

scientific data

OPEN
DATA DESCRIPTOR



Global data on earthworm abundance, biomass, diversity and corresponding environmental properties

Helen R. P. Phillips *et al.*[#]

Earthworms are an important soil taxon as ecosystem engineers, providing a variety of crucial ecosystem functions and services. Little is known about their diversity and distribution at large spatial scales, despite the availability of considerable amounts of local-scale data. Earthworm diversity data, obtained from the primary literature or provided directly by authors, were collated with information on site locations, including coordinates, habitat cover, and soil properties. Datasets were required, at a minimum, to include abundance or biomass of earthworms at a site. Where possible, site-level species lists were included, as well as the abundance and biomass of individual species and ecological groups. This global dataset contains 10,840 sites, with 184 species, from 60 countries and all continents except Antarctica. The data were obtained from 182 published articles, published between 1973 and 2017, and 17 unpublished datasets. Amalgamating data into a single global database will assist researchers in investigating and answering a wide variety of pressing questions, for example, jointly assessing aboveground and belowground biodiversity distributions and drivers of biodiversity change.

Background & Summary

Soils are considered to be one of the most biodiverse terrestrial habitats^{1–3}. Despite this, very little is known about the biodiversity that resides there compared to aboveground biodiversity, especially at the global scale^{1,4,5}. This is surprising given the large number of local-scale biodiversity datasets available in the published literature. A number of studies have amalgamated local scale datasets, primarily for aboveground or marine organisms e.g.^{6,7}, which can then be used for large-scale analyses e.g.^{8,9}. Belowground biodiversity data are often overlooked in these large biodiversity databases⁴, and thus separate efforts to collate data are just now starting to emerge for certain belowground taxa, particularly microbes e.g.^{10,11}.

Earthworms are involved in a large number of ecosystem functions and services, such as decomposition¹², nutrient cycling¹³ and climate regulation¹⁴, amongst others¹³. In addition, they are often used as bioindicators of soil biodiversity and health¹⁵. Earthworms are relatively easy to sample; thus, a large amount of data are available¹⁶. Nevertheless, previous attempts to collate earthworm datasets have been geographically restricted^{17,18} or focused on country or regional species lists (e.g., DriloBASE; <http://taxo.drilobase.org>). By collating site-level diversity measures, we can also collect information on factors that might determine community composition, for example, measurements of soil properties or land use and cover.

Here, we describe a global database of local earthworm diversity and associated site-level characteristics from 10,840 sites in 60 countries (Fig. 1)¹⁹. Site-level information includes at least one sampled soil property, land use, and habitat cover for just over 58% of sites. Measurements of earthworm species richness (including species lists where available), total abundance, and biomass were collected at the site-level, and for some species occurrences i.e., abundance and biomass of the species recorded at a site. In addition, using expert opinion and details given by data providers, we classified each earthworm species into ecological groups based on their feeding and burrowing behaviours (epigeics, endogeics, anecics, epi-endogeics; more details below²⁰).

[#]A full list of authors and their affiliations appears at the end of the paper.

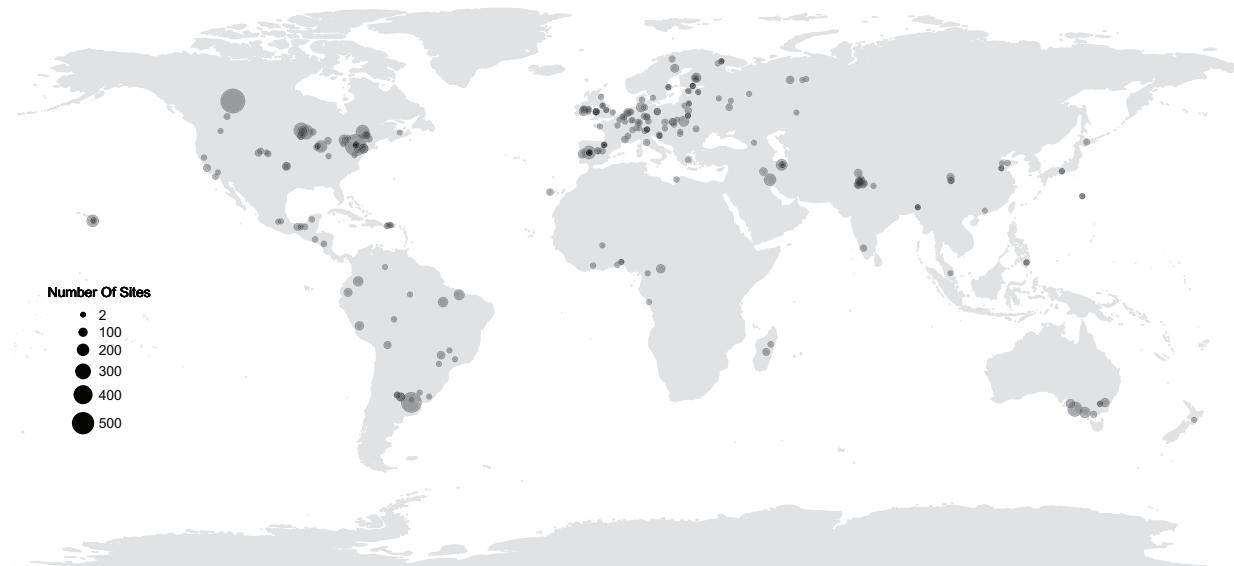


Fig. 1 Locations of the 276 studies included in the database. Each circle represents the centre of a study (a collection of sites where earthworms were sampled with a consistent method). The size of the circle indicates the number of sites within the study. Transparency is used only for aiding visualisation.

The compilation of this dataset is timely. It can be used to answer long-standing questions in ecology in relation to this important belowground faunal group (e.g., global diversity patterns¹⁶). And in light of the IPBES Global Assessment²¹ and the loss of biodiversity, the dataset has the potential to be used to address the pressing issue of the consequences of environmental change on soil biodiversity. These data are suitable for linking with other soil databases, such as BETSI (<http://betsi.cesab.org/>), a database of soil organism traits²². Linking trait information with site-level diversity would then allow analyses of functional diversity. In addition, as nearly all sites have geographic coordinates, other environmental data layers (e.g., related to climate variables, land use or soil abiotic factors) could be linked to the site-level diversity measures (e.g.¹⁶). Belowground diversity measures could also be linked to similar diversity measurements aboveground, thus enabling investigations across ecosystems to identify patterns of diversity and biodiversity changes²³.

Methods

This work was conceptualised and discussed during two ‘sWorm’ workshops in 2016 and 2017, funded by sDiv, the synthesis centre of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig. More than 20 international scientists with expertise in earthworms, soil science, and/or data management met at each of the workshops.

On 18th December 2016, Web of Science was used to search the available literature for articles that had sampled the earthworm community. Keywords were used that captured measurements of diversity of all taxa within Oligochaetes: ((Earthworm* OR Oligochaeta OR Megadril* OR Haplotaxida OR Annelid* OR Lumbric* OR Clitellat* OR Acanthodril* OR Ailoscoleci* OR Almid* OR Benhamiin* OR riodriliid* OR Diplocard* OR Enchytraeid* OR Eudrilid* OR Exxid* OR Glossoscolecid* OR Haplotaxid* OR Hormogastrid* OR Kynotid* OR Lutodrilid* OR Megascolecid* OR Microchaetid* OR Moniligastrid* OR Ocnerodrilid* OR Octochaet* OR Sparganophilid* OR Tumakid*) AND (Diversity OR “Species richness” OR “OTU” OR Abundance OR individual* OR Density OR “tax* richness” OR “Number” OR Richness OR Biomass))

This search returned 7,783 papers. All titles and abstracts of papers post-2000 were screened (6140 papers), and were excluded if they did not make reference to data suitable for the analysis. As it was most likely that raw data would need to be requested, papers in the literature search published before 2000 were not screened and excluded, as it was unlikely that available author contact details were up-to-date. After this initial screening, PDFs of all remaining papers ($n = 986$) were manually screened to determine whether data were suitable (see below). 477 papers made reference to data that was suitable.

In addition, to find unpublished data or to target underrepresented regions, inquiries were made to specific earthworm researchers regarding suitable datasets (e.g., by directly contacting researchers, giving presentations at the Second Global Soil Biodiversity Conference and the International Symposium of Earthworm Ecology). No date restrictions were placed on such datasets, and thus, some were published prior to 2000.

In order to be included in the database, the individual article was required to have sampled earthworm diversity using an appropriate quantitative methodology (such as hand-sorting of a soil quadrat e.g.²⁴, or chemical expulsion e.g.²⁵) at two or more sites that varied in their land-use/habitat cover or soil properties. At a minimum, we required data on the total abundance or fresh biomass of earthworms at each site, and if possible, the number of species (ideally with species binomials), and the abundance and biomass of each species. In addition, geographic coordinates of the sites were required, and at each site, data collectors ideally had sampled at least one of the following soil properties: soil pH (in H₂O, KCl, CaCl₂), soil organic carbon (%), soil organic matter (%), sand/

silt/clay content (%), soil texture (USDA classification²⁶), Cation Exchange Capacity (CEC), Base Saturation (%), Carbon:Nitrogen ratio, soil moisture (%), and soil type (WRB/FAO classification²⁷).

Where possible, available data were extracted from the suitable articles. For each suitable article, the meta-data (e.g., the article title and DOI) was compiled (Online-only Table 1). Data were extracted from the article text, tables, figures, or supplementary material (e.g., using ImageJ²⁸). Where data were not given but were required (Online-only Table 2), authors of the articles were contacted and the raw data (or missing information) were requested. If the authors did not respond, and the required information could not be obtained using an alternate method, the data were not entered into the database. All data were extracted into online data templates, with data from one article (i.e., a dataset) being entered into an individual template, referred to as a ‘file’. Each file was given a unique ID, and in total 199 files were created and made open-access.

A file could contain multiple ‘studies’, where each study was either a different sampling event i.e., multiple samples taken at the same site over time, and/or different sampling methodology. Each study was assigned a unique study ID. Sampled diversity of earthworms is highly dependent on the extraction method used²⁹. If a dataset did not contain consistent sampling methodologies across all sites (i.e., some sites sampled with hand sorting and others hand sorting + chemical extraction), thus making it inappropriate to compare earthworm communities, the dataset was split into a separate study for each consistent methodology. If sites had been sampled multiple times, either across multiple years or within years, and the data were available for each sampling period, then only data from the first and the last sampling period were used. Each sampling period was entered as a study, which can help prevent temporal autocorrelation during analysis, e.g., when using a mixed-effects modelling approach.

A site was defined as a single location where the earthworm community was sampled using an appropriate quantitative methodology. Within each study, each site was given a unique ID (usually based on an ID given in the original source). For each site, information on the sampling methodology, soil properties, and land-use/habitat cover, along with the diversity measurements (site-level species richness, abundance and/or biomass) were entered into the data template (see Online-only Table 2 for full list of variables and the format that was required for the data template). Where possible, data were entered into the data template in the same format as given in the original source. To help enable this, columns often had separate fields to record the units. However, for some fields, values needed to be standardised prior to data entry, such as for the site coordinates and some soil properties (e.g., sand/silt/clay content).

All available and required soil properties for each site were entered into the template. Where a site had soil properties sampled at different depths (e.g., at 0–15, 15–30, and 30–40 cm), the weighted average of the values was entered into the templates. The value was then indicated as being a mean (Online-only Table 2).

The fields for habitat cover, land-use, and management system were predefined categories based on ESA CCI-LC (<https://www.esa-landcover-cci.org/>), the Land-use Harmonization dataset^{30,31} (Fig. 2), and expert opinion (during the sWorm workshops), respectively. These classification systems were chosen based on knowledge of what external pressures might be important for explaining earthworm communities, whilst also ensuring consistency across all regions of the globe. Based on information given within the published article, or from the data providers directly, every site was classified into one of the categories for each of these fields. When information was missing, sites were classified as “unknown”. Additional information on the land use and management system classification definitions shown in Tables 1 and 2, respectively.

As sampling effort also impacts diversity measurements³², the sampling effort at each site was recorded. Effort was recorded in two ways:

1. The area that was sampled, e.g., of a quadrat or soil block, or the area across all e.g., quadrats. This depended on how the data were presented.
2. The number of times a site was sampled, either temporally or spatially. If a site was sampled over multiple time periods, it would be the number of occasions the site was sampled. If the site had multiple samples (e.g., multiple quadrats) and the diversity measure is an average, the sampling effort would be 1. If the diversity is a total measure (e.g., the total number of species across all quadrats) the sampling effort would be the total number of e.g., quadrats.

When datasets contained information at a higher resolution than total abundance or biomass of earthworms at a site (i.e., at ecological group, genus, or species level), this information was entered into the species occurrence table (Online-only Table 3). Each row contained a measurement of an observation (e.g. species, morphospecies, genus, life stage or ecological group) at a single site. The measurement could be the presence only, abundance, or fresh biomass of the record. Where possible, for each row we also included the life stage (adult or juvenile), whether the species was native to the location or not, and the ecological group (epigeic, endogeic, anecic, epi-endogeic). Thus, if the diversity measure was for all the juveniles at the site regardless of species, columns such as the species binomial and genus would be empty, but life stage completed. Every species binomials and ecological group assignment were checked using DrilobASE and by earthworm taxonomists (GB, MJIB, MLCB, PL), see ‘Technical Validation’.

Where site-level diversity measures were given by the data provider, these were entered into the site-level sheet. Where site-level diversity measures were not given, but could be calculated from the species occurrence information, that was done in R³³, following data entry and prior to subsequent analyses. The species present at each site, as given in the species occurrence data, were used for calculating species richness, this included species identified as sub-species. If data collectors identified a specimen as a morphospecies (i.e., a species delineation based solely on morphological characteristics, typically identified to genus level with a unique ID differentiating from other species of the same genus, as determined by the original data collector), it was included in the species richness estimate as an additional species. Unidentified species grouped as ‘unknown’ were excluded (Fig. 3). As

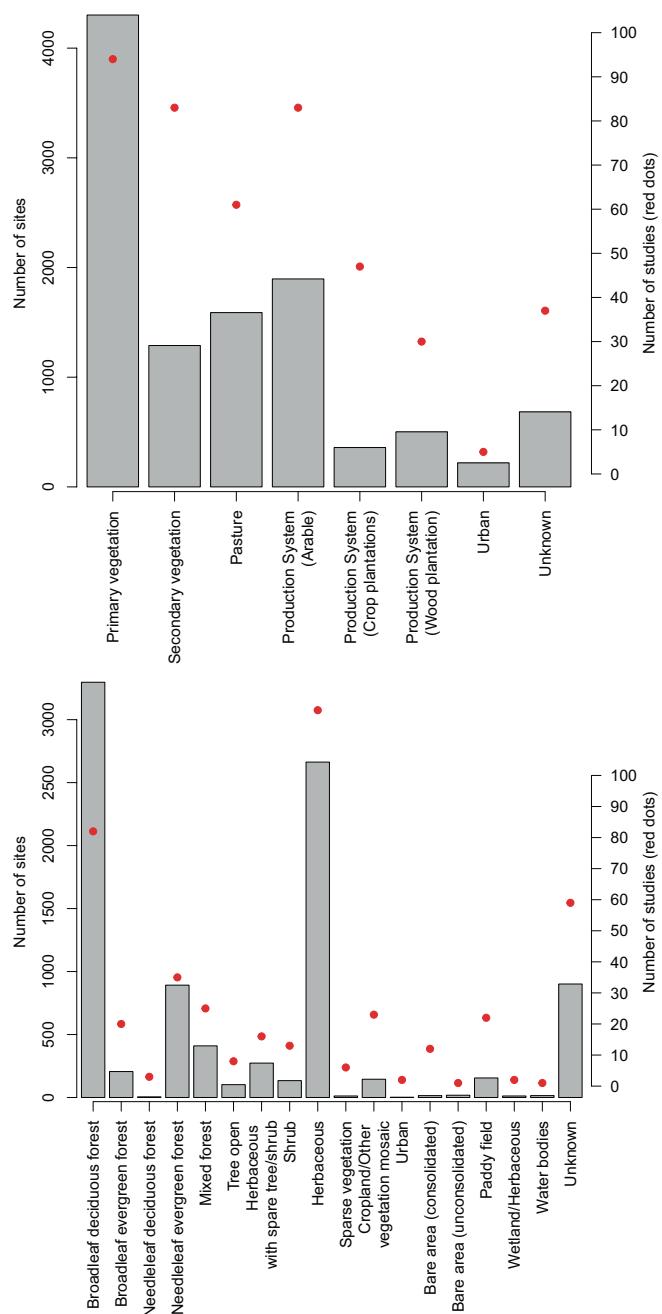


Fig. 2 The number of sites (grey bars) and the number of studies (red dots) for each category in (a) the land-use system, and (b) the habitat-cover system. Sites could only be categorised within one category, but studies do contain sites that span multiple categories.

juveniles of many earthworm species are hard to identify to species level^{29,34}, juveniles were excluded from the calculation (even identified at family level). All earthworms (including juveniles) found at a site were included in the total biomass and abundance calculations.

After the ecological grouping (epigaeic, endogeic, anecic, and epi-endogeic) of each species had been assigned and/or checked by the earthworm taxonomists, diversity measures within each ecological group at a site were also calculated. As with the site-level metrics, the species richness within each ecological group was calculated using only species with binomials or morphospecies. Biomass and abundance of each ecological group at a site was calculated regardless of species identity. The total number of the ecological groups at each site was calculated regardless of abundance, biomass, life stage or native status of the species included (maximum ecological group richness = 4).

Data Records

The data presented here are available in the iDiv data portal (<https://doi.org/10.25829/ivid.1880-17-3189>. Dataset ID: 1880)¹⁹ in a static form. In addition, the full dataset will be hosted by Edaphobase (www.portal.edaphobase). In the future, the version in Edaphobase might change (i.e., with species names revisions, or requests from the data providers) and will hopefully be added to with additional earthworm records (or other soil taxa).

Land use category	Definition
Primary	Relatively undisturbed natural habitat
Secondary	Recovering, previously disturbed natural habitat
Pasture	Land used for the grazing of livestock
Production - Arable	Land used for crop production (e.g., wheat, rice, corn)
Production - Plantations crops	Land used for plantations crops (e.g., coffee, vineyards, oil palm)
Production – Wood plantations	Land used for timber production (e.g., teak)
Urban	Land converted to dense urban settlement
Unknown	If the land use is not given or is not clear

Table 1. Definitions for the land use category. The land use classification was based on the Land-use Harmonization dataset^{30,31}, to map to the original classification system, ‘Production – Wood plantations’ and ‘Production – Plantation crops’ would be ‘Secondary’ and ‘Production – Arable’ would be ‘Cropland’.

Management Intensity measure	Annual crops	Integrated systems	Perennial crops	Pastures (grazed lands)	Tree plantations
Tillage	×	×			
Pesticide	×	×	×	×	×
Fertilizer	×	×	×	×	×
Selectively harvested			×		×
Clear cut			×		×
Fire	×	×	×	×	×
Stocking rate				×	
Grazing all-year				×	
Rotation	×	×		×	
Monoculture	×	×	×	×	×
Planted				×	

Table 2. A management classification system was created during the sWorm workshops. For each managed site (i.e., not natural vegetation) the management system could also be identified (table headers), and additional management intensity variables could be also captured (table rows). However, not every management intensity variable was applicable for each management system, thus restrictions were placed. ‘×’ indicates which management intensity variable was applicable to each management system.

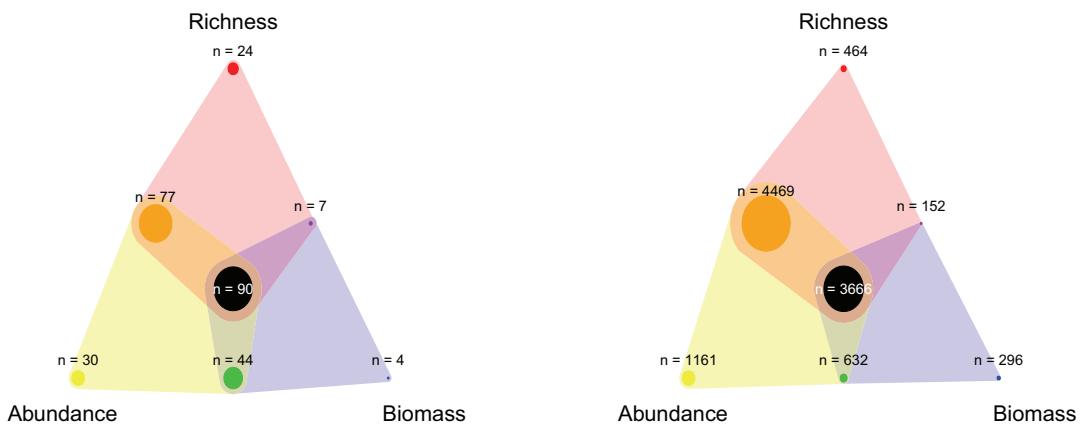


Fig. 3 The number of (a) studies and (b) sites that measured each of the three community metrics. The points at the vertices indicate the number of studies or sites with only one community metric. The points on the edges indicates the number of studies or sites with the community metrics represented at the connecting two vertices. Finally, the point in the centre indicates the number of studies or sites with all three community metrics. For example, in (a), 145 studies measured biomass, shown in the blue polygon. 4 studies measured only biomass, 7 measured biomass and species richness, 44 measured biomass and abundance, and 90 measured all three metrics.

The data is stored in three tables; meta-data (Online-only Table 1), site-level (Online-only Table 2), and species occurrence (Online-only Table 3). The file ID links the meta-data to the site-level data, and the Study ID and the Site ID, link the site-level data to the species occurrence table.

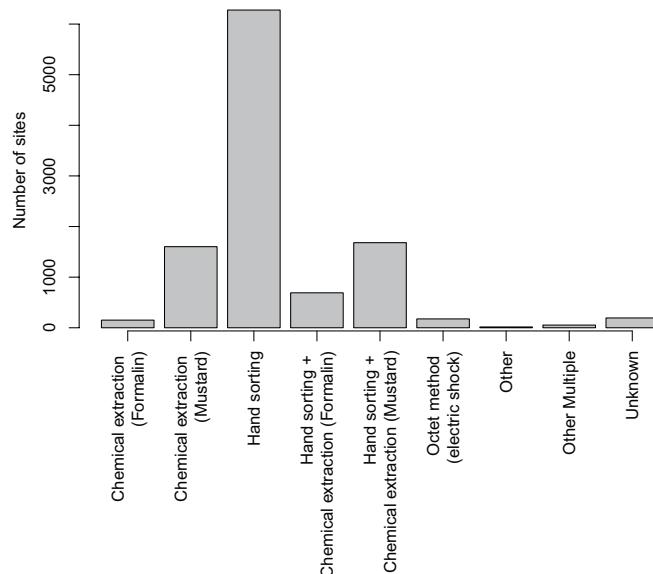


Fig. 4 The number of sites sampled with each sampling method across the different earthworm studies.

For all suitable datasets, the meta-data information was completed. The meta-data contains bibliographic information on the original paper which analysed, or published, the data, as well as contact information of the person who provided the raw data (not included in the release of the database for privacy reasons). The meta-data also included the number of sites and studies within the file, so that validation checks could be completed. Online-only Table 1 shows all fields within the meta-data, personal information of data providers has not been made available.

Information on all sampled sites within each dataset was recorded in the site-level table (Online-only Table 2). Each row represents a single site within a study, with information on the sampling methodology, soil properties, and how the land was used, managed, and covered. The site-level earthworm community metrics (species richness, abundance and biomass) are also included if available.

Site-level species lists, or abundance, and/or biomass measures for individual records are given in the species occurrence table (Online-only Table 1). Each row is a measurement of an observation at a site (22,690 non-zero observations in total). An observation could relate to a species (with a scientific binomial, e.g., the abundance of *Lumbricus terrestris* at a site, or a morphospecies identification), a genus, life stage, ecological group, or native/non-native group (e.g., the abundance of all non-native species at a site). Details of native/non-native status of a species was only available when provided by the original data collector.

Technical Validation

Templates used to enter the individual datasets were designed so that fields were only allowed certain values and formats where possible. This helped to reduce spelling errors, slight inconsistencies, and incorrect values being entered. Data providers were contacted if details within their raw data were unclear. As multiple people entered data into the templates, detailed documentation was created at the start of the project to ensure consistency amongst those involved. In addition, a subset of datasets was checked by several curators.

All earthworm species names were checked against DrilоБASE (<http://taxo.drilobase.org>) to identify potential synonyms and spelling mistakes. Following that, earthworm specialists and taxonomists (GB, MJIB, MLCB and PL) checked the scientific names, removed synonyms and updated names if taxonomies had changed. Where ecological groupings were missing, the earthworm taxonomists also added them where possible, based on the available literature.

Usage Notes

Land-use fields were based on classification schemes, and may not be the most suitable for the analysis of earthworms. We included a free-text field (“Habitat as described”) that could be used by future researchers to define their own classification scheme for land-use or habitat cover.

As diversity measures are highly influenced by sampling methodology, we included information on sampling methods in the database (Fig. 4). In addition, we would expect that variation in diversity would differ between the individual datasets due to, for example, inter-observer variability. We highly recommend that statistical methods used on this database take these between-dataset variations into account.

Despite our efforts to obtain a global dataset, there is a geographic bias (Fig. 1), such that sites are highly clustered in certain regions (e.g., Europe), sparse in others (e.g., South America), or lacking (e.g., southern Africa, northern Russia). To reduce such biases, we attempted to contact as many researchers as possible in such areas to acquire data. Although this helped to improve the data coverage, it did not remove the gaps. We hope to address these gaps in the future, but in the meantime, researchers should be aware of the influence these biases might have on their analyses^{35,36}.

Code availability

All code used to format and clean the dataset for publication is available on GitHub (www.github.com/helenphillips).

Received: 14 August 2020; Accepted: 1 April 2021;

Published online: 21 May 2021

References

1. Giller, P. S. The diversity of soil communities, the poor man's tropical rainforest? *Biodivers. Conserv.* **5**, 135–168 (1996).
2. Decaëns, T., Jiménez, J. J., Gioia, C., Measey, G. J. & Lavelle, P. The values of soil animals for conservation biology. *Eur. J. Soil Biol.* **42**, S23–S38 (2006).
3. Bardgett, R. D. & van der Putten, W. H. Belowground biodiversity and ecosystem functioning. *Nat.* **515** 505, 505–511 (2014).
4. Phillips, H. R. P. *et al.* Red list of a black box. *Nat. Ecol. Evol.* **1**, 0103 (2017).
5. Orgiazzi, A. *et al.* *Global Soil Biodiversity Atlas*. European Commission, Publications (2016).
6. Dornelas, M. *et al.* BioTIME: A database of biodiversity time series for the Anthropocene. *Glob. Ecol. Biogeogr.* **27**, 760–786 (2018).
7. Hudson, L. N. *et al.* The database of the PREDICTS (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems) project. *Ecol. Evol.* **7**, 145–188 (2017).
8. Dornelas, M. *et al.* Assemblage time series reveal biodiversity change but not systematic loss. *Science* **344**, 296–299 (2014).
9. Newbold, T. *et al.* Global effects of land use on local terrestrial biodiversity. *Nature* **520**, 45–50 (2015).
10. Ramirez, K. S. *et al.* Detecting macroecological patterns in bacterial communities across independent studies of global soils. *Nat. Microbiol.* **3**, 189–196 (2018).
11. Delgado-Baquerizo, M. *et al.* A global atlas of the dominant bacteria found in soil. *Science* **359**, 320–325 (2018).
12. Milcu, A., Partsch, S., Scherber, C., Weisser, W. W. & Scheu, S. Earthworms and legumes control litter decomposition in a plant diversity gradient. *Ecology* **89**, 1872–1882 (2008).
13. Blouin, M. *et al.* A review of earthworm impact on soil function and ecosystem services. *Eur. J. Soil Sci.* **64**, 161–182 (2013).
14. Zhang, W. *et al.* Earthworms facilitate carbon sequestration through unequal amplification of carbon stabilization compared with mineralization. *Nat. Commun.* **4**, 2576 (2013).
15. Paoletti, M. G. The role of earthworms for assessment of sustainability and as bioindicators. *Agric. Ecosyst. Environ.* **74**, 137–155 (1999).
16. Phillips, H. R. P. *et al.* Global distribution of earthworm diversity. *Science* **366**, 480–485 (2019).
17. Rutgers, M. *et al.* Mapping earthworm communities in Europe. *Appl. Soil Ecol.* **97**, 98–111 (2016).
18. Burkhardt, U. *et al.* The Edaphobase project of GBIF-Germany-A new online soil-zoological data warehouse. *Appl. Soil Ecol.* **83**, 3–12 (2014).
19. Phillips, H. R. P. *et al.* *Global data on earthworm abundance, biomass, diversity and corresponding environmental properties. (iDiv Data Repository)* German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig <https://doi.org/10.25829/ivid.1880-17-3189> (2020).
20. Bouché, M. B. Strategies lombriennes. *Ecol. Bull.* 122–132 (1977).
21. IPBES. Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. 56 (2019).
22. Pey, B. *et al.* Current use of and future needs for soil invertebrate functional traits in community ecology. *Basic Appl. Ecol.* **15**, 194–206 (2014).
23. Cameron, E. K. *et al.* Global mismatches in aboveground and belowground biodiversity. *Conserv. Biol.* **430** (2019).
24. Anderson, J. M. & Ingram, J. S. I. Tropical Soil Biology and Fertility: A handbook of methods. *Trop. Soil Biol. Fertil. A Handb. methods* 2 Ed., 88–91 (1993).
25. ISO. *Soil quality – Sampling of soil invertebrates – Part 1: Hand-sorting and extraction of earthworms (ISO/FDIS 23611-1:2012)*. (2012).
26. USDA. Soil Survey Manual Agriculture. Handbook 18. USDA, Nat. Resour. Conserv. Serv. (2017).
27. FAO/WRB. *World reference base for soil resources 2014. World Soil Resources Reports No. 106* (2014).
28. Schindelin, J. *et al.* Fiji: an open-source platform for biological-image analysis. *Nat. Methods* **9**, 676–682 (2012).
29. Bartlett, M. D. *et al.* A critical review of current methods in earthworm ecology: From individuals to populations. *Eur. J. Soil Biol.* **46**, 67–73 (2010).
30. Hoskins, A. J. *et al.* Downscaling land-use data to provide global 30" estimates of five land-use classes. *Ecol. Evol.* **6**, 3040–3055 (2016).
31. Hurt, G. C. *et al.* Harmonization of land-use scenarios for the period 1500–2100: 600 years of global gridded annual land-use transitions, wood harvest, and resulting secondary lands. *Clim. Change* **109**, 117–161 (2011).
32. Magurran, A. E. *Measuring biological diversity*. (John Wiley & Sons, 2004).
33. R Core Team. *R: A language and environment for statistical computing*. (2016).
34. Sims, R. W. & Gerard, B. M. Earthworms. Keys and notes for the identification and study of the species. *New Zeal. J. Zool.* **15**, 447–448 (1988).
35. Gonzalez, A. *et al.* Estimating local biodiversity change: a critique of papers claiming no net loss of local diversity. *Ecology* **97**, 1949–1960 (2016).
36. Cameron, E. K. *et al.* Global gaps in soil biodiversity data. *Nat. Ecol. Evol.* **2**, 1042–1043 (2018).

Acknowledgements

This database and paper are a product of two sWorm workshops at iDiv, the synthesis center at iDiv. We thank M. Winter and the sDiv team for their help in organizing the sWorm workshops, and the Biodiversity Informatics Unit (BDU) at iDiv for their assistance in making the data open access. H.R.P.P., B.K.-R., and the sWorm workshops were supported by the sDiv [Synthesis Centre of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig (DFG FZT 118)]. H.R.P.P., O.F. and N.E. acknowledge funding by the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement no. 677232 to NE). K.S.R. and W.H.v.d.P. were supported by ERC-ADV grant 323020 to W.H.v.d.P. Also supported by iDiv (DFG FZT118) Flexpool proposal 34600850 (C.A.G. and N.E.); the Academy of Finland (285882) and the Natural Sciences and Engineering Research Council of Canada (postdoctoral fellowship and RGPIN-2019-05758) (E.K.C.); German Federal Ministry of Education and Research (01LO0901A) (D.J.R.); ERC-AdG 694368 (M.R.); the TULIP Laboratory of Excellence (ANR-10-LABX-41) (M.L); and the BBSRC David Phillips Fellowship to F.T.d.V. (BB/L02456X/1). In addition, data collection was funded by the Russian Foundation for Basic Research (12-04-01538-a, 12-04-01734-a, 14-44-03666-r_center_a, 15-29-02724-ofi_m,

16-04-01878-a 19-05-00245, 19-04-00-609-a); Tarbiat Modares University; Aurora Organic Dairy; UGC(NERO) (F. 1-6/Acctt./NERO/2007-08/1485); Natural Sciences and Engineering Research Council (RGPIN-2017-05391); Slovak Research and Development Agency (APVV-0098-12); Science for Global Development through Wageningen University; Norman Borlaug LEAP Programme and International Atomic Energy Agency (IAEA); São Paulo Research Foundation - FAPESP (12/22510-8); Oklahoma Agricultural Experiment Station; INIA - Spanish Agency (SUM 2006-00012-00-0); Royal Canadian Geographical Society; Environmental Protection Agency (Ireland) (2005-S-LS-8); University of Hawai'i at Mānoa (HAW01127H; HAW01123M); European Union FP7 (FunDivEurope, 265171; ROUTES 265156); U.S. Department of the Navy, Commander Pacific Fleet (W9126G-13-2-0047); Science and Engineering Research Board (SB/SO/AS-030/2013) Department of Science and Technology, New Delhi, India; Strategic Environmental Research and Development Program (SERDP) of the U.S. Department of Defense (RC-1542); Maranhão State Research Foundation (FAPEMA 03135/13, 02471/17); Coordination for the Improvement of Higher Education Personnel (CAPES 3281/2013); Ministry of Education, Youth and Sports of the Czech Republic (LTT17033); Colorado Wheat Research Foundation; Zone Atelier Alpes, French National Research Agency (ANR-11-BSV7-020-01, ANR-09-STRA-02-01, ANR 06 BIODIV 009-01); Austrian Science Fund (P16027, T441); Landwirtschaftliche Rentenbank Frankfurt am Main; Welsh Government and the European Agricultural Fund for Rural Development (Project Ref. A AAB 62 03 qA731606); SÉPAQ, Ministry of Agriculture and Forestry of Finland; Science Foundation Ireland (EEB0061); University of Toronto (Faculty of Forestry); National Science and Engineering Research Council of Canada; Haliburton Forest & Wildlife Reserve; NKU College of Arts & Sciences Grant; Österreichische Forschungsförderungsgesellschaft (837393 and 837426); Mountain Agriculture Research Unit of the University of Innsbruck; Higher Education Commission of Pakistan; Kerala Forest Research Institute, Peechi, Kerala; UNEP/GEF/TSBF-CIAT Project on Conservation and Sustainable Management of Belowground Biodiversity; Ministry of Agriculture and Forestry of Finland; Complutense University of Madrid/European Union FP7 project BioBio (FPU UCM 613520); GRDC; AWI; LWRRDC; DRDC; CONICET (National Scientific and Technical Research Council) and FONCyT (National Agency of Scientific and Technological Promotion) (PICT, PAE, PIP), Universidad Nacional de Luján y FONCyT (PICT 2293 (2006)); Fonds de recherche sur la nature et les technologies du Québec (131894); Deutsche Forschungsgemeinschaft (SCHR1000/3-1, SCHR1000/6-1, 6-2 (FOR 1598), WO 670/7-1, WO 670/7-2, & SCHA 1719/1-2), CONACYT (FONDOS MIXTOS TABASCO/PROYECTO11316); NSF (DGE-0549245, DGE-0549245, DEB-BE-0909452, NSF1241932, LTER Program DEB-97-14835); Institute for Environmental Science and Policy at the University of Illinois at Chicago; Dean's Scholar Program at UIC; Garden Club of America Zone VI Fellowship in Urban Forestry from the Casey Tree Endowment Fund; J.E. Weaver Competitive Grant from the Nebraska Chapter of The Nature Conservancy; The College of Liberal Arts and Sciences at Depaul University; Elmore Hadley Award for Research in Ecology and Evolution from the UIC Dept. of Biological Sciences, Spanish CICYT (AMB96-1161; REN2000-0783/GLO; REN2003-05553/GLO; REN2003-03989/GLO; CGL2007-60661/BOS); Yokohama National University; MEXT KAKENHI (25220104); Japan Society for the Promotion of Science KAKENHI (25281053, 17KT0074, 25252026); ADEME (0775C0035); Ministry of Science, Innovation and Universities of Spain (CGL2017-86926-P); Syngenta Philippines; UPSTREAM; LT'SER (Val Mazia/Matschertal); Marie Skłodowska Curie Postdoctoral Fellowship (747607); National Science & Technology Base Resource Survey Project of China (2018FY100306); McKnight Foundation (14-168); Program of Fundamental Researches of Presidium of Russian Academy of Sciences (AAAA-A18-118021490070-5); Brazilian National Council for Scientific and Technological Development (CNPq 310690/2017-0, 404191/2019-3, 307486/2013-3); French Ministry of Foreign and European Affairs; Bavarian Ministry for Food, Agriculture and Forestry (Project No B62); INRA AIDY project; MIUR PRIN 2008; Idaho Agricultural Experiment Station; Estonian Science Foundation; Ontario Ministry of the Environment, Canada; Russian Science Foundation (16-17-10284); National Natural Science Foundation of China (41371270); Australian Research Council (FT120100463); USDA Forest Service-IITF. The authors would like to thank all supervisors, students, collaborators, technicians, data analysts, land owners/managers, and anyone else involved with the collection, processing, and/or publication of the primary datasets, both for this manuscript and¹⁶. Namely: Peter M. Kotanen, Jessica G. Davis, S.N. Ramanujam, J.M. Julka, Csaba Csuzdi, P. Bescansa, M. Moriones, C. González, Creighton Litton, Danielle Celentano, Sandriel Sousa, Samuel James, C. Hakseth, C. Mills, Hirohi Takeda, Sandriel Sousa Costa, Kyungsoo Yoo, Sébastien De Danieli, Philippe Choler, Pierre Taberlet, Lauric Cecillon, Erwin Meyer, Felix Gerlach, Doris Beutler, Christina Marley, Rhun Fychan, Ruth Sanderson, Mervi Nieminen, Taisto Sirén, Mariana Alem, Carlos Regalsky, Tara Sackett, Erin Bayne, Sarah Hamilton, Alexander Rief, Catarina Praxedes, Rosana Sandler, Julianne Palm, Anne Zangerlé, Anne-Kathrin Schneider, Erwin Zehe, David H. Wise, Liam Heneghan, Yoshikazu Kawaguchi, Irene L. López-Sañudo, Almudena Mateos, Pilar Meléndez, Raquel Santos, Marta Yebrá, Tamara Vsevolodova-Perel, Maxim Bobrovsky, Natalya Ivanova, Eufemio Rasco Jr., Robert W. Myslajek, Jianxiong Li, Jiangping Qiu, A. Barne, Antonio Gómez-Sal, Tanya Handa, Mark Vellend, Hans de Wandeler, Sarah Placella, Lee Frelich, Peter Reich. Open Access funding enabled and organized by Projekt DEAL.

Author contributions

The sWorm workshops were organised by N.E., E.K.C. and H.R.P.P., with funding acquired by N.E., E.K.C. and M.P.T. Data collation and formatting was led by H.R.P.P., with assistance from J.K., M.J.I.B., G.B., K.B.G. and B.S. Harmonisation of earthworm species names was completed by G.B., M.J.I.B., M.L.C.B. and P.L. Advice and feedback on data collation protocols was provided by E.M.B., M.J.I.B., G.B., O.F., C.A.G., B.K.R., A.O., D.R., and D.H.W. Writing of the manuscript was led by H.R.P.P. All authors provided input and comments on the manuscript. The majority of authors provided data to the database.

Competing interests

The authors declare no competing interests.

Additional information

Correspondence and requests for materials should be addressed to H.R.P.P.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

The Creative Commons Public Domain Dedication waiver <http://creativecommons.org/publicdomain/zero/1.0/> applies to the metadata files associated with this article.

© The Author(s) 2021

Helen R. P. Phillips^{1,2,3}✉, Elizabeth M. Bach^{4,5}, Marie L. C. Bartz^{6,7}, Joanne M. Bennett^{1D,8,9}, Rémy Beugnon^{1,2}, Maria J. I. Briones¹⁰, George G. Brown¹¹, Olga Ferlian^{1,2}, Konstantin B. Gongalsky^{12,13}, Carlos A. Guerra^{1,8}, Birgitta König-Ries^{1,14}, Julia J. Krebs^{1,2}, Alberto Orgiazzi¹⁵, Kelly S. Ramirez¹⁶, David J. Russell¹⁷, Benjamin Schwarz¹⁸, Diana H. Wall^{1D,4,5}, Ulrich Brose^{1,19}, Thibaud Decaëns²⁰, Patrick Lavelle²¹, Michel Loreau²², Jérôme Mathieu^{23,24}, Christian Mulder^{1D,25}, Wim H. van der Putten^{1D,16,26}, Matthias C. Rillig^{1D,27}, Madhav P. Thakur^{1D,16}, Franciska T. de Vries^{1D,28}, David A. Wardle²⁹, Christian Ammer^{1D,30,31}, Sabine Ammer³², Miwa Arai³³, Fredrick O. Ayuke^{34,35}, Geoff H. Baker³⁶, Dilmar Baretta³⁷, Dietmar Barkusky³⁸, Robin Beauséjour³⁹, Jose C. Bedano⁴⁰, Klaus Birkhofer⁴¹, Eric Blanchart⁴², Bernd Blossey⁴³, Thomas Bolger^{44,45}, Robert L. Bradley³⁹, Michel Brossard⁴², James C. Burtis⁴⁶, Yvan Capowiez⁴⁷, Timothy R. Cavagnaro⁴⁸, Amy Choi⁴⁹, Julia Clause⁵⁰, Daniel Cluzeau⁵¹, Anja Coors⁵², Felicity V. Crotty^{53,54}, Jasmine M. Crumsey⁵⁵, Andrea Dávalos⁵⁶, Darío J. Díaz Cosín⁵⁷, Annise M. Dobson⁵⁸, Anahí Domínguez^{1D,40}, Andrés Esteban Duhour⁵⁹, Nick van Eeckeren⁶⁰, Christoph Emmerling⁶¹, Liliana B. Falco⁶², Rosa Fernández⁶³, Steven J. Fonte^{1D,64}, Carlos Fragoso⁶⁵, André L. C. Franco⁶⁶, Abegail Fusilero^{67,68}, Anna P. Geraskina⁶⁹, Shaieste Gholami⁷⁰, Grizelle González^{1D,71}, Michael J. Gundale⁷², Mónica Gutiérrez López⁵⁷, Branimir K. Hackenberger⁷³, Davorka K. Hackenberger⁷³, Luis M. Hernández⁷⁴, Jeff R. Hirth⁷⁵, Takuo Hishi⁷⁶, Andrew R. Holdsworth⁷⁷, Martin Holmstrup⁷⁸, Kristine N. Hopfensperger⁷⁹, Esperanza Huerta Lwanga^{1D,80,81}, Veikko Huhta⁸², Tunsisa T. Hurisso^{64,83}, Basil V. Iannone III⁸⁴, Madalina Iordache⁸⁵, Ulrich Irmiger⁸⁶, Mari Ivask⁸⁷, Juan B. Jesús⁵⁷, Jodi L. Johnson-Maynard⁸⁸, Monika Joschko³⁸, Nobuhiro Kaneko⁸⁹, Radoslava Kanińska⁹⁰, Aidan M. Keith^{1D,91}, Maria L. Kernecker⁹², Armand W. Koné^{1D,93}, Yahya Kooch⁹⁴, Sanna T. Kukkonen⁹⁵, H. Lalthanzara⁹⁶, Daniel R. Lammel²⁷, Iurii M. Lebedev^{12,13,97}, Edith Le Cadre⁹⁸, Noa K. Lincoln⁹⁹, Danilo López-Hernández¹⁰⁰, Scott R. Loss¹⁰¹, Raphael Marichal¹⁰², Radim Matula¹⁰³, Yukio Minamiya¹⁰⁴, Jan Hendrik Moos^{105,106}, Gerardo Moreno^{1D,107}, Alejandro Morón-Ríos¹⁰⁸, Hasegawa Motohiro¹⁰⁹, Bart Muys¹¹⁰, Johan Neirynck¹¹¹, Lindsey Norgrove¹¹², Marta Novo⁵⁷, Visa Nuutinen¹¹³, Victoria Nuzzo¹¹⁴, P. Mujeeb Rahman¹¹⁵, Johan Pansu^{116,117}, Shishir Paudel^{101,118}, Guénola Pérès^{51,119}, Lorenzo Pérez-Camacho¹²⁰, Jean-François Ponge^{1D,121}, Jörg Prietzel^{1D,122}, Irina B. Rapoport^{1D,123}, Muhammad Imtiaz Rashid^{1D,124}, Salvador Rebollo^{1D,120}, Miguel Á. Rodríguez¹²⁵, Alexander M. Roth^{126,127}, Guillaume X. Rousseau^{74,128}, Anna Rozen¹²⁹, Ehsan Sayad⁷⁰, Loes van Schaik⁸¹, Bryant Scharenbroch^{130,131}, Michael Schirrmann¹³², Olaf Schmidt^{1D,133,134}, Boris Schröder¹³⁵, Julia Seeber^{136,137}, Maxim P. Shashkov^{1D,138,139}, Jaswinder Singh¹⁴⁰, Sandy M. Smith⁴⁹, Michael Steinwandter¹³⁷, Katalin Szlavecz¹⁴¹, José Antonio Talavera¹⁴², Dolores Trigo⁵⁷, Jiro Tsukamoto¹⁴³, Sheila Uribe-López¹⁴⁴, Anne W. de Valença¹⁴⁵, Iñigo Virto¹⁴⁶, Adrian A. Wackett¹⁴⁷, Matthew W. Warren¹⁴⁸, Emily R. Webster¹⁴⁹, Nathaniel H. Wehr¹⁵⁰, Joann K. Whalen¹⁵¹, Michael B. Wironen¹⁵², Volkmar Wolters¹⁵³, Pengfei Wu¹⁵⁴, Irina V. Zenkova¹⁵⁵, Weixin Zhang^{1D,156}, Erin K. Cameron^{3,157,158} & Nico Eisenhauer^{1D,1,2,158}

¹German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstrasse 4, 04103, Leipzig, Germany. ²Institute of Biology, Leipzig University, Puschstrasse 4, 04103, Leipzig, Germany. ³Department of Environmental Science, Saint Mary's University, Halifax, Nova Scotia, Canada. ⁴Global Soil Biodiversity Initiative and School of Global Environmental Sustainability, Colorado State University, Fort Collins, CO, 80523, USA. ⁵Department of Biology, Colorado State University, Fort Collins, CO, 80523, USA. ⁶Universidade Positivo, Rua Prof. Pedro Viriato Parigot de Souza, 5300, Curitiba, PR, 81280-330, Brazil. ⁷Center of Functional Ecology, Department of Life Sciences, University of Coimbra, Calçada Martins de Freitas, 3000-456, Coimbra, Portugal. ⁸Institute of Biology, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, 06108, Halle (Saale), Germany. ⁹Centre for Applied Water Science, Institute for Applied Ecology, Faculty of Science and Technology, University of Canberra, Canberra, Australia. ¹⁰Departamento de Ecología y Biología Animal, Universidad de Vigo, 36310, Vigo, Spain. ¹¹Embrapa Forestry, Estrada da Ribeira, km. 111, C.P. 231, Colombo, PR, 83411-000, Brazil. ¹²A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky pr., 33, Moscow, 119071, Russia. ¹³M.V. Lomonosov Moscow State University, Leninskie Gory, 1, Moscow, 119991, Russia. ¹⁴Institute of Computer Science, Friedrich Schiller University Jena, Ernst-Abbe-Platz 2, 07743, Jena, Germany. ¹⁵European Commission, Joint Research Centre (JRC), Ispra, Italy. ¹⁶Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), 6700, Wageningen, AB, The Netherlands. ¹⁷Senckenberg Museum for Natural History Görlitz, Department of Soil Zoology, 02826, Görlitz, Germany. ¹⁸Biometry and Environmental System Analysis, University of Freiburg, Tennenbacher Str. 4, 79106, Freiburg, Germany. ¹⁹Institute of Biodiversity, Friedrich Schiller University Jena, Dornburger-Str. 159, 07743, Jena, Germany. ²⁰CEFE, Univ Montpellier, CNRS, EPHE, IRD, Univ Paul Valéry Montpellier 3, Montpellier, France. ²¹Sorbonne Université, Institut d'Ecologie et des Sciences de l'Environnement, 75005, Paris, France. ²²Centre for Biodiversity Theory and Modelling, Theoretical and Experimental Ecology Station, CNRS, 09200, Moulis, France. ²³Sorbonne Université, Institute of Ecology and Environmental Sciences of Paris (UMR 7618 IES-Paris, CNRS, INRA, UPMC, IRD, UPEC), 4 place Jussieu, 75000, Paris, France. ²⁴INRA, IRD, Institut d'Ecologie et des Sciences de l'Environnement de Paris, F-75005, Paris, France. ²⁵Department of Biological, Geological and Environmental Sciences, University of Catania, Via Androne 81, 95124, Catania, Italy. ²⁶Laboratory of Nematology, Wageningen University, PO Box 8123, 6700, Wageningen, ES, The Netherlands. ²⁷Institute of Biology, Freie Universität Berlin, 14195, Berlin, Germany. ²⁸Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands. ²⁹Asian School of the Environment, Nanyang Technological University, Singapore, 639798, Singapore. ³⁰Centre of Biodiversity and Sustainable Landuse, University of Göttingen, Büsgenweg 1, Göttingen, Germany. ³¹Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, Büsgenweg 1, Göttingen, Germany. ³²Forest Sciences and Forest Ecology, University of Göttingen, Büsgenweg 1, Göttingen, Germany. ³³Institute for Agro-Environmental Sciences, National Agriculture and Food Research Organization, 3-1-3 Kan-nondai, Tsukuba, Ibaraki, Japan. ³⁴Land Resource Management and Agricultural Technology, University of Nairobi, Kapenguria Road, Off Naivasha Road, P.O Box 29053, Nairobi, Kenya. ³⁵Rwanda Institute for Conservation Agriculture, KG 541, Kigali, Rwanda. ³⁶Health & Biosecurity, CSIRO, PO Box 1700, Canberra, Australia. ³⁷Department of Animal Science, Santa Catarina State University, Chapecó, SC, 89815-630, Brazil. ³⁸Experimental Infrastructure Platform (EIP), Leibniz Centre for Agricultural Landscape Research, Eberswalder Str. 84, Müncheberg, Germany. ³⁹Département de biologie, Université de Sherbrooke, Sherbrooke, Québec, Canada. ⁴⁰Geology Department, FCEFQyN, ICBIA-CONICET (National Scientific and Technical Research Council), National University of Rio Cuarto, Ruta 36 Km, 601, Río Cuarto, Argentina. ⁴¹Department of Ecology, Brandenburg University of Technology, Konrad-Wachsmann-Allee 6, Cottbus, Germany. ⁴²Eco&Sols, Univ Montpellier, IRD, INRAE, CIRAD, Institut Agro, Montpellier, France. ⁴³Natural Resources, Cornell University, Ithaca, NY, USA. ⁴⁴Earth Institute, University College Dublin, Belfield, Dublin, 4, Ireland. ⁴⁵School of Biology and Environmental Science, University College Dublin, Belfield, Dublin, Ireland. ⁴⁶Department of Entomology, Cornell University, 3132, Comstock Hall, Ithaca, NY, USA. ⁴⁷EMMAH, UMR 1114, INRA, Site Agroparc, Avignon, France. ⁴⁸The School of Agriculture, Food and Wine, The Waite Research Institute, The University of Adelaide, PMB 1, Glen Osmond, Australia. ⁴⁹Faculty of Forestry, University of Toronto, 33 Willcocks Street, Toronto, Canada. ⁵⁰Laboratoire Écologie et Biologie des Interactions, équipe EES, UMR CNRS 7267, Université de Poitiers, 5 rue Albert Turpaine, Poitiers, France. ⁵¹UMR ECOBIO (Ecosystems, Biodiversity, Evolution) CNRS-Université de Rennes, Station Biologique, 35380, Paimpont, France. ⁵²ECT Oekotoxikologie GmbH, Boettgerstr. 2-14, Floersheim, Germany. ⁵³Institute of Biological, Environmental and Rural Sciences, Aberystwyth University, Plas Gogerddan, Aberystwyth, SY24 3EE, United Kingdom. ⁵⁴School for Agriculture, Food and the Environment, Royal Agricultural University, Stroud Road, Cirencester, GL7 6JS, United Kingdom. ⁵⁵Odum School of Ecology, University of Georgia, 140 E Green Street, Athens, USA. ⁵⁶Department of Biological Sciences, SUNY Cortland, 1215 Bowers Hall, Cortland, USA. ⁵⁷Biodiversity, Ecology and Evolution, Faculty of Biology, University Complutense of Madrid, José Antonio Novais, 12, Madrid, Spain. ⁵⁸Yale School of the Environment, Yale University, 370 Prospect St, New Haven, CT, USA. ⁵⁹Departamento de Ciencias Básicas, Universidad Nacional de Luján, Argentina - INEDES (Universidad Nacional de Luján - CONICET), Luján, Argentina. ⁶⁰Louis Bolk Institute, Kosterijland 3-5, Bunnik, The Netherlands. ⁶¹Department of Soil Science, University of Trier, Campus II, Behringstraße 21, Trier, Germany. ⁶²Departamento de Ciencias Básicas, Instituto de Ecología y Desarrollo Sustentable, Universidad Nacional de Luján, Av. Constitución y Ruta 5, Luján, Argentina. ⁶³Animal Biodiversity and Evolution, Institute of Evolutionary Biology, Passeig Marítim de la Barceloneta 37, Barcelona, Spain. ⁶⁴Department of Soil and Crop Sciences, Colorado State University, 1170 Campus Delivery, Fort Collins, CO, USA. ⁶⁵Biodiversity and Systematic Network, Institute of Ecology A.C., El Haya, Xalapa, Veracruz, 91070, Mexico. ⁶⁶Department of Biology, Colorado State University, 200 West Lake Street, Fort Collins, CO, USA. ⁶⁷Department of Biological Sciences and Environmental Studies, University of the Philippines Mindanao, Tugbok District, Davao, Philippines. ⁶⁸Laboratory of Environmental Toxicology and Aquatic Ecology, Environmental Toxicology Unit - GhEnToxLab, Ghent University, Campus Coupure, Coupure Links 653, Ghent, Belgium. ⁶⁹Center for Forest Ecology and Productivity RAS, Profsoyuznaya st. 84/32 bldg. 14, Moscow, Russia. ⁷⁰Razi University, Kermanshah, Iran. ⁷¹United States Department of Agriculture, Forest Service, International Institute of Tropical Forestry, 1201 Ceiba Street, San Juan, Puerto Rico. ⁷²Department of Forest Ecology and

Management, Swedish University of Agricultural Sciences, Skogsmarksgrand 17, 901 83, Umeå, Sweden.
⁷³Department of Biology, University of Osijek, Cara Hadrijana 8A, Osijek, Croatia. ⁷⁴Agriculture engineering, Agroecology Postgraduate Program, Maranhão State University, Avenida Lourenço Vieira da Silva 1000, São Luis, Brazil. ⁷⁵Department of Jobs, Precincts and Regions, Agriculture Victoria, Chiltern Valley Road, Rutherglen, Australia.
⁷⁶Faculty of Agriculture, Kyushu University, 394 Tsubakuro, Sasaguri, Fukuoka, 811-2415, Japan. ⁷⁷Minnesota Pollution Control Agency, 520 Lafayette Road, St Paul, MN, USA. ⁷⁸Department of Bioscience, Aarhus University, Vejlsøvej 25, Aarhus, Denmark. ⁷⁹Department of Biological Science, Northern Kentucky University, 1 Nunn Drive, Highland Heights, KY, USA. ⁸⁰Agricultura Sociedad y Ambiente, El Colegio de la Frontera Sur, Av. Polígono s/n Cd. Industrial Lerma, Campeche, Campeche, Mexico. ⁸¹Soil Physics and Land Management Group, Wageningen University & Research, Droevedaalsteeg 4, Wageningen, The Netherlands. ⁸²Dept. of Biological and Environmental Sciences, University of Jyväskylä, Box 35, Jyväskylä, Finland. ⁸³College of Agriculture, Environmental and Human Sciences, Lincoln University of Missouri, Jefferson City, MO, 65101, USA. ⁸⁴School of Forest Resources and Conservation, University of Florida, Gainesville, USA. ⁸⁵Sustainable Development and Environmental Engineering, University of Agricultural Sciences and Veterinary Medicine of Banat "King Michael the 1st of Romania" from Timisoara, Calea Aradului 119, Timisoara, Romania. ⁸⁶Institute for Ecosystem Research, University of Kiel, Olshausenstrasse 40, 24098, Kiel, Germany. ⁸⁷Tartu College, Tallinn University of Technology, Puiestee 78, Tartu, Estonia. ⁸⁸Department of Soil and Water Systems, University of Idaho, 875 Perimeter Drive MS, 2340, Moscow, USA. ⁸⁹Faculty of Food and Agricultural Sciences, Fukushima University, Kanayagawa 1, Fukushima, Japan. ⁹⁰Department of Environment, Faculty of Natural Sciences, Matej Bel University, Tajovského 40, Banská Bystrica, Slovakia. ⁹¹UK Centre for Ecology & Hydrology, Library Avenue, Bailrigg, Lancaster, United Kingdom. ⁹²Land Use and Governance, Leibniz Centre for Agricultural Landscape Research, Eberswalder Str. 84, Müncheberg, Germany. ⁹³UFR Sciences de la Nature, UR Gestion Durable des Sols, Université Nangui Abrogoua, Abidjan, Côte d'Ivoire. ⁹⁴Faculty of Natural Resources and Marine Sciences, Tarbiat Modares University, 46417-76489, Noor, Mazandaran, Iran. ⁹⁵Production Systems, Natural Resources Institute Finland, Survontie 9 A, Jyväskylä, Finland. ⁹⁶Department of Zoology, Pachhunga University College, Aizawl, Mizoram, India. ⁹⁷Skolkovo Institute of Science and Technology, 30-1 Bolshoy Boulevard, Moscow, 121205, Russia. ⁹⁸SAS, INRAE, Institut Agro, 35042, Rennes, France. ⁹⁹Tropical Plant and Soil Sciences, College of Tropical Agriculture and Human Resources, University of Hawai'i at Manoa, 3190 Maile Way, St. John 102, Honolulu, USA. ¹⁰⁰Ecología Aplicada, Instituto de Zoología y Ecología Tropical, Universidad Central de Venezuela, Los Chaguaramos, Ciudad Universitaria, Caracas, Venezuela. ¹⁰¹Department of Natural Resource Ecology and Management, Oklahoma State University, 008C, Ag Hall, Stillwater, USA. ¹⁰²UPR Systèmes de Pérennes, CIRAD, Univ Montpellier, TA B-34/02 Avenue Agropolis, Montpellier, France. ¹⁰³Department of Forest Ecology, Faculty of Forestry and Wood Technology, Czech University of Life Sciences Prague, Kamýcká 129, Prague, Czech Republic. ¹⁰⁴Tochigi Prefectural Museum, 2-2 Mutsumi-cho, Utsunomiya, Japan. ¹⁰⁵Thuenen-Institute of Biodiversity, Bundesallee 65, Braunschweig, Germany. ¹⁰⁶Thuenen-Institute of Organic Farming, Trenthorst 32, Westerau, Germany. ¹⁰⁷Plant Biology, Ecology and Earth Science, INDEHESA, University of Extremadura, Plasencia, Spain. ¹⁰⁸Conservación de la Biodiversidad, El Colegio de la Frontera Sur, Av. Rancho, poligono 2A, Cd. Industrial de Lerma, Campeche, Mexico. ¹⁰⁹Department of Environmental Systems Science, Faculty of Science and Engineering, Doshisha University, Kyoto, 602-8580, Japan. ¹¹⁰Department of Earth & Environmental Sciences, Division of Forest, Nature and Landscape, KU Leuven, Celestijnlaan 200E Box, 2411, Leuven, Belgium. ¹¹¹Research Institute for Nature and Forest, Gaverstraat 35, 9500, Geraardsbergen, Belgium. ¹¹²School of Agricultural, Forest and Food Sciences, Bern University of Applied Sciences, Länggasse 85, Zollikofen, Switzerland. ¹¹³Soil Ecosystems, Natural Resources Institute Finland (Luke), Tietotie 4, Jokioinen, Finland. ¹¹⁴Natural Area Consultants, 1 West Hill School Road, Richford, NY, USA. ¹¹⁵Department of Zoology, PSMO College, Tirurangadi, Malappuram, Kerala, India, Malappuram, India. ¹¹⁶CSIRO Ocean and Atmosphere, CSIRO, New Illawarra Road, Lucas Heights, NSW, Australia. ¹¹⁷UMR7144 Adaptation et Diversité en Milieu Marin, Station Biologique de Roscoff, CNRS/Sorbonne Université, Place Georges Teissier, Roscoff, France. ¹¹⁸Phipps Conservatory and Botanical Gardens, Pittsburgh, PA, 15213, USA. ¹¹⁹UMR SAS, INRAE, Institut Agro Agrocampus Ouest, 35000, Rennes, France. ¹²⁰Forest Ecology and Restoration Group, Department of Life Sciences, University of Alcalá, 28805, Alcalá De Henares, Spain. ¹²¹Adaptations du Vivant, CNRS UMR 7179, Muséum National d'Histoire Naturelle, 4 Avenue du Petit Château, Brunoy, France. ¹²²Department of Ecology and Ecosystem Management, Technical University of Munich, Emil-Ramann-Str. 2, 85354, Freising, Germany. ¹²³Tembotov Institute of Ecology of Mountain Territories, Russian Academy of Sciences, I. Armand, 37a, Nalchik, Russia. ¹²⁴Center of Excellence in Environmental Studies, King Abdulaziz University, P.O Box 80216, Jeddah, 21589, Saudi Arabia. ¹²⁵Global Change Ecology and Evolution Research Group (GloCEE), Department of Life Sciences, University of Alcalá, 28805, Alcalá De Henares, Spain. ¹²⁶Department of Forest Resources, University of Minnesota, 1530, Cleveland Ave. N, St. Paul, USA. ¹²⁷Friends of the Mississippi River, 101 E 5th St. Suite 2000, St Paul, USA. ¹²⁸Biology, Biodiversity and Conservation Postgraduate Program, Federal University of Maranhão, Avenida dos Portugueses 1966, São Luis, Brazil. ¹²⁹Institute of Environmental Sciences, Jagiellonian University, Gronostajowa 7, Kraków, Poland. ¹³⁰College of Natural Resources, University of Wisconsin, Stevens Point, WI, 54481, USA. ¹³¹The Morton Arboretum, 4100 Illinois Route 53, Lisle, IL, 60532, USA. ¹³²Department Engineering for Crop Production, Leibniz Institute for Agricultural Engineering and Bioeconomy (ATB), Max-Eyth-Allee 100, Potsdam, Germany. ¹³³School of Agriculture and Food Science, University College Dublin, Agriculture and Food Science Centre, Dublin, Ireland. ¹³⁴UCD Earth Institute, University College Dublin, Dublin, Ireland. ¹³⁵Landscape Ecology and Environmental Systems Analysis, Institute of Geoecology, Technische Universität Braunschweig, Langer Kamp 19c, Braunschweig, Germany. ¹³⁶Department of Ecology, University of Innsbruck, Technikerstrasse 25, Innsbruck, Austria. ¹³⁷Institute for Alpine Environment, Eurac Research, Viale Druso 1, Bozen/Bolzano, Italy. ¹³⁸Laboratory of Ecosystem Modelling, Institute of Physicochemical and Biological Problems in Soil Science of the Russian Academy of Sciences, Institutskaya str., 2, Pushchino, Russia. ¹³⁹Laboratory of Computational Ecology, Institute of Mathematical Problems of Biology RAS – the Branch of Keldysh Institute of Applied Mathematics of the Russian Academy of Sciences, Vitkevicha str., 1, Pushchino, Russia. ¹⁴⁰Department of Zoology, Khalsa College Amritsar, Amritsar, Punjab, India.

¹⁴¹Department of Earth and Planetary Sciences, Johns Hopkins University, 3400 N. Charles Street, Baltimore, USA.
¹⁴²Department of animal biology, edaphology and geology, Faculty of Sciences (Biology), University of La Laguna, La Laguna, Santa Cruz De Tenerife, Spain. ¹⁴³Forest Science, Kochi University, Monobe Otsu 200, Nankoku, Japan.
¹⁴⁴Juárez Autonomous University of Tabasco, Nanotechnology Engineering, Multidisciplinary Academic Division of Jalpa de Méndez, Carr. Estatal libre Villahermosa-Comalcalco, Km 27 S/N, C.P. 86205 Jalpa de Méndez, Tabasco, Mexico. ¹⁴⁵Unit Food & Agriculture, WWF-Netherlands, Driebergseweg 10, Zeist, The Netherlands. ¹⁴⁶Dpto. Ciencias, IS-FOOD, Universidad Pública de Navarra, Edificio Olivos - Campus Arrosadia, Pamplona, Spain. ¹⁴⁷Department of Soil, Water and Climate, University of Minnesota, 1991 Upper Buford Circle, St Paul, USA. ¹⁴⁸Earth Innovation Institute, 98 Battery Street Suite 250, San Francisco, USA. ¹⁴⁹University of California Davis, 1 Shields Avenue, Davis, USA. ¹⁵⁰Natural Resources & Environmental Management, University of Hawaii at Manoa, 1910 East West Rd, Honolulu, USA. ¹⁵¹Natural Resource Sciences, McGill University, 2111 Lakeshore Road, Ste-Anne-de-Bellevue, Canada. ¹⁵²The Nature Conservancy, 4245 Fairfax Drive, Arlington, USA. ¹⁵³Animal Ecology, Justus Liebig University, Heinrich-Buff-Ring 26, Giessen, Germany. ¹⁵⁴Institute of Qinghai-Tibetan Plateau, Southwest Minzu University, Chengdu, China. ¹⁵⁵Laboratory of terrestrial ecosystems, Federal Research Centre "Kola Science Centre of the Russian Academy of Sciences", Institute of North Industrial Ecology Problems (INEP KSC RAS), Akademgorodok, 14a, Apatity, Murmansk, Province, Russia. ¹⁵⁶Key Laboratory of Geospatial Technology for the Middle and Lower Yellow River Regions (Henan University), Ministry of Education, College of Environment and Planning, Henan University, Kaifeng, China. ¹⁵⁷Faculty of Biological and Environmental Sciences, Post Office Box 65, FI 00014, University of Helsinki, Helsinki, Finland. ¹⁵⁸These authors contributed equally: Erin K. Cameron, Nico Eisenhauer.
✉e-mail: helen.phillips@smu.ca