

Land management modulates the environmental controls on global earthworm communities

Article

Accepted Version

Johnston, A. S. A. (2019) Land management modulates the environmental controls on global earthworm communities. *Global Ecology and Biogeography*, 28 (12). pp. 1787-1795. ISSN 1466-8238 doi: <https://doi.org/10.1111/geb.12992>
Available at <http://centaur.reading.ac.uk/85572/>

It is advisable to refer to the publisher's version if you intend to cite from the work. See [Guidance on citing](#).

To link to this article DOI: <http://dx.doi.org/10.1111/geb.12992>

Publisher: Wiley

All outputs in CentAUR are protected by Intellectual Property Rights law, including copyright law. Copyright and IPR is retained by the creators or other copyright holders. Terms and conditions for use of this material are defined in the [End User Agreement](#).

www.reading.ac.uk/centaur

CentAUR

Central Archive at the University of Reading

Reading's research outputs online

1 **Land management modulates the environmental controls on global earthworm**
2 **communities**

3 Alice S.A. Johnston^{1*}

4

5 ¹ School of Biological Sciences, University of Reading, UK.

6 * Corresponding Author:

7 alice.johnston@reading.ac.uk; +44 (0)118 378 6439

8 School of Biological Sciences, University of Reading, Reading, RG6 6AH

9

10 **Running title:** Global patterns in earthworm communities

11

12 **Abstract**

13 **Aim:** Soils and their biological communities face increasing pressure from multiple global
14 drivers, including land management and climate change. In soils, earthworms play key roles
15 in ecosystem functioning, but the environmental controls on their global communities are not
16 fully understood. Here, an earthworm dataset was compiled to investigate the effects of
17 environmental variables and land management on global earthworm communities.

18 **Location:** 40 ° S – 65 ° N.

19 **Time period:** 1962 to 2016.

20 **Major taxa studied:** Earthworms

21 **Methods:** A dataset of 899 earthworm community observations, together with environmental
22 variables, was compiled across 169 globally distributed sites. Sites included natural forest
23 and grassland or managed arable, pasture and plantation ecosystems. Total, anecic,
24 endogeic and epigeic abundances and total species richness were compared in natural and
25 managed ecosystems to quantify the effects of land management across climates. A
26 hierarchical model was used to test the importance of environmental controls in predicting
27 the relationship between total earthworm species richness and abundance at a global scale.

28 **Results:** Land management prompted little change in total earthworm abundance at the
29 global scale, but reduced species richness and shifted community composition. Endogeic
30 earthworms were more abundant in managed ecosystems, while anecic and epigeic
31 earthworms show variable responses across ecosystem types. Global relationships between
32 total earthworm species richness and abundance were explained by climate, soil pH and
33 land management.

34 **Main conclusions:** Land management modulates the effects of environmental controls on
35 global earthworm communities, through direct disturbance and indirect changes in edaphic
36 conditions.

37

38 **Keywords:** earthworms; community composition; species richness; land management; soil
39 pH; climate.

40

41 **1. Introduction**

42 Global environmental drivers are placing increasing pressures on soils, with shifts in soil
43 biodiversity and community composition reducing ecosystem resilience (Wagg *et al.*, 2014;
44 Smith *et al.*, 2016). In soils, earthworms act as important ecosystem engineers. By
45 burrowing through the soil, earthworms influence soil aggregation and structure (Lavelle *et*
46 *al.*, 2006) while their feeding and casting activities stimulate the decomposition of plant
47 material and encourage other beneficial soil organisms (Blouin *et al.*, 2013). As 'nature's
48 plough', the activities of earthworms are particularly beneficial in managed ecosystems
49 (Darwin, 1881), and conservation management practices often aim to optimise soil
50 environmental conditions (e.g. soil organic carbon (SOM) and soil moisture) for earthworm
51 proliferation (Rounsevell *et al.*, 2010). In turn the effects of earthworm activity on soil
52 aggregate stability, water regulation and carbon and nutrient cycling improve crop yields and
53 soil carbon storage (Shuster *et al.*, 2001; van Groenigen *et al.*, 2014). Exotic earthworm
54 species, on the other hand, have invaded most areas of the globe (Hendrix *et al.*, 2008), and

55 when introduced into previously unoccupied areas can act as strong drivers of ecosystem
56 change (Hendrix, 2006; Eisenhauer, 2010; Craven *et al.*, 2017).

57

58 Despite the long known impact of earthworms on soil fertility (Darwin, 1881), relatively few
59 attempts have been made to investigate large-scale patterns in earthworm communities
60 (Decaëns, 2010). Generally, earthworm communities are thought to become more complex
61 and diverse towards the equator (Lavelle, 1983). Climatic factors (temperature and
62 precipitation) are considered fundamental drivers of these latitudinal trends in earthworm
63 communities (Brussaard *et al.*, 2012; Rutgers *et al.*, 2016), but such inferences are based on
64 limited data (Fierer *et al.*, 2009; Decaëns, 2010; Brussaard *et al.*, 2012). Other
65 environmental variables have also been reported to structure earthworm communities. For
66 instance, earthworm abundance increases with soil organic carbon (SOC) content across
67 ecosystem types and management intensity (Hendrix *et al.*, 1992), while species richness
68 tends to decline with increasing SOC availability (Bouché, 1972). Earthworm community
69 responses to disturbance through soil management show much more general trends at
70 regional and global scales (Decaëns & Jiménez, 2002; Decaëns *et al.*, 2003; Spurgeon *et al.*,
71 2013). In a global meta-analysis, Briones and Schmidt (2017) found that earthworm
72 population abundance and biomass declined with increasing tillage intensity, but also
73 depended on variations in soil, environmental, climatic and management conditions as well
74 as the different sensitivities of earthworm ecological groups.

75

76 Earthworms are typically classified into three broad ecological groups (epigeic, anecic and
77 endogeic), which play different roles in ecosystem functioning and display different
78 responses to management and environmental changes (Blouin *et al.*, 2013). Epigeic
79 (surface-living) and anecic (vertical burrowing) earthworms rely on leaf litter for habitat and
80 food, and when this is disturbed by management practices such as tillage, their numbers are
81 largely reduced (Briones & Schmidt, 2017; Johnston *et al.*, 2018). Thus, managed soils are
82 often dominated by endogeic species, which live in temporary horizontal burrows in the

83 mineral soil (Riley *et al.*, 2008). Although endogeic earthworms do offer beneficial soil
84 functions in managed soils, more diverse earthworm populations are needed in order to
85 optimise ecosystem functioning under sustainable land management (Eisenhauer &
86 Schädler, 2011; Blouin *et al.*, 2013). For instance, anecic earthworms are particularly
87 beneficial for enhancing plant production (van Groenigen *et al.*, 2014), through greater
88 mineralisation of carbon and nutrients from plant material (Postma-Blaauw *et al.*, 2006).
89 Mineralisation of SOC, on the other hand, is enhanced by endogeic and not anecic
90 earthworms (Postma-Blaauw *et al.*, 2006), while the feeding and burrowing activities of
91 epigeic and anecic earthworms increase water infiltration rates but endogeics do not
92 (Spurgeon *et al.*, 2013).

93

94 Anticipating the effects of global environmental changes on earthworm communities and
95 their activities requires a more comprehensive understanding of the environmental controls
96 on their global distribution, in both natural and managed ecosystems. Previous studies on
97 large-scale biogeographical distributions of soil microbes (bacteria and fungi) have revealed
98 strong relationships between soil pH and soil organic matter (Fierer & Jackson, 2006;
99 Tedersoo *et al.*, 2014; Malik *et al.*, 2018) whereas those on soil animals suggest a closer
100 relationship with climatic conditions (Wall *et al.*, 2008; Bates *et al.*, 2013; Gibb *et al.*, 2015).
101 Here, the working hypothesis was that biogeographic patterns in earthworm communities are
102 fundamentally similar to other soil animals, with climatic variables structuring earthworm
103 communities in both natural and managed ecosystems. In managed ecosystems, declines in
104 species richness and shifts in community composition to endogeic earthworm dominance
105 was also expected (Kladivko, 2001). To test these hypotheses, a global earthworm dataset
106 was compiled across boreal, temperate, mediterranean and tropical climates, covering both
107 natural (forests and grasslands) and managed (arable, pasture and plantation) ecosystems.

108

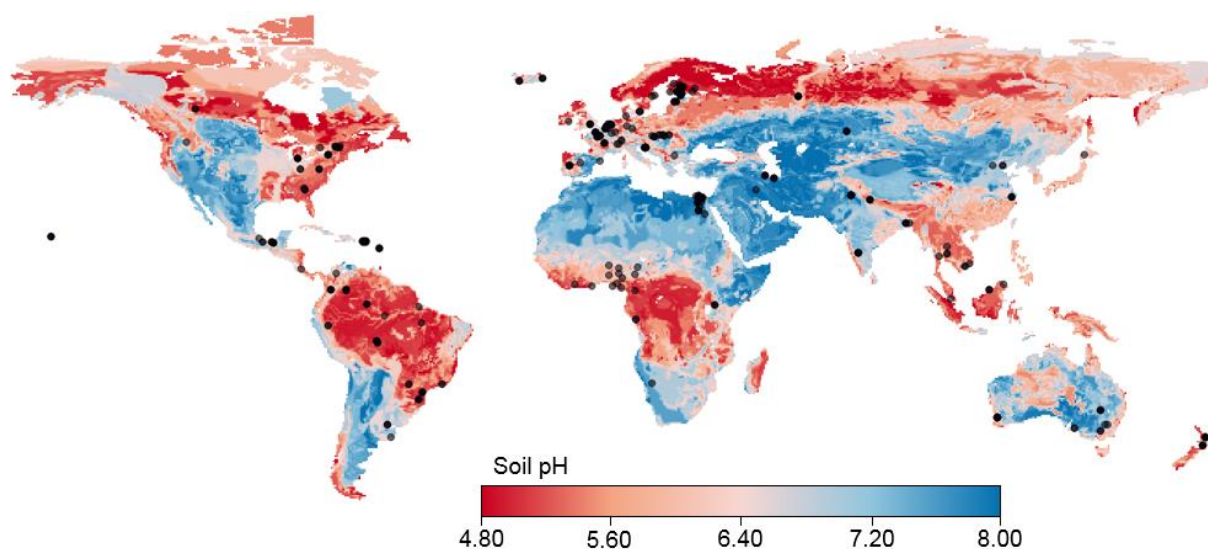
109 **2. Methods and Material**

110

111 **2.1. Data collection**

112 Studies of earthworm field populations and communities were synthesised, using ISI Web of
113 Knowledge (www.webofknowledge.com). To be included in the dataset, studies had to report
114 field-collected population abundances and/or species richness in un-manipulated field
115 conditions. That is, mesocosm experiments and experimental field trials that manipulated
116 environmental variables were excluded. Search terms included macrofauna, earthworm or
117 oligochaete and excluded the terms laboratory, microcosm or mesocosm in the title.
118 Additional search terms for the topic included: population or community; abundance, density,
119 number or species richness; and field, forest, grassland, arable, plantation, pasture,
120 agricultural, managed or natural. Field studies were also excluded if they did not report
121 essential site information such as latitude, longitude or site location, or the year/month of
122 earthworm collection to extract climatic data. Following the initial literature search, data gaps
123 for under-represented climates or ecosystems (e.g. natural ecosystems in mediterranean or
124 managed ecosystems in boreal climates) were addressed using specific search terms in
125 Web of Knowledge to ensure comparable sample sizes between climates. A total of 135
126 studies met the search criteria, which covered 169 globally distributed study sites (Figure 1)
127 over a period spanning 1962 to 2016.

128



129

130 **Figure 1.** Geographic distribution of study sites ($n = 169$) across 135 studies compiled in the earthworm dataset,
 131 displayed over a world soil pH map (IGBP-DIS, 1998).

132

133 **2.2. Data summary**

134 Most studies combined hand sorting and formaldehyde extraction methods for earthworm
 135 sampling, and abundance was typically measured as individuals m^{-2} . Cocoons were rarely
 136 reported and so not included in average abundance measures, whereas adults and juveniles
 137 were summed to give total species abundance where relevant. The raw earthworm dataset
 138 ($N = 1583$), reported seasonal earthworm population abundances and species richness
 139 where available, and seasonal or annual population dynamics by species, ecological group
 140 or total earthworm community. Where seasonal earthworm measurements were provided,
 141 and when replicates were given for the same sites, population abundances were averaged
 142 to give annual and site-specific measurements. If species richness measurements were not
 143 provided but species-specific abundances were reported, the number of species recorded
 144 was included in the dataset. Ecological group data ($N = 398$) were summarised by
 145 classifying earthworm species by their broad ecological group (anecic, endogeic and
 146 epigeic) and summing species-specific earthworm abundances in each group for single
 147 sites. Total earthworm community data ($N = 501$), were summed for ecological groups

148 recorded at a single site, alongside measurements for total earthworm abundance and
149 species richness.

150

151 Environmental variables include mean annual temperature (MAT), mean annual precipitation
152 (MAP), soil moisture, pH, litter layer, soil organic carbon (SOC), total C, N and P, C:N, N:P
153 and C:P ratios. If soil organic matter (SOM, %) measurements were available, the standard
154 conversion factor of $SOC = SOM \times 0.58$ was used (Guo & Gifford, 2002). When soil
155 properties were reported according to soil layer, an average value for all soil layers was
156 calculated. Missing climate data were filled using global climate databases if latitude and
157 longitude and study month/s and/or year were reported. Monthly air temperatures (study
158 temperature, ST) and precipitation (study precipitation, SP) measurements, together with
159 MAT and MAP if not reported, were compiled from local NOAA weather stations
160 (<https://www.ncdc.noaa.gov/cdo-web/datatools/findstation>).

161

162 The data were finally summarised by categorising study sites as boreal, temperate,
163 mediterranean and tropical climates and ecosystem type (natural forests or grasslands, or
164 managed arable, pasture or plantation ecosystems). Extrapolation was necessary in some
165 cases, for instance by including subtropical studies within the tropical climate category and
166 managed grasslands or forests as pastures or plantations, respectively. Managed
167 ecosystems also included a variety of management practices. For instance, arable fields
168 ranged from organic and conservation agriculture to conventional management schemes.

169

170 **2.3. Data analysis**

171 Data analysis was performed in the R environment software (RCoreTeam 2018) and
172 focused on explaining relationships between global earthworm communities and
173 environmental variables. First, differences in total earthworm species richness and
174 abundance and ecological group abundance were analysed across climates, ecosystem
175 types and management groups. Then, a hierarchical model was used to test the importance

176 of environmental controls in predicting the relationship between total earthworm species
177 richness and abundance at a global scale.

178

179 **2.3.1. Land management effects on global earthworm communities**

180 Differences in total earthworm species richness and abundance and ecological group
181 abundance across climates, ecosystem types and management groups were analysed using
182 all available measurements in the datasets. The effect of land management on total
183 earthworm abundance and species richness was tested using independent-samples t-tests,
184 with $p < 0.05$ supporting a difference between the two groups (natural vs managed
185 ecosystems). The effects of climate (tropical, mediterranean, temperate and boreal) and
186 ecosystem type (forest, grassland, arable, pasture or plantation) on total earthworm species
187 richness and abundance, and the effects of both land management and climate on
188 ecological group (anecic, endogeic, epigeic) abundance, were tested using one-way
189 ANOVA's and again taking $p < 0.05$ to support a difference between groups.

190

191 Earthworm and environmental data were then summarised according to ecosystem type (N
192 = 18) to investigate general relationships across climates and natural or managed
193 ecosystems. The effects of land management on total, anecic, endogeic and epigeic
194 earthworm abundance were summarised by comparing observed abundances in different
195 climates and ecosystems. Management effect sizes were calculated by comparing mean
196 earthworm abundances in natural grasslands with abundances in managed arable or
197 pasture ecosystems, and mean abundances in natural forests were compared with
198 abundances in managed plantation ecosystems. Comparisons between mean abundances
199 across ecosystem types and managed and natural ecosystems were further made at the
200 global scale.

201

202 **2.3.1. Multiple controls on global earthworm communities**

203 Scaling relationships between earthworm species richness (*SR*) and abundance (*A*) were
204 analysed to investigate differences between climates and ecosystem type. First, the *SR* – *A*
205 relationship was analysed without, and then with, interactions between *A* and climate
206 (boreal, temperate, mediterranean, tropical) and *A* and management (natural or managed).
207 Hierarchical models were then used to test the importance of environmental variables in
208 predicting differences in earthworm species richness and abundance relationships at a
209 global scale. The hierarchy of terms tested followed an order similar to that suggested by de
210 Vries *et al.* (2012), in which ‘controls’ are added before ‘function’. That is, variables that
211 cause variations in multiple soil properties (e.g. climate) were added first, so that if ‘controls’
212 explain the variation in ‘functions’ then addition of these variables do not improve model
213 likelihood. Terms were added in the order: climate (MAT, MAP, ST, SP and component 1 of
214 PCA’s for each combination of the four variables), soil type (pH, soil moisture, SOC and
215 PCA’s), management (natural or managed) and nutrients (C:N, N:P, C:P and PCA’s). Each
216 variable was added as a linear or quadratic term, with and without interactions with *A*.
217 Models were then compared by testing their influence on goodness of fit (Akaike’s
218 Information Criterion, AIC), model likelihood (Chi-square $p < 0.05$) and parsimony ($\Delta AIC > 2$
219 for additional degrees of freedom). Models that met these criteria were tested with the
220 subsequent environmental variables. All regression models were performed with averaged
221 *SR* and *A* measurements for each ecosystem type ($N = 18$) and weighted using the
222 reciprocal of the variance of *SR* to account for differences in sample sizes. The independent
223 effects of key environmental variables, identified by the hierarchical model, were then
224 illustrated by correcting species richness for abundance and the other explanatory
225 environmental variables in the hierarchical model.

226

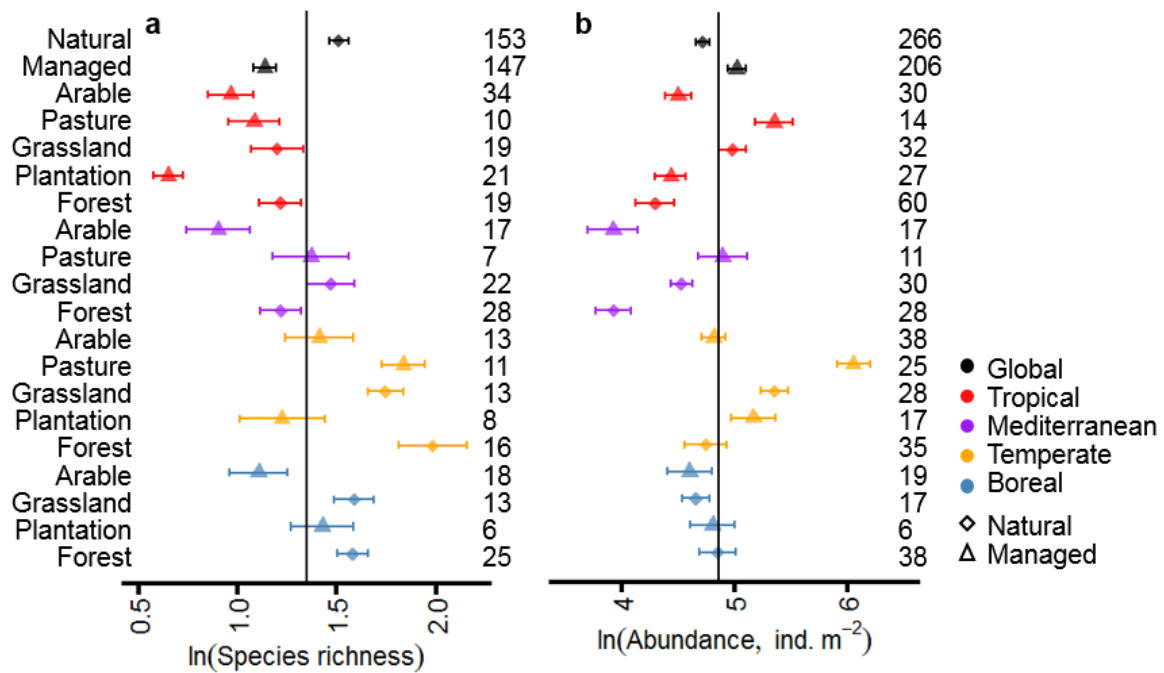
227 **3. Results**

228

229 **3.1. Land management effects on global earthworm communities**

230 Total earthworm species richness and abundance differed significantly with climate (ANOVA
231 for species richness: $F = 18.62$, $p < 0.0001$; and abundance: $F = 16.84$, $p < 0.0001$) and
232 ecosystem type (species richness: $F = 7.90$, $p < 0.0001$; and abundance: $F = 24.68$, $p <$
233 0.0001) (Figure 2). At a global scale, total earthworm species richness and abundance
234 differed in natural and managed ecosystems (independent-samples t-test for species
235 richness: $t = 4.58$, $p < 0.0001$; and abundance: $t = -2.86$, $p = 0.005$) (Figure 2). Shifts in
236 species richness and abundance, however, were highly variable across ecosystem types.
237 For instance, earthworm species richness declined in most managed compared to natural
238 ecosystems within climates (Figure 2a), whereas total earthworm abundance displayed a
239 much more variable response (Figure 2b).

240



241

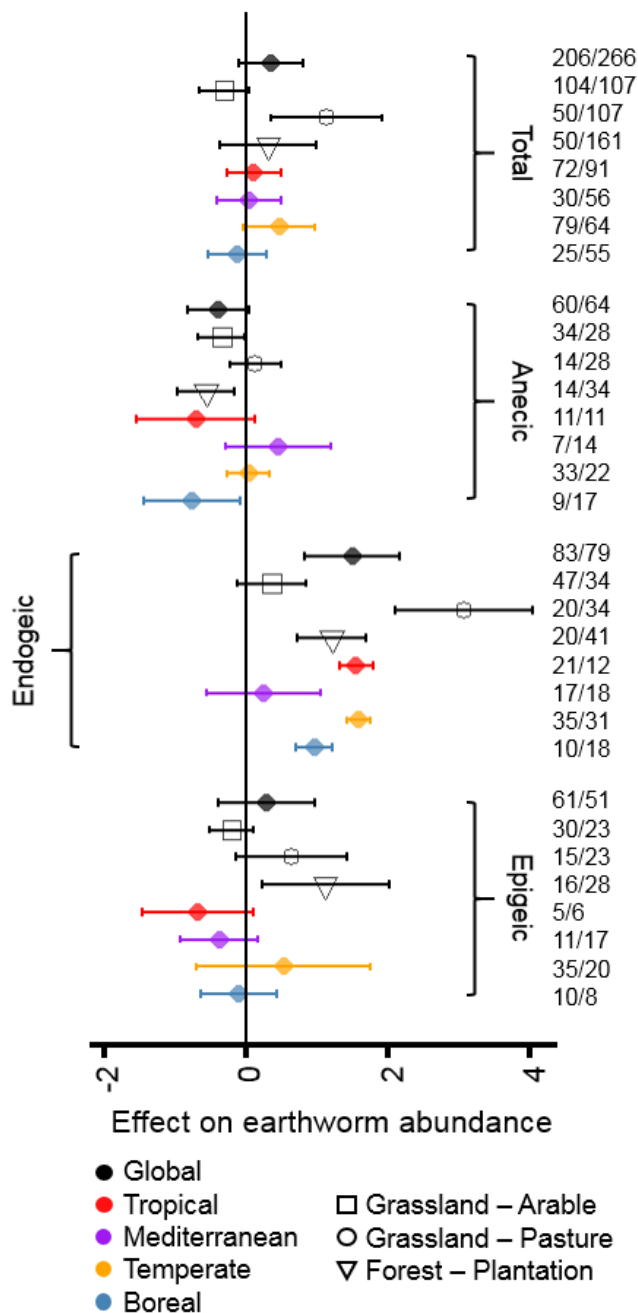
242 **Figure 2:** Earthworm species richness and total abundance across global ecosystems (black: global, red:
 243 tropical, purple: mediterranean, orange: temperate, blue: boreal climates and diamonds: natural, triangles:
 244 managed ecosystems). Presented values are average a) earthworm species richness and b) total abundance
 245 with standard error bars. Solid black vertical lines indicate global averages across climates and ecosystem types.
 246 Number of data points are presented on the right-hand side of each plot.

247

248 Earthworm community composition was summarised by the relative abundance of the three
 249 ecological groups of earthworms: anecic, endogeic and epigeic, which reflect different
 250 habitat needs and so sensitivity to soil disturbance. Analysis of the available ecological
 251 group data (N = 398) revealed that anecic, endogeic and epigeic abundances interacted
 252 significantly with climate ($F = 4.96, p < 0.0001$), ecosystem type ($F = 18.43, p < 0.0001$) and
 253 land management ($F = 10.38, p < 0.0001$). At a global scale, total, endogeic and epigeic
 254 earthworm abundance increased, while anecic earthworm abundance declined, in response
 255 to land management (Figure 3). Similar to total earthworm abundance (Figure 2), however,
 256 ecological group abundance was highly variable across different ecosystem types (Table
 257 S1). For instance, although there was little difference in total earthworm abundance in
 258 natural and managed ecosystems across the different climates, there were greater declines
 259 in abundance in arable compared to grassland ecosystems and increases in abundance in

260 pasture compared to grassland ecosystems (Figure 3). Effects on total earthworm
261 abundance also disguised greater declines in anecic and epigeic earthworms in managed
262 ecosystems due to increases in endogeic earthworm abundance in all managed compared
263 to natural ecosystems, particularly pastures (Figure 3).

264



266

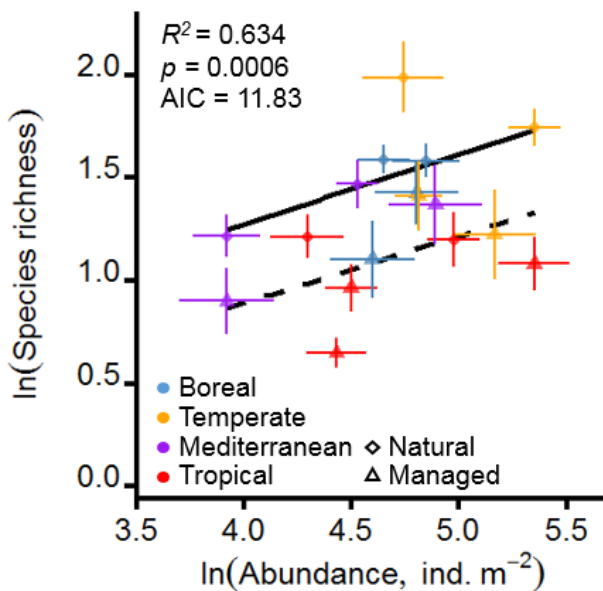
267 **Figure 3.** Land management effects on total earthworm, anecic, endogeic and epigeic abundance. Effect sizes
 268 are calculated by comparing abundances in natural and managed ecosystems at a global scale (black symbols)
 269 or across climates (red: tropical, purple: mediterranean, orange: temperate, blue: boreal climates) and between
 270 specific natural and managed ecosystem types (square symbols: grassland and arable, circle symbols: grassland
 271 and pasture, triangle symbols: forest and plantation). Presented values are average effect sizes with standard
 272 error bars. Number of data points are presented on the right-hand side for the natural and managed ecosystems.

273

274 **3.2. Multiple controls on global earthworm communities**

275 Divergent earthworm responses to land management resulted in different scaling
276 relationships between earthworm species richness and total abundance at a global scale
277 (Figure 4). That is, the relationship between earthworm species richness and abundance
278 was better explained by differences between natural and managed ecosystems than null or
279 climate models (Table S2). There was no significant interaction between abundance and
280 management, however, as abundance was generally unaffected by land management at a
281 global scale (Figure 3).

282



283

284 **Figure 4.** Scaling relationships between earthworm species richness and total abundance across climates (red:
285 tropical, purple: mediterranean, orange: temperate, blue: boreal) and ecosystem types (diamonds: natural,
286 triangles: managed) (N = 18). Linear regressions between abundance and species richness differed in natural
287 (diamond symbols and solid line) and managed (triangle symbols and broken line) ecosystems (Table S2).

288

289 A hierarchical model was used to test the importance of environmental controls on global
290 relationships between earthworm species richness and abundance (Figure 4 and Table S1).
291 Addition of three terms improved the hierarchical model fits in comparison to the null model
292 (Table 1, AIC = 23.77), with the condition that adding an additional term must be met with a
293 goodness of fit of $\Delta AIC > 2$ and Chi-square $p < 0.05$. Climate PCA, measured as component

294 1 of a PCA conducted with MAT, MAP, ST and SP explained the effects of climate better
295 than MAT, MAP, ST or SP separately, or any other PCA between the variables. Overall, the
296 quadratic climate term explained 56 % of the variation in species richness-abundance
297 relationships compared to the null model. An interaction term with soil pH and management
298 explained an additional 8 and 10 % of the variation in global earthworm patterns
299 respectively. The final model had a greatly improved goodness of fit to the data and model
300 likelihood compared to the null model ($\Delta AIC = 46.46$, Chi-square $p < 0.0001$). The
301 hierarchical model also showed an improved goodness of fit and model likelihood in
302 comparison to the management model (Figure 4, $\Delta AIC = 34.52$, Chi-square $p < 0.0001$).
303 Importantly, the hierarchical model further revealed the environmental variables
304 underpinning shifts in the relationship between global earthworm species richness and
305 abundance with climate and land management.
306

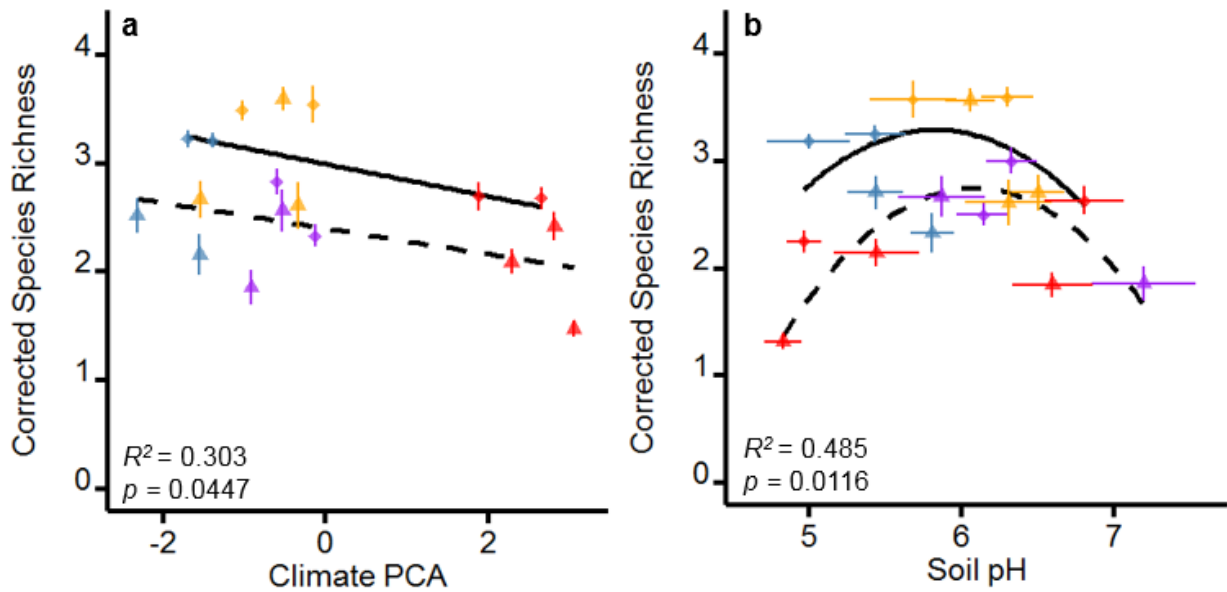
Table 1. Comparison of models used to explain global patterns in the relationship between earthworm species richness (*SR*) and abundance (*A*). The null model does not include interactions between earthworm abundance with environmental variables or management, while the following models indicate additional terms added to a hierarchical model. Chi-square *p*-value < 0.05 indicate increased model likelihood following the addition of each term. Overall goodness of fit is determined by AIC values, where lower AIC's indicate a better fit to the data. Δ AIC's present the difference in AIC values between the different models and the final hierarchical model (Table S3).

Term added	Model	df	Chi-square <i>p</i>	AIC	Δ AIC	<i>R</i> ₂	<i>p</i>
Null	SR ~ A	3		23.77	46.46	0.222	0.0278
Climate PCA	SR ~ A + Climate PCA + Climate PCA ²	5	< 0.0001	2.64	25.32	0.780	< 0.0001
pH	SR ~ A + Climate PCA + Climate PCA ² × pH	7	0.0129	-3.19	19.50	0.851	< 0.0001
Management	SR ~ A + Climate PCA + Climate PCA ² × pH × Management	11	< 0.0001	-22.69	0	0.952	< 0.0001

308

309 The independent effects of climate (component 1 of a PCA conducted with MAT, MAP, ST
310 and SP) and soil pH were illustrated by correcting species richness for abundance and the
311 other explanatory environmental variables in the hierarchical model (Figure 5). For example,
312 climate effects were assessed by correcting species richness for abundance, soil pH, and
313 management effects according to regression coefficients. Then, linear and quadratic models
314 between corrected species richness and the independent variable were tested with and
315 without interaction terms between the environmental variable and management. Results
316 revealed linear declines in corrected abundance with increasing Climate PCA (increasing
317 MAT, MAP, ST and SP) (Figure 5a) and a polynomial relationship between corrected
318 species richness with soil pH (Figure 5b), and significant interactions between natural and
319 managed ecosystems.

320



321

322 **Figure 5.** Relationships between corrected earthworm species richness with a) climate PCA and b) soil pH
 323 across natural (solid lines) or managed (broken lines) ecosystems and climates (symbol colours and shapes as in
 324 Figure 4). Species richness data were corrected for non-fixed explanatory variables as described in the text.

325

326 4. Discussion

327 Compilation of a global dataset in this study (Figure 1) reveals surprising similarities and
 328 expected differences in earthworm communities between natural and managed ecosystems.
 329 Across four climates total earthworm abundance showed little response to land
 330 management, while species richness was consistently reduced in managed compared to
 331 natural ecosystems (Figure 2). These patterns can be largely explained by shifts in
 332 earthworm community composition in managed ecosystems, which are generally composed
 333 of fewer anecic and epigeic and more endogeic earthworms than natural ecosystems (Figure
 334 3). Scaling relationships between earthworm species richness and total abundance differed
 335 in natural and managed ecosystems (Figure 4). A hierarchical model was used to show that
 336 climate, soil pH and land management best explained global variations in earthworm
 337 communities (Table 1 and Figure 5).

338

339 Earthworm species richness and total abundance were highest in temperate and lowest in
 340 mediterranean climates, while abundance was comparable in tropical and boreal but species

341 richness higher in boreal than tropical climates (Figure 2). Climate thus strongly influences
342 global earthworm communities, as hypothesised, through individual physiological and
343 behavioural responses to temperature and soil water extremes (Johnston *et al.*, 2018).
344 Interestingly, this study indicates non-linear latitudinal shifts in earthworm species richness,
345 previously thought to increase from high to low latitudes (Lavelle, 1983). Nevertheless, these
346 global patterns reflect known relationships between soil biodiversity with temperature and
347 precipitation regimes (Brussaard *et al.*, 2012). Temperate climates, however, have been
348 more extensively studied than any of the other climates investigated here. Differences in
349 sampling timing in colder climates will also introduce some bias as they were typically
350 sampled in the growing season, and earthworm species are known to display varying
351 sensitivities to soil temperature and water fluctuations (Briones *et al.*, 2009). General gaps in
352 earthworm taxonomy (Decaëns, 2010) further limits the current dataset not only to measures
353 of abundance and species richness, but also to those earthworms that have been identified
354 at the species level.

355

356 Overall, earthworm abundance increased in managed compared to natural ecosystems
357 globally and across all but boreal climates (Figure 3). This global pattern could be largely
358 explained by expected shifts in earthworm community composition to greater abundances of
359 endogeic earthworms in managed ecosystems (Riley *et al.*, 2008; Kanianska *et al.* 2016).
360 Anecic and epigeic earthworm responses to land management, in comparison, were less
361 extreme than expected given the higher vulnerability of these ecological groups to soil
362 disturbance (Briones & Schmidt, 2017). Although anecic and epigeic abundances declined in
363 arable compared to grassland ecosystems globally, both ecological groups responded
364 positively to pasture compared to grassland ecosystems alongside endogeic earthworms
365 (Figure 3). Livestock grazing is well known to increase earthworm density through the
366 creation of earthworm hotspots of all ecological groups around dung pats (Bacher *et al.*,
367 2018), but the global extent of this pattern has not been previously reported. Epigeic
368 earthworms also responded positively to temperate plantation compared to forest

369 ecosystems (Figure 3 and Table S1), suggesting a competitive advantage of epigeic
370 earthworms in managed forests. Much less data, however, was available for ecological
371 groups compared to total earthworm abundances across the range of ecosystems studied
372 here.

373

374 Global relationships between earthworm species richness and abundance in natural and
375 managed ecosystems (Figure 4) were best explained by climate, soil pH and land
376 management (Table 1). Illustrating the independent effects of climate and soil pH in Figure 5
377 shows how corrected species richness declines with increasing temperature and
378 precipitation (which are positively correlated with climate PCA, Figure 5a) and changes
379 according to a polynomial relationship with soil pH (Figure 5b). Climate PCA captures
380 increasing mean annual and study temperatures and mean annual and study precipitations
381 (except for a decline in mediterranean climates) from boreal to tropical climates. Earthworm
382 species richness thus declines with greater monthly temperatures ($> 12\text{ }^{\circ}\text{C}$) and with both
383 lower ($< 40\text{ mm}$) and greater monthly precipitation ($> 130\text{ mm}$). Although species richness
384 measurements will be influenced by greater sampling effort in moderate climatic conditions,
385 similar patterns in natural and managed ecosystems suggest consistent climate effects on
386 earthworms (Figure 5a). On the other hand, the decline in earthworm species richness
387 between natural and managed ecosystems was greater in more acidic soils ($\text{pH} < 6$)
388 compared to near-neutral soils ($\text{pH} > 6$) (Figure 5b).

389

390 Reduced species richness in managed ecosystems is typically associated with an increase
391 in soil pH at the ecosystem scale. For instance, species richness of earthworm communities
392 was reduced across all climates in arable fields compared to grasslands while soil pH was
393 usually higher in arable compared to grassland ecosystems. In contrast, greater species
394 richness in temperate pastures compared to grasslands was associated with a decline in soil
395 pH (Table S1). Different soil pH changes in managed ecosystems tend to reflect varying
396 management intensities (Malik *et al.*, 2018). Reductions in soil pH in tropical arable

397 compared to grassland ecosystems could therefore indicate the widespread adoption of
398 conservation agriculture (based on minimum soil disturbance) in these regions due to the
399 greater potential of tropical soil erosion under intensive management (Labrière *et al.*, 2015).
400 More intensive management practices, such as tillage, have direct effects on earthworm
401 communities through direct mortality, the removal of plant litter and destruction of habitat
402 (Briones & Schmidt, 2017). Relationships between earthworm communities and soil pH in
403 this study are thus expected to reflect varying extents of plant litter removal and subsequent
404 changes in SOC accumulation in managed ecosystems.

405

406 Plant functional traits likely underpin the relationship between climate, soil pH and
407 earthworm communities in both natural and managed ecosystems (Figure 5). In temperate
408 forests, for example, Reich *et al.* (2005) found variation in leaf litter calcium concentrations to
409 be a key driver of long-term changes in soil pH, earthworm abundance and biomass, and
410 litter decomposition rates. Although relationships between soil C:N:P stoichiometry and
411 earthworm communities were not identified in this study, soil pH reflects the availability of
412 multiple nutrients (e.g. Mulder and Elser (2009)). Different relationships between earthworm
413 ecological groups and soil pH may further indicate successional feedback relationships
414 between plant traits and earthworm communities. Earthworm invasions into previously
415 unoccupied forests, for example, are typically initiated by epigeic species which show a
416 greater tolerance for acidic soils (Hendrix, 2006). Earthworms then feedback to the plant
417 community by accelerating plant litter decomposition and nutrient mineralisation rates and
418 altering microbial community composition (Craven *et al.*, 2017). Earthworm invasions are
419 therefore typically associated with successions in both plant quality and earthworm
420 community composition (Bohlen *et al.*, 2004). Future shifts in temperature and precipitation
421 regimes, alongside changes in land management, will thus alter feedbacks between plant
422 traits, earthworms and multiple soil functions (Wardle *et al.*, 2004).

423

424 Disentangling the effects of climatic, edaphic, management and biotic factors on global
425 earthworm distributions requires a better understanding of the mechanisms linking individual
426 species to their populations in site-specific conditions and species populations to earthworm
427 communities at the ecosystem and global scale. Building global soil community databases at
428 the species- and site-specific level could help unravel the mechanisms linking earthworm
429 communities to their environments. First, however, focused empirical studies are needed to
430 address current knowledge gaps in earthworm macroecology. Seasonal fluctuations in
431 earthworm communities in boreal ecosystems and earthworm communities in mediterranean
432 and tropical ecosystems, for example, need to be accounted for. Overall, the results of this
433 study show that global earthworm communities are strongly linked to climate and soil pH,
434 and that land management modulates global relationships between earthworm species
435 richness and environmental controls. Better understanding of macroecological patterns in
436 earthworm communities are needed to aid prediction of the large-scale impacts of land
437 management and climate changes on soil ecosystems.

438

439 **Acknowledgements.** This research has been financially supported by a NERC Soil Security
440 Programme fellowship (NE/N019504/1). Thanks go to T. Sizmur for feedback on the
441 manuscript, E.L. Gardner for discussions on the analysis and the editor and two anonymous
442 reviewers for helpful suggestions which greatly improved the manuscript.

443

444 **Data availability statement.** The dataset compiled and analysed in this study is available
445 from Dryad (<https://doi.org/10.5061/dryad.4fn50k3>).

446

447 **References**

448 Bacher, M. G., Fenton, O., Bondi, G., Creamer, R. E., Karmarkar, M., & Schmidt, O. (2018).
449 The impact of cattle dung pats on earthworm distribution in grazed pastures. *BMC*
450 *Ecology*, 18, 59.

451 Bates, S.T., Clemente, J.C., Flores, G.E., Walters, W.A., Parfrey, L.W., Knight, R. & Fierer,
452 N. (2013) Global biogeography of highly diverse protistan communities in soil. *The*
453 *ISME Journal*, 7, 652.

454 Blouin, M., Hodson, M.E., Delgado, E.A., Baker, G., Brussaard, L., Butt, K.R., Dai, J.,
455 Dendooven, L., Peres, G. & Tondoh, J.E. (2013) A review of earthworm impact on
456 soil function and ecosystem services. *European Journal of Soil Science*, 64, 161-182.

457 Bohlen, P.J., Groffman, P.M., Fahey, T.J., Fisk, M.C., Suarez, E., Pelletier, D.M. & Fahey,
458 R.T. (2004) Ecosystem Consequences of Exotic Earthworm Invasion of North
459 Temperate Forests. *Ecosystems*, 7, 1-12.

460 Bouché, M.B. (1972) Lombriciens de France: écologie et systématique. *Soil Science*, 119,
461 252.

462 Briones, M.J.I. & Schmidt, O. (2017) Conventional tillage decreases the abundance and
463 biomass of earthworms and alters their community structure in a global meta-
464 analysis. *Global Change Biology*, 23, 4396-4419.

465 Briones, M.J.I., Ostle, N.J., McNamara, N.P. & Poskitt, J. (2009) Functional shifts of
466 grassland soil communities in response to soil warming. *Soil Biology and*
467 *Biochemistry*, 41, 315-322.

468 Brussaard, L., Aanen, D., Briones, M., Decaëns, T., De Deyn, G., Fayle, T., James, S. &
469 Nobre, T. (2012) Biogeography and phylogenetic community structure of soil
470 invertebrate ecosystem engineers, global to local patterns, implications for
471 ecosystem, functioning and services and global, environmental change impacts. *Soil*
472 *Ecology Ecosystems Services*, pp. 201-232. Oxford University Press.

473 Chan, K. (2001) An overview of some tillage impacts on earthworm population abundance
474 and diversity—implications for functioning in soils. *Soil and Tillage Research*, 57,
475 179-191.

476 Craven, D., Thakur, M.P., Cameron, E.K., Frelich, L.E., Beauséjour, R., Blair, R.B., Blossey,
477 B., Burtis, J., Choi, A. & Dávalos, A. (2017) The unseen invaders: introduced

478 earthworms as drivers of change in plant communities in North American forests (a
479 meta-analysis). *Global Change Biology*, 23, 1065-1074.

480 Daniel, O. (1991) Leaf-litter consumption and assimilation by juveniles of *Lumbricus*
481 *terrestris* L.(Oligochaeta, Lumbricidae) under different environmental conditions.
482 *Biology and Fertility of Soils*, 12, 202-208.

483 Darwin, C. (1881) *The formation of vegetable mould through the action of worms: with*
484 *observations on their habits*. John Murray, London.

485 Decaëns, T. (2010) Macroecological patterns in soil communities. *Global Ecology and*
486 *Biogeography*, 19, 287-302.

487 Decaëns, T. & Jiménez, J.J. (2002) Earthworm communities under an agricultural
488 intensification gradient in Colombia. *Plant and Soil*, 240, 133-143.

489 Decaëns, T., Bureau, F. & Margerie, P. (2003) Earthworm communities in a wet agricultural
490 landscape of the Seine Valley (Upper Normandy, France): The 7th international
491 symposium on earthworm ecology · Cardiff · Wales · 2002. *Pedobiologia*, 47, 479-
492 489.

493 Decaëns, T., Margerie, P., Aubert, M., Hedde, M. & Bureau, F. (2008) Assembly rules within
494 earthworm communities in North-Western France—A regional analysis. *Applied Soil*
495 *Ecology*, 39, 321-335.

496 Decaëns, T., Jiménez, J., Barros, E., Chauvel, A., Blanchart, E., Fragoso, C. & Lavelle, P.
497 (2004) Soil macrofaunal communities in permanent pastures derived from tropical
498 forest or savanna. *Agriculture, Ecosystems & Environment*, 103, 301-312.

499 de Vries, F.T., Manning, P., Tallowin, J.R., Mortimer, S.R., Pilgrim, E.S., Harrison, K.A.,
500 Hobbs, P.J., Quirk, H., Shipley, B. & Cornelissen, J.H. (2012) Abiotic drivers and
501 plant traits explain landscape-scale patterns in soil microbial communities. *Ecology*
502 *Letters*, 15, 1230-1239.

503 Eisenhauer, N. (2010) The action of an animal ecosystem engineer: identification of the main
504 mechanisms of earthworm impacts on soil microarthropods. *Pedobiologia*, 53, 343-
505 352.

506 Eisenhauer, N. & Schädler, M. (2011) Inconsistent impacts of decomposer diversity on the
507 stability of aboveground and belowground ecosystem functions. *Oecologia*, 165, 403-
508 415.

509 Eisenhauer, N., Stefanski, A., Fisichelli, N.A., Rice, K., Rich, R. & Reich, P.B. (2014)
510 Warming shifts 'worming': effects of experimental warming on invasive earthworms in
511 northern North America. *Scientific Reports*, 4, 6890.

512 Fierer, N. & Jackson, R.B. (2006) The diversity and biogeography of soil bacterial
513 communities. *Proceedings of the National Academy of Sciences of the United States*
514 *of America*, 103, 626-631.

515 Fierer, N., Strickland, M.S., Liptzin, D., Bradford, M.A. & Cleveland, C.C. (2009) Global
516 patterns in belowground communities. *Ecology Letters*, 12, 1238-1249.

517 Gibb, H., Sanders, N.J., Dunn, R.R., Watson, S., Photakis, M., Abril, S., Andersen, A.N.,
518 Angulo, E., Armbrrecht, I., Arnan, X., Baccaro, F.B., Bishop, T.R., Boulay, R.,
519 Castracani, C., Del Toro, I., Delsinne, T., Diaz, M., Donoso, D.A., Enríquez, M.L.,
520 Fayle, T.M., Feener, D.H., Fitzpatrick, M.C., Gómez, C., Grasso, D.A., Groc, S.,
521 Heterick, B., Hoffmann, B.D., Lach, L., Lattke, J., Leponce, M., Lessard, J.-P.,
522 Longino, J., Lucky, A., Majer, J., Menke, S.B., Mezger, D., Mori, A., Munyai, T.C.,
523 Paknia, O., Pearce-Duvet, J., Pfeiffer, M., Philpott, S.M., de Souza, J.L.P., Tista, M.,
524 Vasconcelos, H.L., Vonshak, M. & Parr, C.L. (2015) Climate mediates the effects of
525 disturbance on ant assemblage structure. *Proceedings of the Royal Society B:*
526 *Biological Sciences*, 282, 20150418.

527 Guo, L.B. & Gifford, R. (2002) Soil carbon stocks and land use change: a meta analysis.
528 *Global Change Biology*, 8, 345-360.

529 Hendrix, P.F. (2006) Biological invasions belowground—earthworms as invasive species.
530 *Biological Invasions Belowground: Earthworms as Invasive Species*, pp. 1-4.
531 Springer.

532 Hendrix, P.F., Mueller, B.R., Bruce, R.R., Langdale, G.W. & Parmelee, R.W. (1992)
533 Abundance and distribution of earthworms in relation to landscape factors on the
534 Georgia Piedmont, U.S.A. *Soil Biology and Biochemistry*, 24, 1357-1361.

535 Hendrix, P.F., Callahan Jr, M.A., Drake, J.M., Huang, C.-Y., James, S.W., Snyder, B.A. &
536 Zhang, W. (2008) Pandora's box contained bait: the global problem of introduced
537 earthworms. *Annual Review of Ecology, Evolution, and Systematics*, 39, 593-613.

538 IGBP-DIS (1998) A program for creating global soil-property databases. *IGBP Global Soils*
539 *Data Task, France*.

540 Johnston, A.S., Sibly, R.M. & Thorbek, P. (2018) Forecasting tillage and soil warming effects
541 on earthworm populations. *Journal of Applied Ecology*, 55, 1498-1509.

542 Kanianska, R., Jaďud'ová, J., Makovníková, J. & Kizeková, M. (2016) Assessment of
543 relationships between earthworms and soil abiotic and biotic factors as a tool in
544 sustainable agricultural. *Sustainability*, 8, 906.

545 Kladivko, E.J. (2001) Tillage systems and soil ecology. *Soil and Tillage Research*, 61, 61-76.

546 Labrière, N., Locatelli, B., Laumonier, Y., Freycon, V., & Bernoux, M. (2015). Soil erosion in
547 the humid tropics: A systematic quantitative review. *Agriculture, Ecosystems &*
548 *Environment*, 203, 127-139.

549 Lavelle, P. (1983) The structure of earthworm communities. *Earthworm ecology*, pp. 449-
550 466. Springer.

551 Lavelle, P., Decaens, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P.
552 & Rossi, J.P. (2006) Soil invertebrates and ecosystem services. *European Journal of*
553 *Soil Biology*, 42, S3-S15.

554 Malik, A.A., Puissant, J., Buckeridge, K.M., Goodall, T., Jehmlich, N., Chowdhury, S.,
555 Gweon, H.S., Peyton, J.M., Mason, K.E., van Agtmaal, M., Blaud, A., Clark, I.M.,
556 Whitaker, J., Pywell, R.F., Ostle, N., Gleixner, G. & Griffiths, R.I. (2018) Land use
557 driven change in soil pH affects microbial carbon cycling processes. *Nature*
558 *Communications*, 9, 3591.

559 Mulder, C. & Elser, J.J. (2009) Soil acidity, ecological stoichiometry and allometric scaling in
560 grassland food webs. *Global Change Biology*, 15, 2730-2738.

561 Postma-Blaauw, M.B., Bloem, J., Faber, J.H., van Groenigen, J.W., de Goede, R.G.M. &
562 Brussaard, L. (2006) Earthworm species composition affects the soil bacterial
563 community and net nitrogen mineralization. *Pedobiologia*, 50, 243-256.

564 R Core Team (2013) R: A language and environment for statistical computing.

565 Reich, P.B., Oleksyn, J., Modrzyński, J., Mrozinski, P., Hobbie, S.E., Eissenstat, D.M.,
566 Chorover, J., Chadwick, O.A., Hale, C.M. & Tjoelker, M.G. (2005) Linking litter
567 calcium, earthworms and soil properties: a common garden test with 14 tree species.
568 *Ecology Letters*, 8, 811-818.

569 Riley, H., Pommeresche, R., Eltun, R., Hansen, S. & Korsath, A. (2008) Soil structure,
570 organic matter and earthworm activity in a comparison of cropping systems with
571 contrasting tillage, rotations, fertilizer levels and manure use. *Agriculture,*
572 *Ecosystems & Environment*, 124, 275-284.

573 Rosseel, Y. (2012) Lavaan: An R package for structural equation modeling and more.
574 Version 0.5–12 (BETA). *Journal of Statistical Software*, 48, 1-36.

575 Rounsevell, M.D.A., Dawson, T.P. & Harrison, P.A. (2010) A conceptual framework to
576 assess the effects of environmental change on ecosystem services. *Biodiversity and*
577 *Conservation*, 19, 2823-2842.

578 Rutgers, M., Orgiazzi, A., Gardi, C., Römbke, J., Jänsch, S., Keith, A.M., Neilson, R., Boag,
579 B., Schmidt, O. & Murchie, A.K. (2016) Mapping earthworm communities in Europe.
580 *Applied Soil Ecology*, 97, 98-111.

581 Shuster, W.D., Subler, S. & McCoy, E.L. (2001) Deep-burrowing earthworm additions
582 changed the distribution of soil organic carbon in a chisel-tilled soil. *Soil Biology and*
583 *Biochemistry*, 33, 983-996.

584 Smith, P., House, J.I., Bustamante, M., Sobocká, J., Harper, R., Pan, G., West, P.C., Clark,
585 J.M., Adhya, T. & Rumpel, C. (2016) Global change pressures on soils from land use
586 and management. *Global Change Biology*, 22, 1008-1028.

587 Smith, R.G., McSwiney, C.P., Grandy, A.S., Suwanwaree, P., Snider, R.M. & Robertson,
588 G.P. (2008) Diversity and abundance of earthworms across an agricultural land-use
589 intensity gradient. *Soil and Tillage Research*, 100, 83-88.

590 Spurgeon, D.J., Keith, A.M., Schmidt, O., Lammertsma, D.R. & Faber, J.H. (2013) Land-use
591 and land-management change: relationships with earthworm and fungi communities
592 and soil structural properties. *BMC Ecology*, 13, 46.

593 Tedersoo, L., Bahram, M., Põlme, S., Kõljalg, U., Yorou, N.S., Wijesundera, R., Ruiz, L.V.,
594 Vasco-Palacios, A.M., Thu, P.Q., Suija, A., Smith, M.E., Sharp, C., Saluveer, E.,
595 Saitta, A., Rosas, M., Riit, T., Ratkowsky, D., Pritsch, K., Põldmaa, K., Piepenbring,
596 M., Phosri, C., Peterson, M., Parts, K., Pärtel, K., Otsing, E., Nouhra, E., Njouonkou,
597 A.L., Nilsson, R.H., Morgado, L.N., Mayor, J., May, T.W., Majuakim, L., Lodge, D.J.,
598 Lee, S.S., Larsson, K.-H., Kohout, P., Hosaka, K., Hiiesalu, I., Henkel, T.W., Harend,
599 H., Guo, L.-d., Greslebin, A., Grelet, G., Geml, J., Gates, G., Dunstan, W., Dunk, C.,
600 Drenkhan, R., Dearnaley, J., De Kesel, A., Dang, T., Chen, X., Buegger, F., Brearley,
601 F.Q., Bonito, G., Anslan, S., Abell, S. & Abarenkov, K. (2014) Global diversity and
602 geography of soil fungi. *Science*, 346, 1256688.

603 van Groenigen, J.W., Lubbers, I.M., Vos, H.M.J., Brown, G.G., De Deyn, G.B. & van
604 Groenigen, K.J. (2014) Earthworms increase plant production: a meta-analysis.
605 *Scientific Reports*, 4, 6365.

606 Wagg, C., Bender, S.F., Widmer, F. & van der Heijden, M.G. (2014) Soil biodiversity and soil
607 community composition determine ecosystem multifunctionality. *Proceedings of the
608 National Academy of Sciences*, 111, 5266-5270.

609 Wall, D.H., Bradford, M.A., St John, M.G., Trofymow, J.A., Behan-Pelletier, V., Bignell, D.E.,
610 Dangerfield, J.M., Parton, W.J., Rusek, J., Voigt, W., Wolters, V., Gardel, H.Z.,
611 Ayuke, F.O., Bashford, R., Beljakova, O.I., Bohlen, P.J., Brauman, A., Flemming, S.,
612 Henschel, J.R., Johnson, D.L., Jones, T.H., Kovarova, M., Kranabetter, J.M., Kutny,
613 L.E.S., Lin, K.-C., Maryati, M., Masse, D., Pokarzhevskii, A., Rahman, H., SabarÁ,
614 M.G., Salamon, J.-A., Swift, M.J., Varela, A., Vasconcelos, H.L., White, D.O.N. &

615 Zou, X. (2008) Global decomposition experiment shows soil animal impacts on
616 decomposition are climate-dependent. *Global Change Biology*, 14, 2661-2677.
617 Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H. & Wall, D.H.
618 (2004) Ecological Linkages Between Aboveground and Belowground Biota. *Science*,
619 304, 1629-1633.
620