Global distribution of earthworm diversity

One sentence summary (max. 125 characters):

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53 Abstract (max. 125 words)

54 Soil organisms are crucial for ecosystem services that support human life. However, little is

55 known about the distribution, diversity and threats facing them. Here, we compiled a global

56 dataset of sampled earthworm communities from over 7000 sites in 56 countries to predict

57 patterns in earthworm diversity, abundance, and biomass. Further, we identify the

58 environmental drivers shaping these patterns. Local species richness and abundance typically

59 peaked at higher latitudes, while biomass peaked in the tropics, patterns opposite to that

60 observed in many aboveground taxa. But similar to many aboveground taxa, climate variables

61 were more important in shaping earthworm communities than variables relating to soil or habitat

62 cover. These findings highlight that, while the environmental drivers are similar, conservation

63 strategies to conserve aboveground biodiversity might not be appropriate for earthworm

64 diversity.

65 Main Text

66 Despite repeated calls for large-scale biogeographic studies of soil organisms (*1–3*), global

67 biodiversity patterns remain relatively unknown, with most efforts focused on soil microbes (*4–*

68 *6*), the smallest of the soil organisms. Consequently, the drivers of soil biodiversity, particularly

69 soil fauna, remain unknown at global scales. Nevertheless, soils harbour high biodiversity (*7–*

70 *11*), and are responsible for a large number of ecosystem functions and services that we rely

71 upon for our well-being (*9, 10, 12, 13*).

72

73 Here we analyse global patterns in diversity, abundance and biomass of earthworms (hereafter

74 'community metrics'). Earthworms are considered ecosystem engineers (*14*) in many habitats,

75 and contribute to soil quality (e.g., nutrient availability through decomposition *15–17*). They also

76 directly provide a variety of vital ecosystem functions and services (*18*). Whereas most

77   biodiversity-ecosystem functioning studies focus on species richness as a diversity measure

78   (*19–21*), the provisioning of ecosystem functions by earthworms is likely to vary depending on

79   abundance (*22*), biomass (*23–25*), and ecological group of the earthworm species (*24, 26, 27*;

80   see Supplementary Materials and Methods). Consequently, understanding global patterns in

81   community metrics for earthworms is critical.

82

83   Our ecological understanding of global biodiversity patterns (e.g., latitudinal diversity gradients

84   *28, 29*) are largely based on the distribution of aboveground taxa only. For many aboveground

85   taxa, variables relating to climate (*30–33*) or energy (e.g., primary productivity *34*;

86   evapotranspiration *35, 36*) are often the most important predictors of diversity across large

87   scales. At large scales, climatic drivers also shape belowground communities (*5, 37–41*), but

88   the response to these drivers in belowground communities may differ from those seen

89   aboveground (*5, 42, 43*). For example, mean annual temperature positively correlates

90   aboveground diversity (*44*), but negatively correlates with the diversity of many classes of fungi

91   (*5*), likely due to the optimum temperature of the latter being exceeded (*45*).

92

93   From small scale field studies we know that soil properties such as pH and soil carbon will

94   influence earthworm diversity (*40, 46, 47*). For example, lower pH values constrain the diversity

95   of earthworms by reducing calcium availability (*48*), and soil carbon provides resources that

96   sustain diversity (*46*). Alongside the many interacting soil properties (*40*), there are a variety of

97   other drivers can shape earthworm diversity, such as climate and habitat cover (*46, 49, 50*).

98   However, to date, no single framework focused on soil fauna has integrated a comprehensive

99   set of environmental drivers to identify the most important ones.

100

101   As many soil organisms have shown global diversity patterns that differ from aboveground

102   organisms (*5, 42, 43, 51*), we anticipate that earthworm community metrics (particularly

103   diversity) will not follow global patterns seen aboveground. This would be consistent with

104   previous studies at smaller scales, which have shown that species richness of earthworms

105   increases with latitude (*40*, *50*). Because studies have shown that local earthworm communities

106   are highly influenced by soil properties, we furthermore expect soil properties (e.g., pH and soil

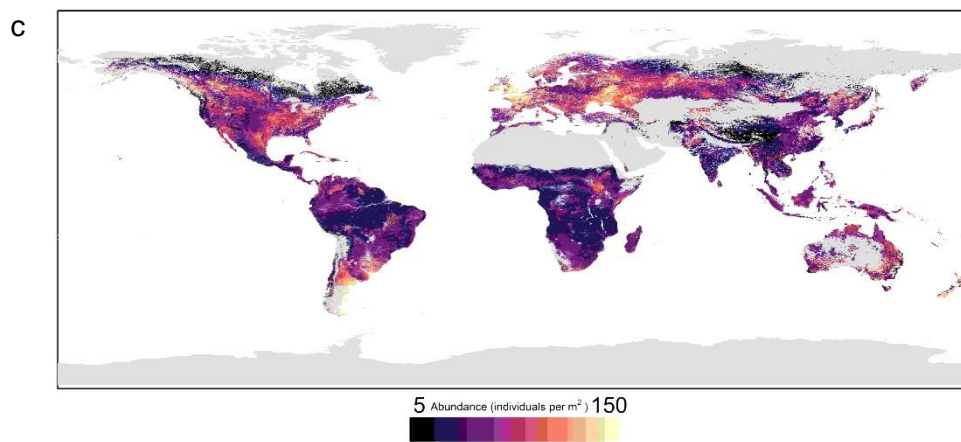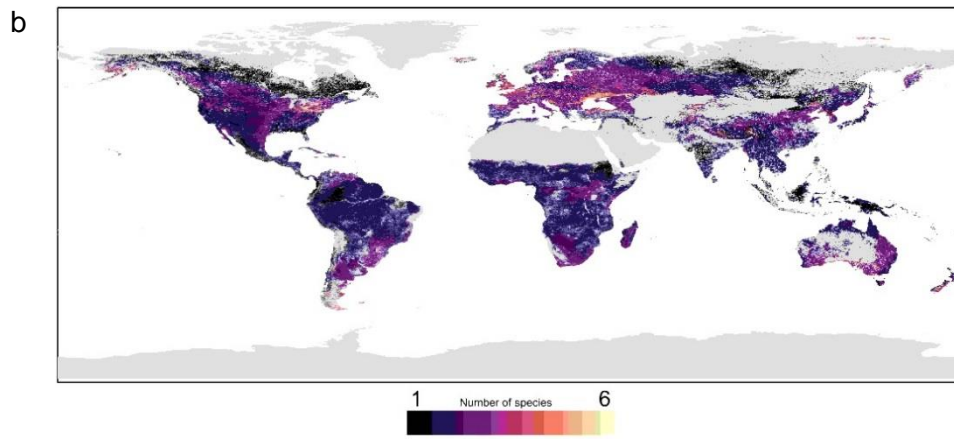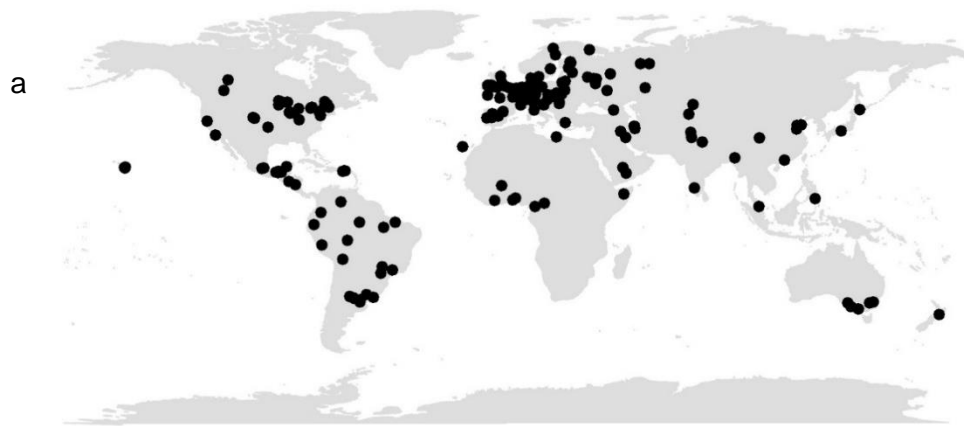107   organic carbon) to be key environmental drivers of earthworm communities.

108

109   We collated 181 earthworm diversity datasets from the literature and unpublished field studies

110   (162 and 19, respectively) to create a dataset spanning 56 countries (all continents except

111   Antarctica) and 7048 sites (Figure 1a). We used this raw data to explore key characteristics of

112   earthworm communities (species richness, abundance and biomass), and determine the

113   environmental drivers that shape earthworm biodiversity. We then used the relationships

114   between earthworm community metrics and environmental drivers to predict local earthworm

115   communities across the globe. Here, we present the first global maps describing earthworm

116   biodiversity, distilled into three earthworm community metrics: diversity, abundance, and

117   biomass.

118

119   Three mixed effects models were constructed for each of the three community metrics; species

120   richness (calculated within a site, ~1m^2), abundance per m^2, and biomass per m^2. Each model

121   contained 12 environmental variables as main effects (Supplementary Table 2) which were

122   grouped into six themes; 'soil', 'precipitation', 'temperature', 'water retention', 'habitat cover' and

123   'elevation' (see Supplementary Materials and Methods). Within each theme, each model

124   contained interactions between the variables. Following model simplification, all models retained

125   most of the original variables, but some interactions were removed (Supplementary Table 3). All

126   models performed well in cross-validation (Supplementary Figure 2) with relatively high R^2

127   values (Supplementary Table 4 a and c, see Supplementary Material for further details).

128

a

b

1   Number of species   6

c

5   Abundance (individuals per m^2)   150
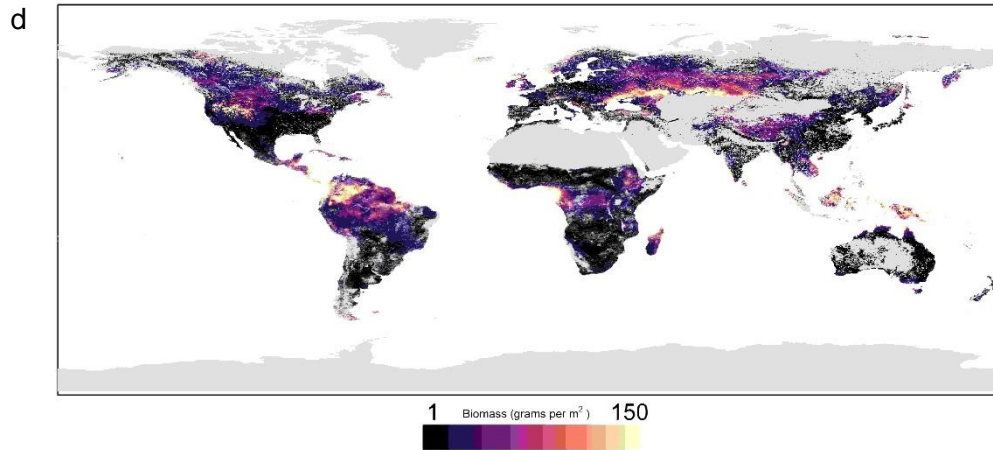
d

1　Biomass (grams per m^7)　150

Figure 1 (a) Map of the distribution of data, showing any record that was used in at least one of the three models (species richness, abundance, and biomass). Each black dot represents the centre of a 'study' (i.e., a set of data with consistent methodology, see Supplementary Materials and Methods). In total, 229 studies were included (from 181 datasets), which equated to 7048 sites across 56 countries. (b-d): The globally predicted values from the three biodiversity models, species richness (within site, ~1m^2; panel b), abundance (panel c; individuals per m^2), and biomass (panel d; grams per m^2). Areas of high diversity are shown in yellow colours, and areas of low diversity are shown in dark purple colours. Grey areas are habitat cover categories which lacked samples of earthworm commuties, thus lack predictions. To prevent outliers skewing the visualization of results, the colour of maps were curtailed at the extreme low and high values. Curtailing was based on where the majority of values laid. Thus, values lower or higher than that number marked on the scale are coloured the same but may represent a large range of values.

129

130　Predicting across global environmental data layers, local diversity of earthworms was estimated

131　to range between 1 and 4 species across most of the terrestrial globe (Figure 1b) (mean: 1.98

132　species; SD: 0.55). These values are in line with previous suggestions (*47*). The lowest values

133　of species richness occurred across the boreal/subarctic regions, which was expected based on

134　aboveground biodiversity patterns. However, low diversity also occurred in subtropical and

135　tropical areas, such as India and Indonesia, in contrast with commonly observed

136　macroecological patterns. This low earthworm diversity could be due to these regions typically

137　being outside of the optimal temperature range (12-20˚C *52*) for earthworms. Areas of high local

138   species richness were at mid-latitudes, such as the southern tip of South America, and the

139   southern regions of Australia and New Zealand. Europe (particularly north of the Black Sea) and

140   northeastern USA also had particularly high local species richness. While this pattern contrasts

141   with the latitudinal diversity patterns found in many aboveground organisms (*28, 29, 53*), it is

142   consistent with patterns found in some belowground organisms (ectomycorrhizal fungi *5*,

143   bacteria *41*, nematodes *54, 55*), but not all (arbuscular mycorrhizal fungus *39*, oribatid mites

144   *56*). The mismatch between above- and belowground biodiversity has been predicted (*42, 51*,

145   *57*). This work highlights the fact that it is important that soil organism diversity patterns are

146   examined in concert with those of aboveground taxa if we want to fully understand large-scale

147   patterns of biodiversity and their underlying drivers (*43, 58*).

148

149   However, the patterns seen could be as a result of past climates, in particular glaciation in the

150   last ice age. With the expectation that regions in the mid- to high latitudes that were previously

151   glaciated would be re-colonised by earthworm species with high dispersal capabilities and large

152   geographic ranges (*50*). Thus mid-latitude communities would have high local diversity but

153   minimal beta-diversity, and the opposite would be true in the tropical regions. When the number

154   of unique species within each 5 degree latitude band was calculated (i.e., regional richness,

155   Figure 2a) there was no evidence of a latitudinal diversity gradient once sampling effects have

156   been accounted for (Figure 2b). This highlights that even with relatively low sampling effort in

157   the tropics (Figure 2a), endemism of earthworms (*59*) and beta diversity within the region (i.e.,

158   across the sites; *50, 60*) must be considerably higher than within the well-sampled temperate

159   region.

160

161   Across the globe, predicted total abundance of the local community of earthworms typically

162   ranged between 5 and 150 individuals per m^2, in line with estimates from Curry (*46*) (Figure 1c;

163   mean: 57.00 individuals per m^2; SD: 43.59). There was a slight tendency for areas of higher
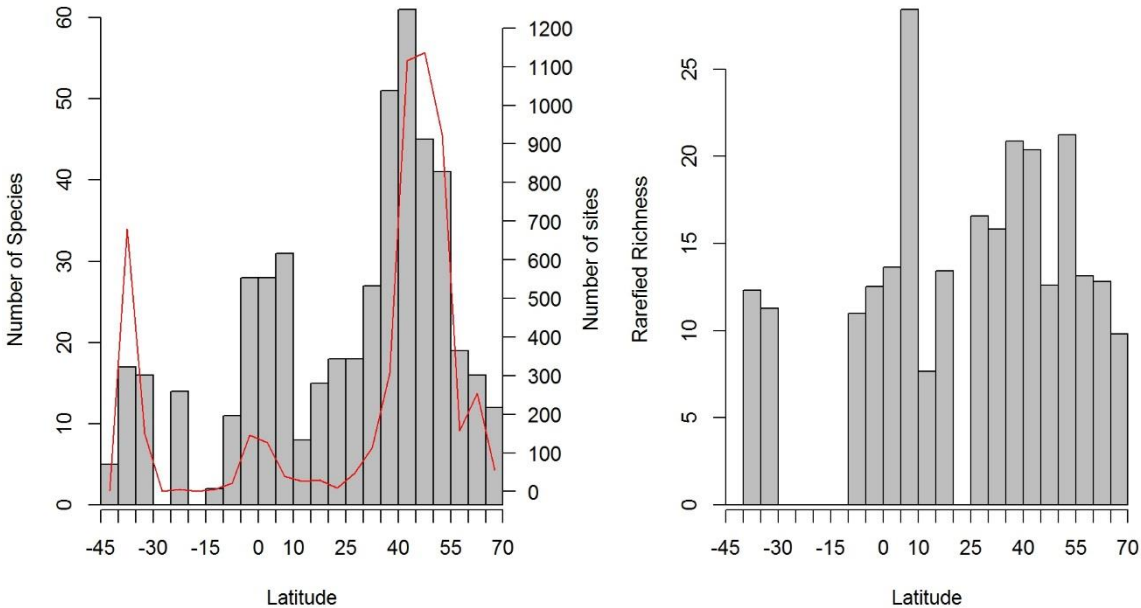
Figure 2 (a) The number of unique species within each 5 degree latitude band (grey bars) and the number of sampled sites within the same latitude band (red line). (b) Sampled-based rarefied species richness within each 5 degree latitude band. Latitude bands with less than 22 sites were not included in the analysis.

164

165   community abundance to not be in the tropics, but in temperate areas such as Europe

166   (particularly the UK, France and Ukraine), New Zealand, and part of the Pampas and

167   surrounding region (South America). Lower community abundance occurred in many of the

168   tropical and sub-tropical regions, such as Brazil, central Africa, and parts of China. In regions of

169   lower earthworm abundance the relationship between community abundance and ecosystem

170   function (*61–63*) implies a lower provision of the ecosystem services performed by these

171   organisms. Further research is needed to disentangle whether these functions are in fact

172   reduced or whether they are carried out by other soil taxa (*64*).

173

174   The predicted total biomass of the local earthworm community across the globe typically ranged

175   between 1 g and 150 g per m^2 (Figure 1d; mean: 380.86g; SD: 47684.3, see Supplementary

176   Materials and Methods for discussion in regards to extreme values). The areas of high

177   earthworm biomass were spread across the globe, but concentrated in the tropics (particularly
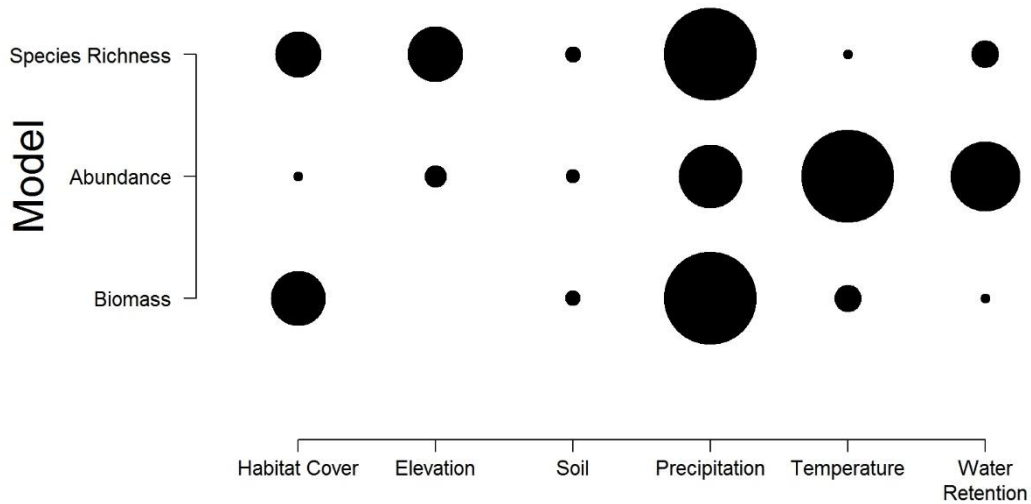
Figure 3: Based on RandomForest models, the importance of the six variable themes from the three biodiversity models. Each row shows the results of each model (top: species richness, middle: abundance, bottom: biomass). Each column represents a theme of variables that was present in the simplified biodiversity model. In the main plot area, the most important variable group has the largest circle. Within each row, the circle size of the other variable themes are scaled in size depending on the relative change in importance. Thus, the circle size should only be compared within a row. Variable theme importance, calculated from the node impurity, was the weighted average of all variables within each theme, following simplification.

178   Indonesia, parts of Coastal West Africa, Southern Central America, much of Colombia and

179   Western Venezuela), some regions of North America and the Eurasian Steppe. In some

180   regions this was almost the inverse of the abundance patterns (Figure 1c), thus these results

181   may relate to the fact that earthworms decrease in body size towards the poles (*65, 66*), unlike

182   other animals (e.g., birds and mammals *67*). This decrease in earthworm body size might be

183   due to smaller-bodied earthworms with greater dispersal capabilities recolonising northern

184   regions following deglaciation post-ice age (*50*). In northern North America, where there are no

185   native earthworms (*68, 69*), high density and, in some regions, high biomass of earthworms

186   likely reflects the earthworm invasion of these regions. The invasive smaller European

187   earthworm species likely encounter an enormous unused resource pool, which leads to

188   exceptionally high population sizes (*70*). In contrast, in Brazil, where we had a relatively higher

189   sampling density (Figure 1a), patterns of abundance and biomass corresponded with the

190   earthworm species that have been documented there. There are a number of giant earthworm

191   species (*71*) within Brazil (and other countries in the tropics, such as Indonesia, where a similar

192   pattern is shown). These giant earthworms normally occur at low densities and low species

193   richness (*72*), causing the patterns observed of high biomass but low abundance.

194

195   For all three of the community metric models (species richness, abundance, and biomass),

196   climatic variables were the most important drivers (the 'temperature' theme being the most

197   important for both species richness and total biomass models, and 'precipitation' theme for the

198   community abundance model; Figure 3). The importance of climatic variables is consistent with

199   many aboveground taxa (e.g., plants *31*, reptiles/amphibians/mammals *34*) and belowground

200   taxa (bacteria and fungi *5*, *41*, nematodes *55*, springtails *73*) when examined at large scales.

201   This suggests that climate related methods and data, which are typically used for the estimation

202   of aboveground biodiversity by macroecologists, may also be suitable for estimating earthworm

203   communities. However, the strong link between climatic variables and earthworm community

204   metrics is cause for concern, as climate has been and will continue to change due to

205   anthropogenic activities over the coming decades (*74*). Our findings further highlight that

206   changes in temperature and precipitation are likely to influence earthworm diversity (*75–77*)

207   and their distributions (*40*, *78*). The expansion or shifts in distributions may be particularly

208   problematic in the case of invasive earthworms, such as in North America (*68*, *79*). However, a

209   change in climate will most likely affect abundance and biomass of the earthworm communities

210   before diversity, as shifts in the latter depend upon dispersal capabilities, which are relatively

211   low in earthworms: 10m per year (*80*) compared to 600m per year for the average terrestrial

212   organism (*81*). This underscores the need to study earthworms in terms of multiple community

213   metrics in order to accurately assess responses of communities to climate change.

214

215   Habitat cover and soil properties still influenced the earthworm community (Supplementary

216   Figure 3 a and b) and in the case of habitat cover, especially the community structure in relation

217   to the three ecological groups (epigeic, endogeics and anecics, see Supplementary Material

218   and Methods and Supplementary Figure 4). Across larger scales, climate will influence both the

219   habitat cover and the soil properties, all of which will affect earthworm communities. Being able

220   to account for this indirect effect with appropriate methods and data may alter the perceived

221   importance of soil properties and habitat cover (e.g., with pathway analysis *33*). In addition, for

222   soil properties, the mismatch in scale between community metrics and soil properties taken from

223   global layers (for sites where sampled soil properties were missing; see supplementary methods

224   and materials) could also reduce the apparent importance of the theme.

225

226   By compiling a global dataset of earthworm communities we show, for the first time, the global

227   distribution of earthworm diversity, abundance and biomass, and identify key environmental

228   drivers responsible for these patterns. Our findings suggest that climate change might have

229   significant and serious effects on earthworm communities and the functions they provide.

230   Despite earthworm communities being driven by similar environmental drivers as aboveground

231   communities (*31*, *33*), this relationship results in different patterns of diversity. We highlight the

232   need to integrate belowground organisms into the global biodiversity paradigm to fully

233   understand global patterns of biodiversity. Our study creates an avenue for future research:

234   given that climate was the most important predictor of earthworm communities, it is possible for

235   ecologists who have previously focused on modelling aboveground diversity to use similar

236   methods belowground. By modelling both realms, aboveground/belowground comparisons are

237   possible, potentially allowing a clearer view of the biodiversity distribution of whole ecosystems.

238

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243

244   Author contributions:

245   Competing interests:

246   Data and materials availability:

247

References

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249   1.   L. Brussaard, Biodiversity and ecosystem functioning in soil. *Ambio A J. Hum. Environ.*
250   **26**, 563–570 (1997).
251   2.   J. Rusek, Biodiversity of Collembola and their functional role in the ecosystem. *Biodivers.*
252   *Conserv.* **7**, 1207–1219 (1998).
253   3.   N. Eisenhauer *et al.*, Priorities for research in soil ecology. *Pedobiologia.* **63**, 1–7 (2017).
254   4.   K. S. Ramirez *et al.*, Detecting macroecological patterns in bacterial communities across
255   independent studies of global soils. *Nat. Microbiol.* **3**, 189–196 (2018).
256   5.   L. Tedersoo *et al.*, Global diversity and geography of soil fungi. *Science.* **346**, 1256688–
257   1256688 (2014).
258   6.   M. Delgado-Baquerizo *et al.*, A global atlas of the dominant bacteria found in soil.
259   *Science.* **359**, 320–325 (2018).
260   7.   P. S. Giller, The diversity of soil communities, the poor man's tropical rainforest?
261   *Biodivers. Conserv.* **5**, 135–168 (1996).
262   8.   T. Bongers, H. Ferris, Nematode community structure as a bioindicator in environmental
263   monitoring. *Trends Ecol. Evol.* **14**, 224–228 (1999).
264   9.   T. Decaëns, J. J. Jiménez, C. Gioia, G. J. Measey, P. Lavelle, The values of soil animals
265   for conservation biology. *Eur. J. Soil Biol.* **42**, S23–S38 (2006).
266   10.   R. D. Bardgett, W. H. van der Putten, Belowground biodiversity and ecosystem
267   functioning. *Nat. 515.* **505**, 505–511 (2014).
268   11.   W. B. Whitman, D. C. Coleman, W. J. Wiebe, Prokaryotes: The unseen majority. *Proc.*
269   *Natl. Acad. Sci.* **95**, 6578–6583 (1998).
270   12.   D. H. Wall, U. N. Nielsen, J. Six, Perspective Soil biodiversity and human health. *Nature.*
271   **528**, 69–76 (2015).
272   13.   A. Orgiazzi *et al.*, *Global Soil Biodiversity Atlas* (2016).
273   14.   P. Lavelle *et al.*, in *Earthworm Ecology, Second Edition*, C. Edwards, Ed. (CRC Press,
274   2004).
275   15.   G. G. Brown, P. F. Hendrix, M. H. Beare, Influence of earthworms (Lumbricus rubellus)

276   on sorghum litter processing and nitrogen mineralisation in two Ultisols. *Acta Zool. Fenn.*
277   **196**, 55–59 (1995).

278 16.   J. Seeber, G. U. H. Seeber, R. Langel, S. Scheu, E. Meyer, The effect of macro-
279   invertebrates and plant litter of different quality on the release of N from litter to plant on
280   alpine pastureland. *Biol. Fertil. Soils.* **44**, 783–790 (2008).

281 17.   C. A. Edwards, *Earthworm ecology* (2004).

282 18.   M. Blouin *et al.*, A review of earthworm impact on soil function and ecosystem services.
283   *Eur. J. Soil Sci.* **64**, 161–182 (2013).

284 19.   P. Balvanera *et al.*, Quantifying the evidence for biodiversity effects on ecosystem
285   functioning and services. *Ecol. Lett.* **9**, 1146–1156 (2006).

286 20.   D. U. Hooper *et al.*, A global synthesis reveals biodiversity loss as a major driver of
287   ecosystem change. *Nature.* **486**, 105–108 (2012).

288 21.   D. Tilman, F. Isbell, J. M. Cowles, Biodiversity and Ecosystem Functioning. *Annu. Rev.*
289   *Ecol. Evol. Syst.* **45**, 471–493 (2014).

290 22.   J. W. van Groenigen *et al.*, Earthworms increase plant production: a meta-analysis. *Sci.*
291   *Rep.* **4**, 6365 (2014).

292 23.   C. Sheehan, L. Kirwan, J. Connolly, T. Bolger, The effects of earthworm functional group
293   diversity on nitrogen dynamics in soils. *Soil Biol. Biochem.* **38**, 2629–2636 (2006).

294 24.   D. Craven *et al.*, The unseen invaders: introduced earthworms as drivers of change in
295   plant communities in North American forests (a meta-analysis). *Glob. Chang. Biol.* **23**,
296   1065–1074 (2017).

297 25.   F. Schwarzmüller, N. Eisenhauer, U. Brose, "Trophic whales" as biotic buffers: Weak
298   interactions stabilize ecosystems against nutrient enrichment. *J. Anim. Ecol.* **84**, 680–691
299   (2015).

300 26.   O. Ferlian *et al.*, Invasive earthworms erode soil biodiversity: A meta-analysis. *J. Anim.*
301   *Ecol.* **87**, 162–172 (2018).

302 27.   I. M. Lubbers *et al.*, Greenhouse-gas emissions from soils increased by earthworms. *Nat.*
303   *Clim. Chang.* **3** (2013), pp. 187–194.

304 28.   H. Hillebrand, On the Generality of the Latitudinal Diversity Gradient. *Am. Nat.* **163**, 192–
305   211 (2004).

306 29.   M. L. Rosenzweig, *Species diversity in space and time* (Cambridge University Press,
307   1995).

308 30.   J. J. Lennon, J. J. D. Greenwood, J. R. G. Turner, Bird diversity and environmental
309   gradients in Britain: a test of the species-energy hypothesis. *J. Anim. Ecol.* **69**, 581–598
310   (2000).

311 31.   H. Kreft, W. Jetz, Global patterns and determinants of vascular plant diversity. *Proc. Natl.*
312   *Acad. Sci.* **104**, 5925–5930 (2007).

313 32.   J. R. G. Turner, C. M. Gatehouse, C. A. Corey, Does Solar Energy Control Organic
314   Diversity? Butterflies, Moths and the British Climate. *Oikos.* **48**, 195 (1987).

315 33.   A. Rice *et al.*, The global biogeography of polyploid plants. *Nat. Ecol. Evol.* **3**, 265–273
316   (2019).

317 34.   L. Santini *et al.*, Global drivers of population density in terrestrial vertebrates. *Glob. Ecol.*
318   *Biogeogr.* **27**, 968–979 (2018).

319 35.   D. J. Currie, J. T. Fritz, Global Patterns of Animal Abundance and Species Energy Use.
320   *Oikos.* **67**, 56–68 (1993).

321 36.   D. J. Currie, V. Paquin, Large-scale biogeographical patterns of species richness of trees.
322   *Nature.* **329**, 326–327 (1987).

323 37.   H. M. Serna-Chavez, N. Fierer, P. M. Van Bodegom, Global drivers and patterns of
324   microbial abundance in soil. *Glob. Ecol. Biogeogr.* **22**, 1162–1172 (2013).

325 38.   K. Ekschmitt, T. Stierhof, J. Dauber, K. Kreimes, V. Wolters, On the quality of soil
326   biodiversity indicators: abiotic and biotic parameters as predictors of soil faunal richness

327   at different spatial scales. *Agric. Ecosyst. Environ.* **98**, 273–283 (2003).

328 39. J. Davison *et al.*, Global assessment of arbuscular mycorrhizal fungus diversity reveals
329   very low endemism. *Science.* **127**, 970–973 (2015).

330 40. M. Rutgers *et al.*, Mapping earthworm communities in Europe. *Appl. Soil Ecol.* **97**, 98–
331   111 (2016).

332 41. M. Bahram *et al.*, Structure and function of the global topsoil microbiome. *Nature.* **560**,
333   233–237 (2018).

334 42. G. B. De Deyn, W. H. van der Putten, Linking aboveground and belowground diversity.
335   *Trends Ecol. Evol.* **20** (2005), pp. 625–633.

336 43. N. Fierer, M. S. Strickland, D. Liptzin, M. A. Bradford, C. C. Cleveland, Global patterns in
337   belowground communities. *Ecol. Lett.* **12** (2009), pp. 1238–1249.

338 44. R. R. Dunn *et al.*, Climatic drivers of hemispheric asymmetry in global patterns of ant
339   species richness. *Ecol. Lett.* **12**, 324–333 (2009).

340 45. J. Pietikäinen, M. Pettersson, E. Bååth, Comparison of temperature effects on soil
341   respiration and bacterial and fungal growth rates. *FEMS Microbiol. Ecol.* **52**, 49–58
342   (2005).

343 46. J. P. Curry, in *Earthworm Ecology* (2004), pp. 91–113.

344 47. P. F. Hendrix, P. J. Bohlen, Exotic Earthworm Invasions in North America: Ecological and
345   Policy Implications. *Bioscience.* **52**, 801–811 (2002).

346 48. T. G. Piearce, The Calcium Relations of Selected Lumbricidae. *J. Anim. Ecol.* **41**, 167
347   (1972).

348 49. D. J. Spurgeon, A. M. Keith, O. Schmidt, D. R. Lammertsma, J. H. Faber, Land-use and
349   land-management change: relationships with earthworm and fungi communities and soil
350   structural properties. *BMC Ecol.* **13**, 46 (2013).

351 50. J. Mathieu, T. J. Davies, Glaciation as an historical filter of below-ground biodiversity. *J.*
352   *Biogeogr.* **41**, 1204–1214 (2014).

353 51. E. K. Cameron *et al.*, Global mismatches in aboveground and belowground biodiversity.
354   *Conserv. Biol.*, 430 (2019).

355 52. J. W. Reynolds, Earthworms of the world. *Glob. Biodivers.* **4**, 11–16 (1994).

356 53. K. J. Gaston, T. M. Blackburn, *Pattern and process in macroecology* (2007).

357 54. B. Boag, G. W. Yeates, Soil nematode biodiversity in terrestrial ecosystems. *Biodivers.*
358   *Conserv.* **7**, 617–630 (1998).

359 55. D. Song *et al.*, Large-scale patterns of distribution and diversity of terrestrial nematodes.
360   *Appl. Soil Ecol.* **114**, 161–169 (2017).

361 56. M. Maraun, H. Schatz, S. Scheu, Awesome or ordinary? Global diversity patterns of
362   oribatid mites. *Ecography.* **30**, 209–216 (2007).

363 57. T. Decaëns, Macroecological patterns in soil communities. *Glob. Ecol. Biogeogr.* **19**
364   (2010), pp. 287–302.

365 58. A. Shade *et al.*, Macroecology to Unite All Life, Large and Small. *Trends Ecol. Evol.* **33**,
366   731–744 (2018).

367 59. P. Lavelle, E. Lapied, Endangered earthworms of Amazonia: an homage to Gilberto
368   Righi. *Pedobiologia.* **47**, 419–427 (2003).

369 60. T. Decaëns *et al.*, DNA barcoding reveals diversity patterns of earthworm communities in
370   remote tropical forests of French Guiana. *Soil Biol. Biochem.* **92**, 171–183 (2016).

371 61. J. W. Spaak *et al.*, Shifts of community composition and population density substantially
372   affect ecosystem function despite invariant richness. *Ecol. Lett.* **20**, 1315–1324 (2017).

373 62. R. Winfree, J. W Fox, N. M. Williams, J. R. Reilly, D. P. Cariveau, Abundance of common
374   species, not species richness, drives delivery of a real-world ecosystem service. *Ecol.*
375   *Lett.* **18**, 626–635 (2015).

376 63. K. J. Gaston, R. Fuller, Commonness, population depletion and conservation biology.
377   *Trends Ecol. Evol.* **23**, 14–19 (2008).

378   64.   M. Zimmer, G. Kautz, W. Topp, Do woodlice and earthworms interact synergistically in
379   leaf litter decomposition? *Funct. Ecol.* **19**, 7–16 (2005).
380   65.   D. C. Coleman, D. A. Crossley, P. F. Hendrix, in *Fundamentals of Soil Ecology* (Elsevier,
381   2004), pp. 271–298.
382   66.   L. E. Frelich *et al.*, Trophic cascades, invasive species and body-size hierarchies
383   interactively modulate climate change responses of ecotonal temperate-boreal forest.
384   *Philos. Trans. R. Soc. B Biol. Sci.* **367**, 2955–2961 (2012).
385   67.   S. Meiri, T. Dayan, On the validity of Bergmann's rule. *J. Biogeogr.* **30**, 331–351 (2003).
386   68.   L. E. Frelich *et al.*, Earthworm invasion into previously earthworm-free temperate and
387   boreal forests. *Biol. Invasions.* **8**, 1235–1245 (2006).
388   69.   P. J. Bohlen *et al.*, Non-Native Invasive Earthworms as Agents of Change in Northern
389   Temperate Forests. *Front. Ecol. Environ.* **2**, 427 (2004).
390   70.   N. Eisenhauer, J. Schlaghamerský, P. B. Reich, L. E. Frelich, The wave towards a new
391   steady state: Effects of earthworm invasion on soil microbial functions. *Biol. Invasions.*
392   **13**, 2191–2196 (2011).
393   71.   G. G. Brown, S. W. James, Earthworm biodiversity in São Paulo state, Brazil. *Eur. J. Soil
394   Biol.* **42**, S145–S149 (2006).
395   72.   M. Drumond *et al.*, Life history, distribution and abundance of the giant earthworm
396   Rhinodrilus alatus RIGHI 1971: conservation and management implications. *Brazilian J.
397   Biol.* **73**, 699–708 (2013).
398   73.   W. Ulrich, C. Fiera, Original article Environmental correlates of species richness of
399   European springtails (Hexapoda : Collembola). *Acta Oecologica.* **35**, 45–52 (2009).
400   74.   Intergovernmental Panel on Climate Change, "Climate Change 2014 Synthesis Report
401   Summary Chapter for Policymakers" (2014), , doi:10.1017/CBO9781107415324.
402   75.   L. A. Wever, T. J. Lysyk, M. J. Clapperton, The influence of soil moisture and temperature
403   on the survival, aestivation, growth and development of juvenile Aporrectodea tuberculata
404   (Eisen) (Lumbricidae). *Pedobiologia.* **45**, 121–133 (2001).
405   76.   J. M. Perreault, J. K. Whalen, Earthworm burrowing in laboratory microcosms as
406   influenced by soil temperature and moisture. *Pedobiologia.* **50**, 397–403 (2006).
407   77.   D. K. Hackenberger, B. K. Hackenberger, European Journal of Soil Biology Earthworm
408   community structure in grassland habitats differentiated by climate type during two
409   consecutive seasons. *Eur. J. Soil Biol.* **61**, 27–34 (2014).
410   78.   P. Eggleton, K. Inward, J. Smith, D. T. Jones, E. Sherlock, A six year study of earthworm
411   (Lumbricidae) populations in pasture woodland in southern England shows their
412   responses to soil temperature and soil moisture. *Soil Biol. Biochem.* **41**, 1857–1865
413   (2009).
414   79.   H. G. Greiner, D. R. Kashian, S. D. Tiegs, Impacts of invasive Asian (Amynthas
415   hilgendorfi) and European (Lumbricus rubellus) earthworms in a North American
416   temperate deciduous forest. *Biol. Invasions.* **14**, 2017–2027 (2012).
417   80.   J. C. Y. Marinissen, F. van den Bosch, Colonization of new habitats by earthworms.
418   *Oecologia.* **91**, 371–376 (1992).
419   81.   C. Parmesan, G. Yohe, A globally coherent fingerprint of climate change impacts across
420   natural systems. *Nature.* **421**, 37–42 (2003).
421
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Supplementary Materials

424   Materials and methods

425   Table S1 – S3

426   Figures S1 - S4

427   References (X – X)