., Zamioudis, C., Leon-Reyes, A. & Van Wees, S.C. (2012)
708 Hormonal modulation of plant immunity. *Annual Review of Cell and Developmental*
709 *Biology*, **28**, 489–521.

710 Pineda, A., Dicke, M., Pieterse, C.M.J., Pozo, M.J. & Biere, A. (2013) Beneficial microbes in a
711 changing environment: are they always helping plants to deal with insects? *Functional*
712 *Ecology*, **27**, 574–586.

713 Pineda, A., Soler, R., Pozo, M.J., Rasmann, S. & Turlings, T.C. (2015) Editorial:
714 Above-belowground interactions involving plants, microbes and insects. *Frontiers in*
715 *Plant Science*, **6**, 318. doi:10.3389/fpls.2015.00318.

716 Pineda, A., Zheng, S.J., van Loon, J.J., Pieterse, C.M. & Dicke, M. (2010) Helping plants to deal
717 with insects: the role of beneficial soil-borne microbes. *Trends in Plant Science* 15:507–
718 514.

719 Prescott, C. (2005) Decomposition and mineralization of nutrients from litter and humus. In:
720 Nutrient Acquisition by Plants. Springer, pp. 15–41.

721 Puga-Freitas, R., Barot, S., Taconnat, L., Renou, J.P. & Blouin, M. (2012) Signal molecules

722 mediate the impact of the earthworm *Aporrectodea caliginosa* on growth, development
723 and defence of the plant *Arabidopsis thaliana*. *PLoS ONE*, **7**, e49504.

724 Puga-Freitas, R., Belkacem, L., Barot, S., Bertrand, M., Roger-Estrade, J. & Blouin, M. (2016)
725 Transcriptional profiling of wheat in response to take-all disease and mechanisms
726 involved in earthworm's biocontrol effect. *European Journal of Plant Pathology*, **144**,
727 155–165.

728 R Development Core Team (2015) R: A language and environment for statistical computing. R
729 Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL:
730 <http://www.R-project.org>.

731 Rosenberg, M.S. (2005) The file-drawer problem revisited: a general weighted method for
732 calculating fail-safe numbers in meta-analysis. *Evolution*, **59**, 464–468.

733 Rosenthal, J. & Welter, S. (1995) Tolerance to herbivory by a stem-boring caterpillar in
734 architecturally distinct maizes and wild relatives. *Oecologia*, **102**, 146–155.

735 Rosenthal, J.P. & Dirzo, R. (1997) Effects of life history, domestication and agronomic selection
736 on plant defence against insects: evidence from maizes and wild relatives. *Evolutionary*
737 *Ecology*, **11**, 337–355.

738 Scheu, S. (2003) Effects of earthworms on plant growth: patterns and perspectives. *Pedobiologia*,
739 **47**, 846–856.

740 Scheu, S., Theenhaus, A. & Jones, T.H. (1999) Links between the detritivore and the herbivore
741 system: effects of earthworms and Collembola on plant growth and aphid development.
742 *Oecologia*, **119**, 541–551.

743 Schoonhoven, L.M., Van Loon, J.J. & Dicke, M. (2005) *Insect-plant biology*. Oxford University

744 Press.

745 Schwachtje, J. & Baldwin, I.T. (2008) Why does herbivore attack reconfigure primary metabolism?

746 *Plant Physiology*, **146**, 845–851.

747 Seastedt, T. (1984) The role of microarthropods in decomposition and mineralization processes.

748 *Annual Review of Entomology*, **29**, 25–46.

749 Spurgeon, D.J., Keith, A.M., Schmidt, O., Lammertsma, D.R. & Faber, J.H. (2013) Land-use and

750 land-management change: relationships with earthworm and fungi communities and soil

751 structural properties. *BMC ecology*, **13**, 1–13.

752 Stam, J.M., Kroes, A., Li, Y., Gols, R., van Loon, J.J., Poelman, E.H. & Dicke, M. (2014) Plant

753 interactions with multiple insect herbivores: from community to genes. *Annual Review of*

754 *Plant Biology* **65**:689–713.

755 Strauss, S.Y. & Agrawal, A.A. (1999) The ecology and evolution of plant tolerance to herbivory.

756 *Trends in Ecology & Evolution*, **14**, 179–185.

757 Tiffin, P. (2000) Mechanisms of tolerance to herbivore damage: what do we know? *Evolutionary*

758 *Ecology*, **14**, 523-536.

759 Trouve, R., Drapela, T., Frank, T., Hadacek, F. & Zaller, J.G. (2014) Herbivory of an invasive slug

760 in a model grassland community can be affected by earthworms and mycorrhizal fungi.

761 *Biology and Fertility of Soils*, **50**, 13–23.

762 van Groenigen, J.W., Lubbers, I.M., Vos, H.M., Brown, G.G., De Deyn, G.B. & van Groenigen,

763 K.J. (2014) Earthworms increase plant production: a meta-analysis. *Scientific Reports*

764 4:6365. doi:10.1038/srep06365.

765 van Loon, L.C., Bakker, P.A. & Pieterse, C.M. (1998) Systemic resistance induced by rhizosphere

766 bacteria. *Annual Review of Phytopathology*, **36**, 453–483.

767 Viechtbauer, W. (2010) Conducting meta-analyses in R with the metafor package. *Journal of*
768 *Statistical Software*, **36**, 1–48.

769 Walling, L.L. (2000) The Myriad Plant Responses to Herbivores. *Journal of Plant Growth*
770 *Regulation*, **19**, 195–216.

771 Whitehead, S.R., Turcotte, M.M. & Poveda, K. (2017) Domestication impacts on plant-herbivore
772 interactions: a meta-analysis. *Philosophical Transactions of the Royal Society of London.*
773 *Series B: Biological Sciences*, **372**: 20160034

774 Wurst, S. (2010) Effects of earthworms on above- and belowground herbivores. *Applied Soil*
775 *Ecology*, **45**, 123–130.

776 Wurst, S. (2013) Plant-mediated links between detritivores and aboveground herbivores. *Frontiers*
777 *in Plant Science*, **4**.

778 Wurst, S., Allema, B., Duyts, H. & Van Der Putten, W.H. (2008) Earthworms counterbalance the
779 negative effect of microorganisms on plant diversity and enhance the tolerance of grasses
780 to nematodes. *Oikos*, **117**, 711–718.

781 Wurst, S., Dugassa-Gobena, D., Langel, R., Bonkowski, M. & Scheu, S. (2004) Combined effects
782 of earthworms and vesicular-arbuscular mycorrhizas on plant and aphid performance.
783 *New Phytologist*, **163**, 169–176.

784 Wurst, S., Dugassa-Gobena, D. & Scheu, S. (2004) Earthworms and litter distribution affect
785 plant-defensive chemistry. *Journal of Chemical Ecology*, **30**, 691–701.

786 Wurst, S. & Jones, T.H. (2003) Indirect effects of earthworms (*Aporrectodea caliginosa*) on an
787 above-ground tritrophic interaction. *Pedobiologia*, **47**, 91–97.

788 Wurst, S., Langel, R., Reineking, A., Bonkowski, M. & Scheu, S. (2003) Effects of earthworms
789 and organic litter distribution on plant performance and aphid reproduction. *Oecologia*,
790 137, 90–96.

791 Wurst, S., Langel, R., Rodger, S. & Scheu, S. (2006) Effects of belowground biota on primary and
792 secondary metabolites in *Brassica oleracea*. *Chemoecology*, **16**, 69–73.

793 Xiao Z., Wang X., Koricheva J., Kergunteuil A., Le Bayon R., Liu M., Hu F. & Rasmann S. (2017)
794 Data from: Earthworms affect plant growth and resistance against herbivores: a
795 meta-analysis. *Dryad Digital Repository*. <http://doi.org/10.5061/dryad.382k1>

796 Yoshitake, S., Soutome, H. & Koizumi, H. (2014) Deposition and decomposition of cattle dung
797 and its impact on soil properties and plant growth in a cool-temperate pasture. *Ecological*
798 *Research*, **29**, 673–684.

799 Züst, T. & Agrawal, A.A. (2016) Mechanisms and evolution of plant resistance to aphids. *Nature*
800 *Plants*, **2**, 15206.

801 Züst, T. & Agrawal, A.A. (2017) Trade-offs between plant growth and defense against insect
802 herbivory: an emerging mechanistic synthesis. *Annual Review of Plant Biology*. **68**,
803 10.11–10.22.

804

805 **Supporting Information**

806 Additional supporting information may be found in the online version of this article.

807 Supporting Appendix S1: Database and moderator variable

808 Supporting Tables S1-S8: Summary tables for overall effect size, moderator and
809 correlation analyses

810 Supporting Figures S1-S3: additional datapoints, moderator and hierarchical analyses

811

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815

816 **Figure legends**

817 **Fig. 1** The effect size of earthworms on plant growth (a) and nutrients (b) in the

818 presence of herbivores. Error bars denote 95% bias-corrected confidence intervals

819 (CIs). Sample sizes are shown in brackets. The individual effect is significant if the 95%

820 CIs does not include zero.

821

822 **Fig. 2** Moderator analyses of the effect size of earthworm presence on plant resistance

823 against (a) cell-feeders, (b) chewing herbivore and (c) phloem-feeders. Error bars

824 denote 95% bias-corrected confidence intervals (CIs). Sample sizes are shown in

825 brackets. The individual effect is significant if the 95% CIs does not include zero.

826

827 **Fig. 3** The effect size of earthworms on plant chemical defences in the presence of

828 different herbivores. Error bars denote 95% bias-corrected confidence intervals (CIs).

829 Sample sizes are shown in brackets. The individual effect is significant if the 95% CIs

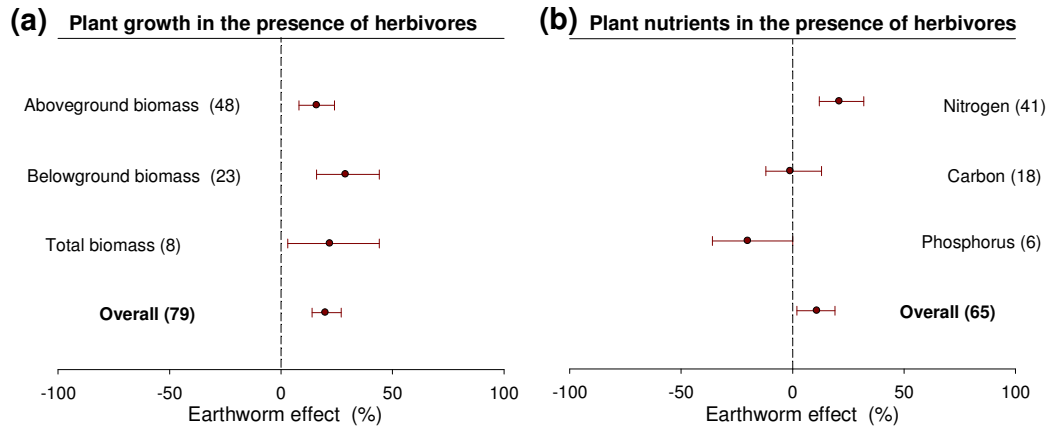
830 does not include zero.

831

832 **Fig. 4** Correlations between the effects of earthworms on (a) plant resistance and
833 growth, (b) chemical defences and growth. Each data point of the correlation
834 corresponded to an lnR. For instance, a significant negative correlation between
835 growth and resistance means that positive effect of earthworm on growth is correlated
836 with negative effect of earthworms on plant resistance, vice versa.
837

838 **Figures:**

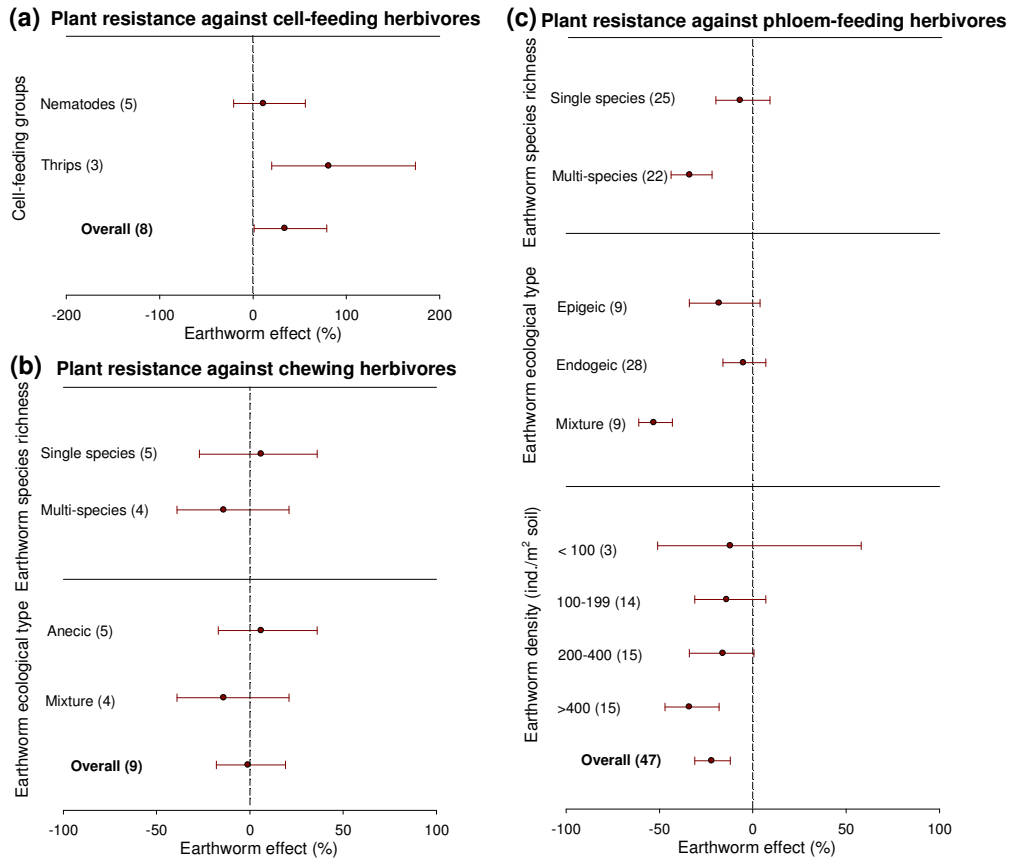
839 **Figure 1.**



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841

842 **Figure 2.**

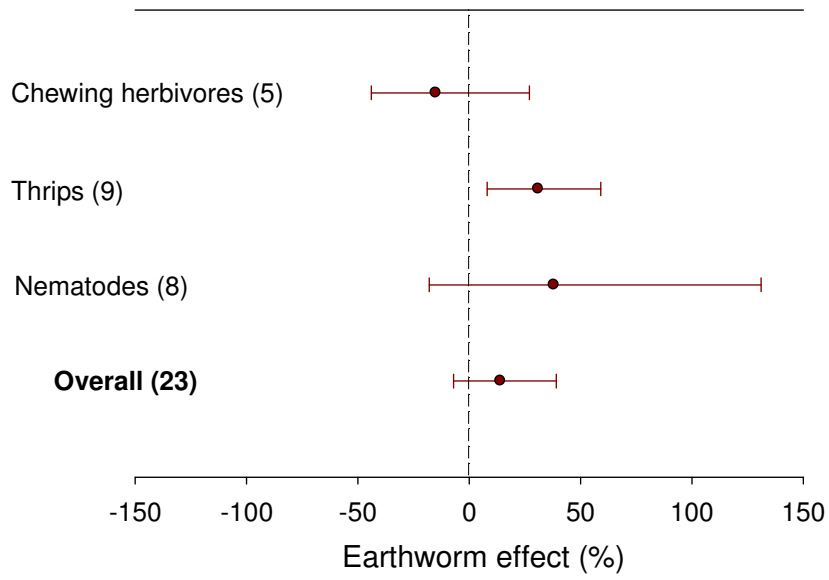


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845 **Figure 3.**

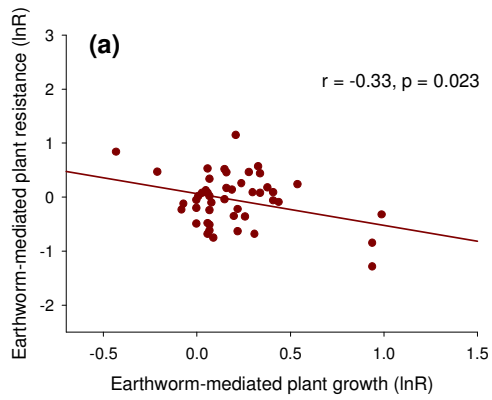
Plant chemical defences in the presence of different herbivores



846

847

848 **Figure 4.**



849

