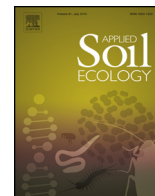




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Earthworm databases and ecological theory: Synthesis of current initiatives and main research directions

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ABSTRACT

Earthworms are a key group of detritivores and ecosystem engineers in many ecosystems worldwide, yet we have a limited understanding of how their diversity varies globally. Synthesis of global data on earthworms would allow a range of important ecological, evolutionary, and applied questions to be addressed. We conducted a survey on global earthworm data at the 10th International Symposium on Earthworm Ecology (ISEE10) and sent an electronic survey to additional earthworm researchers. Respondents were asked about existing databases, research interests, required data, and research locations. Most researchers were aware of at least one database with earthworm data, with a total of 19 current databases being identified. Most of the top questions listed by researchers related to distributions and diversity at global scales, but traits, evolution, genetics, taxonomy, invasions, ecosystem functioning/impacts, ecotoxicology, and bioindicators were also key themes of interest. Correspondingly, distributional, environmental, and trait data were the primary data types required. Global data coverage was poor, with research being especially concentrated in Europe and the United States. Encouragingly, all researchers who currently had data indicated they would be willing to contribute it to a global database. While there are a number of key challenges associated with synthesis of earthworm data on a global scale (data limitations, taxonomic inconsistencies, logistical issues), the wide range of questions involving global data listed by researchers, and their willingness to contribute their own data, suggests there is strong interest in developing a comprehensive global database on earthworms.

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1. Introduction

Global distributions of soil organisms, and the factors driving these distributions, are poorly understood as compared to broad-scale patterns of aboveground biodiversity (Bardgett, 2002; Decaëns, 2010; Wardle et al., 2004). The complex and heterogeneous nature of soil allows for high levels of niche partitioning and local diversity, but how this biodiversity varies over temporal and spatial scales is not clear especially at large scales (Bardgett, 2002; Decaëns, 2010). Very few studies have systematically examined

global patterns of belowground diversity and community structure (Nielsen et al., 2014), despite increasing recognition of the importance of aboveground–belowground feedbacks in controlling ecosystem processes (Wardle et al., 2004). In general, there is a need for hypothesis-driven and synthesizing research in soil ecology to allow an improved understanding of the major factors driving dynamics of belowground systems (Powell et al., 2014).

Earthworms are an important group of soil organisms for which global synthesis is needed. They are essential components of many terrestrial ecosystems and function as key detritivores (Edwards, 2004) and ecosystem engineers (Lavelle et al., 1997). Earthworms often dominate the biomass of invertebrates and initiate decomposition processes by incorporating surface litter into the soil, fragmenting leaf litter, and paving the way for further microbial decay (Edwards, 2004). Furthermore, earthworms

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structure the environment for other soil invertebrates (Brown, 1995; Eisenhauer, 2010) and plants (Scheu, 2003; Van Groenigen et al., 2014). They also have substantial effects on ecosystem functions and services, including greenhouse gas fluxes (Lubbers et al., 2013).

Synthesis of global earthworm data would allow many fundamental questions to be addressed relating to ecology, evolution, ecotoxicology, and conservation. For example, basic macroecological patterns, such as effects of elevational and latitudinal gradients on diversity could be examined with such a dataset. As well, factors that have been demonstrated to determine earthworm distributions at local and regional scales, including climate, habitat type, species' interactions, and anthropogenic activities, could be compared across broad spatial extents. Synthesis of earthworm data available worldwide would also allow identification of regions where little data currently exists and which would greatly benefit from increased research effort. This knowledge would allow research in data-poor regions to be prioritized.

Despite the wide range of research questions that could be examined using global earthworm data, synthesis is likely to be challenging for a number of reasons. Assembling data will be complicated by the fact that sampling techniques are not standardized across different studies, with various extraction methods and sampling plot sizes being used. The taxonomic level to which individuals are identified also varies among datasets, and there are issues with unresolved taxonomies, the use of multiple names for the same species, and the use of the same name for multiple species (i.e., cryptic species). Finally, practical difficulties exist with linking databases that have different formats and data types, or with transferring data from one database to another.

In this paper, we summarize currently available data on earthworms at broad spatial scales and discuss future directions for synthesis of global data. We surveyed earthworm researchers attending the 10th International Symposium on Earthworm Ecology (ISEE10) in Athens, Georgia and also sent a survey to additional earthworm researchers via email. As well, we conducted a workshop on global earthworm data at ISEE10, which informs some of the discussion in this paper.

2. Materials and methods

Paper copies of our questionnaire were distributed to the approximately 113 attendees at the ISEE10 in June 2014, who were asked to return the survey by the end of the day. In August 2014, we also emailed an electronic version of the questionnaire to 174 earthworm researchers, which represents the majority of the international research community, but likely excludes a non-negligible number of Chinese and Russian scientists. A total of approximately 235 unique individuals were contacted, as there was some overlap between conference attendees and the email list, and thus some people received the survey twice. Respondents

were also asked to forward the survey to other interested researchers, but there appear to have been very few, or no, responses from other researchers not on our list, as most respondents included their email address on the survey form. The survey consisted of six open-ended questions (see Table 1 for survey questions). Respondents were asked to indicate any global databases they were aware of that contain information on earthworms, as well as up to five key questions that could be addressed with a global earthworm database and the types of data that should be included in such a database. In addition, we asked where their research was conducted and if they would be willing to contribute their data to a global database or to collect additional data.

Responses to the survey were used to compile a list of current databases (Table 2), which we examined to determine whether they were still being updated and contained publicly available information. To identify major areas of research interest, we divided the key questions listed by respondents into six major categories (listed in Table 3). We then selected the top one to three questions in each of these categories (depending on the overall number of questions within each category). We also grouped the types of data that respondents thought should be included in a database into ten major categories (listed in Table 4). Locations where researchers reported their data from were mapped using ArcGIS 10.0 (ESRI, Redlands, CA).

3. Results

A total of 77 earthworm researchers responded to our survey, including 31 at ISEE10 and the remainder via email. This represents a response rate of 33%, given that approximately 235 individuals received surveys. From the survey, we identified 16 currently existing databases that contain publicly available earthworm data and two databases that do not currently have data freely available online (Table 2). Some respondents also listed citizen science projects, most of which do not presently have data available but might in the future (Table 3). All of the databases included data at the species level and most focused on the global level (75%) rather than on specific countries or regions (25%). The databases included data on large-scale distributions, genetics, taxonomy, traits, and abundance/biomass within plots, with most including only one type of data. More than half of the respondents were aware of at least one database (56%).

A wide range of key research questions were suggested by survey participants, on topics such as distributions, genetics, invasions, ecotoxicology, traits, and ecosystem functioning/impacts (Table 4). Most of the research questions listed concerned large-scale distributions and biodiversity (45%), followed by traits (17%). Consistent with the types of questions that were of greatest interest, the data types most frequently listed as being important to include in a global database were trait, environmental, and distributional data (Table 5). Our question about desired data types

Table 1
List of questions from the survey conducted at ISEE10 and online. In the online survey, we specified that answers to question 1 should include only databases that participants were aware of before reading our email asking for responses, because one database (Drilobase) was discussed in the email.

Questions

- 1 Before reading our email, what databases did you know of that contain information on earthworms? Please indicate the type of data included in each database: (a) Large-scale distributional/geographical; (b) Quantitative plot-level data (density/biomass); (c) Genetics/phylogeny; (d) Traits
- 2 List up to 5 key questions that could be addressed with a global dataset on earthworms
- 3 Which data would you like to be able to extract from a global earthworm database (e.g., morphological traits, behavioural traits, environmental data, ...)?
- 4 Would you be willing to contribute your data to such a database?
- 5 What country or region(s) do you work in/is your data from?
- 6 In the future, would you be willing to collect more data about additional variables at your sites in order to inform key research questions (e.g., data on pH, soil moisture, body size, etc.)?

Table 2

List of existing databases containing earthworm data, the type of data they contain, their extent (global or specific country/region), and link to database website.

Database name	Data type	Extent	Website	Data online
Annelid resources	Taxonomy	Global	www.annelida.net	Yes
BETSI	Traits	France, some Germany/ Finland	http://betsi.cesab.org/node/2	Some
BOLD	Genetic	Global	www.barcodinglife.org	Yes
Discoverlife	Distributions	Global	www.discoverlife.org	Yes
DriloBASE	Distributions, genetic, taxonomy, traits	Global	earthworms.info	Yes
Earthworm species	Taxonomy	Global	earthworm.uw.hu	Yes
ECOFINDERS	Distributions	Europe	http://ecofinders.dmu.dk/	No
Edaphobase	Distributions, quantitative	Global	www.edaphobase.org	Yes
E-FAUNA BC	Distributions	British Columbia	ibis.geog.ubc.ca/biodiversity/efauna	Yes
EOL	Distributions, taxonomy, traits	Global	eol.org	Yes
Fauna Europea	Distributions	Europe	www.faunaeur.org	Yes
GBIF	Distributions	Global	www.gbif.org	Yes
Genbank/NCBI	Genetic	Global	www.ncbi.nlm.nih.gov/genbank	Yes
ITIS	Taxonomy	Global	www.itis.gov	No
Lumbribase	Genetic	Global	earthworms.org	Yes
MACROFAUNA	Distributions, quantitative	Global	macrofauna.earthworms.info	Yes
NMNH Smithsonian	Distributions	Global	collections.nmnh.si.edu	Yes
Nomenclatura Oligochaetologica	Taxonomy	Global	http://www.inhs.illinois.edu/people/mjwetzell/nomenoligo	Yes

Table 3

List of earthworm citizen science programs, their location, and link to their website.

Program	Location	Website
Alberta worm tracker	Alberta	worms.educ.ualberta.ca
Artsdatabanken/NRC	Norway	http://www.forskingsradet.no/en/Newsarticle/Earthworm_research_spurred_pupils_to_action/1253965291544
Earthworms across Kansas	Kansas	http://www.k-state.edu/earthworm/
Great Lakes Worm Watch	USA	www.nrri.umn.edu/worms
OPAL soil and earthworm survey	UK	http://www.opalexplornature.org/soilsurvey
OPVT	France	http://ecobiosoil.univ-rennes1.fr/OPVT_accueil.php

mentioned behavioural traits, morphological traits, and environmental data as examples, which may have influenced the proportion of responses per category. However, a range of other types of data were listed in responses such as taxonomic, genetic, and ecotoxicological data.

All participants who currently had earthworm data (76 out of 77 researchers surveyed) indicated they would be willing to contribute it to a global database. However, three of the people who said that they would contribute data indicated that they would need to wait until it was published, would require permission from their project sponsor, or would only contribute if it was not difficult. The majority of respondents (66%) also said they would be willing to collect additional data for a global database, such as soil moisture, pH, and body size. A further 23% indicated they would be willing to collect additional data if it was feasible and they had enough funding or time to do so. The remainder of the participants were not sure (5%), gave no answer (2.5%), or indicated the question did not apply to their situation (2.5%). Global data coverage, at least as reflected by the answers of survey participants, appears to be fairly poor (Fig. 1). Research is concentrated in Europe and the United States, and data availability is especially limited in parts of Africa and South America, as well as Australia.

4. Discussion

4.1. Priorities for future global research

The broad range of top questions listed by survey respondents suggests that synthesis of global earthworm data could open many productive avenues for future research in the fields of ecology, evolution, and ecotoxicology. Researchers appeared to be most

interested in questions relating to global distributional patterns of earthworms, with many of the suggested key questions relating to diversity patterns and the abiotic and biotic factors driving global distributions of native and non-native species. This lack of information on macroecological patterns of soil fauna has previously been identified as an important research gap (Decaëns, 2010; Nielsen et al., 2014). It should be possible to address a number of these macroecological questions using existing databases on earthworm distributions, but others could be best examined using quantitative plot-level data on abundances or biomasses. Unfortunately, this type of data exists in only two of the current databases: Edaphobase which is largely restricted to Germany, and Macrofauna which is restricted to 843 sites that are mostly in the tropics. Thus, there is a clear need for a new database or an additional module within an existing database to allow questions requiring global quantitative data to be investigated.

A strong emphasis on trait-based approaches was also evident in the list of top questions. Most researchers further indicated that trait data would be important to include in a global database, but similar to the lack of databases focused on quantitative data, only two databases currently include trait data (BETSI and Drilobase). Collection of trait data and input of this data into online databases should be a priority, so that the many research questions relating to traits can be addressed. Linking distribution data and species functional traits can for instance be used to assess how earthworm communities respond to environmental factors at different scales. From a global perspective, this could provide insights into the potential impacts of global change on earthworm communities and the consequences of these impacts on the production of ecosystem services (Pey et al., 2014). In addition, species trait data could be used to examine responses of field communities to contaminants in ecotoxicological studies. Ecotoxicology was also

Table 4
List of top questions that could be addressed using a global database. Questions were grouped into broad categories, and the number of questions suggested per category were counted (participants could suggest up to five questions each; numbers in brackets indicate the counts for each question). From the list of questions, we selected one to three top questions per question category.

Category	Number of questions	Top questions
Distributions/ biogeography	100	1 How are different species of earthworms dispersed across the globe? (47) 2 How will climate change and land use affect earthworm species distributions? (19) 3 What data do we have on earthworm distributions nationally and regionally, and where is this information missing? (7)
Traits	37	1 What are the ecological and morphological properties of a particular earthworm species? (14) 2 Can we identify global co-occurrence patterns within earthworm communities and link them to specific traits? (6) 3 What is the relationship between reproduction, life history, and environmental conditions? (6)
Invasions	25	1 How do native and invasive earthworms interact? (4) 2 How are invasive species distributed and what drivers are important? (13) 3 Are earthworm invaded soils less biodiverse than non-invaded soils? (1)
Evolution/genetics/ taxonomy	23	1 What genetic studies have been conducted on different species? (4) 2 How does earthworm evolution relate to long-term climatic/paleoclimatic trends? (1) 3 How has human transport influenced phylogeographic patterns and microevolution? (7)
Ecosystem functioning/ impacts	20	1 In which types of ecosystems/regions do earthworms significantly modify soil properties and ecosystem services? (7) 2 What is the relationship between earthworms, soil properties, and plant production? (2) 3 What is the role of earthworms in the mineralization process and nutrient cycling? (1)
Bioindicators/ ecotoxicology	15	1 Are earthworms useful bioindicators across large geographical scales? (4) 2 Can earthworms be used for bioremediation? (6)

identified as a major area of interest by researchers, and there is an urgent need to develop the ecological aspects of toxicological studies.

Finally, research on evolution, genetics, and taxonomy was a key priority identified by many researchers. For example, information across broad spatial scales could allow assessment of how phylogeographic patterns and microevolution have been influenced by human transportation and climatic factors. Taxonomic research is especially critical given the importance of consistent species definitions across regions for development of a global dataset. We discuss the taxonomic challenges associated with data synthesis further in Section 4.2 below.

4.2. Challenges for data synthesis

Among survey participants, there was an extremely high willingness to contribute data to a global database. This suggests future synthesis efforts will be able to draw upon a broad base of participants worldwide (Fig. 1B). Although this is encouraging,

actual contribution rates are likely to be considerably lower as time constraints or other issues could limit participation. Some researchers indicated funding limitations may restrict their ability to collect additional types of data (e.g., soil characteristics) for a global dataset, pointing to a need to investigate potential funding for data collection at broad scales if consistent protocols were to be followed across regions. However, compared to most soil invertebrates, earthworms are relatively simple to sample and thus citizen science may be a useful approach for obtaining data on earthworm distributions at a lower cost than data collected by scientists. A number of citizen science programs exist in the United States, Canada, France, the United Kingdom, and Norway, a few of which have been highly successful both in obtaining data and in providing science-based educational opportunities for the public (Table 3).

Our results suggest data is extremely limited in certain regions. Most researchers responding to our survey indicated their data was collected in Europe or the United States. For example, no data was available from eastern or southern Africa, the southern portion of

Table 5
Types of data wanted and number of responses. Number of responses in each subcategory are indicated in brackets. The survey question included several examples of potential data types (environmental, behavioural traits, morphological traits) which are denoted with asterisks.

General category	Subcategory	Number of responses
Distribution	Abundance (9), distribution (21), richness (8)	38
Ecotoxicological	Bioindication (1), ecotoxicology (4)	5
Effects	Effects on environment (3), species (1)	4
Environmental*	climate (5), environmental (33), soil (19), plants (10)	67
Genetics	Sequences/markers (14), phylogenetic (2)	16
Human disturbances	Land use practices (2), agriculture (1)	3
References	Publications (6), type specimens (2)	8
Sampling/storage method	Extraction technique (2), storage media (1)	3
Taxonomic	Taxonomy (6), identification (2)	8
Traits	Behavioural* (14), ecological (17), functional (6), morphological* (27), physiological (6), traits (6)	76

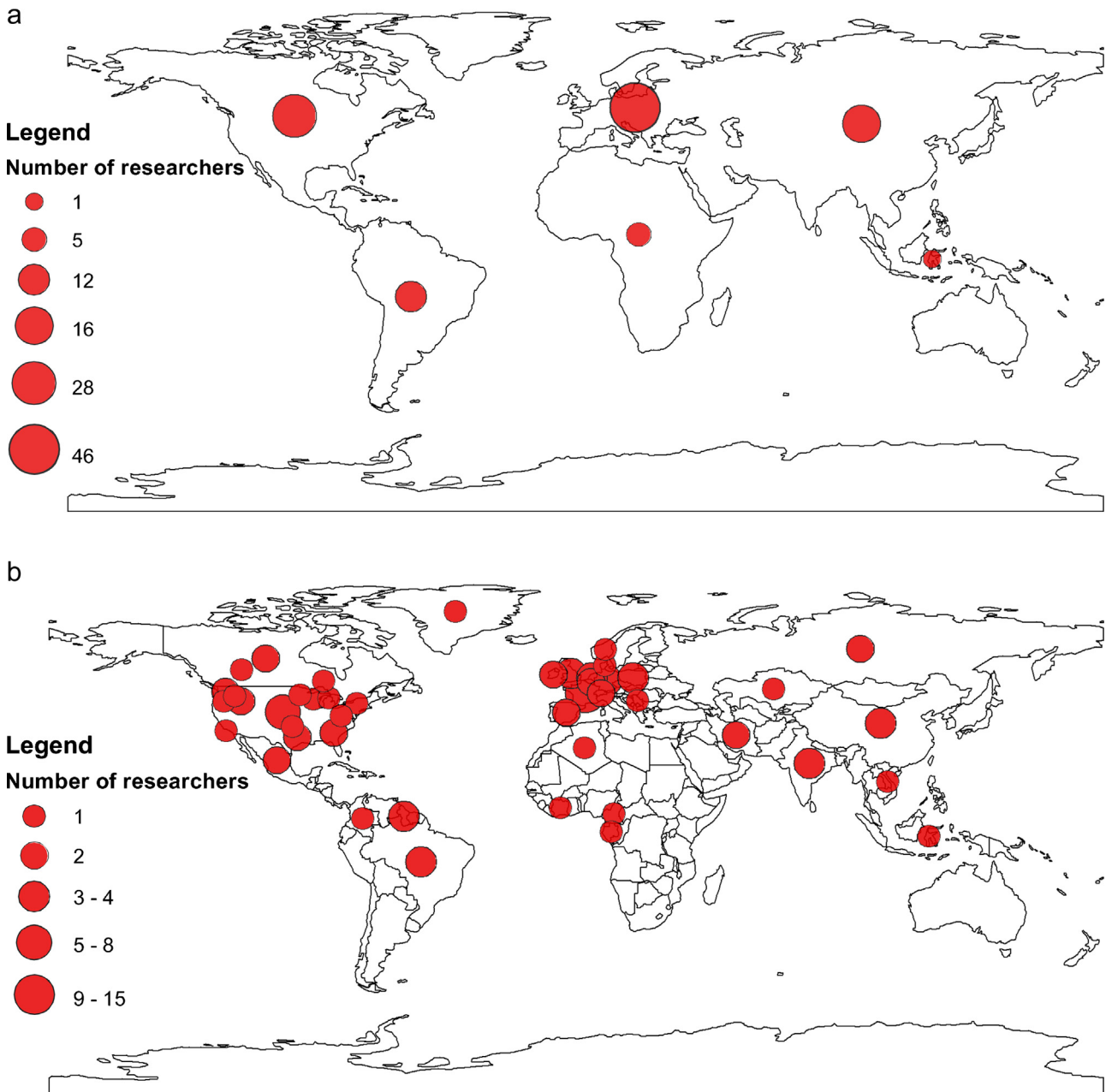


Fig. 1. (A) Number of survey respondents who reported that they have data and/or conduct their research in (A) continents ($N=96$) and (B) countries or regions within a country ($N=95$). Some respondents only provided information on the continent rather than country, and thus that data is not included in (B). Symbol size is proportional to number of respondents.

South America, or Australia. A more thorough examination of the sampling locations of the earthworm data currently in global databases and available in published articles is needed before definitive conclusions can be made about which areas are the most data deficient. However, our results strongly suggest there is a strong spatial bias in the existing data, at least in the English literature. If conclusions about earthworm ecology and evolution are to be drawn at a global scale, this deficiency must be addressed and these understudied areas should be a top priority for future research.

The existence of a range of databases containing global data on earthworms, including general databases, as well as a number of specialized databases, is promising. As well, data from eight European countries was recently harmonized and collated to allow earthworm communities to be mapped across much of Europe

(Rutgers et al., 2016). However, there remain numerous challenges associated with linking existing databases or establishing a new database, which draws upon all existing data. In cases where data is similarly structured, such as in databases containing geolocated occurrence records at the species-level, linking existing databases may be relatively simple. However, when databases with different types of data or data at different resolutions (e.g., data with species vs. functional groups identified) must be linked together, more issues will likely be encountered. The top research questions assembled in Table 1 moreover indicate that many scientists are interested in synthesizing different types of data, such as data on distributions and biodiversity, traits, and environmental conditions at the sampling locations, which would require major efforts to inform and structure databases accordingly as such information is often distributed across different databases with different

scopes. Inclusion of quantitative data may be particularly difficult as very little data of this type is currently in existing databases. As well, differences in sampling methods among studies, which can have strong effects on the quantitative data (earthworm abundances or biomasses) reported, will also make data synthesis challenging. Nonetheless, at our ISEE10 workshop, interest in linking existing databases together was high and was a major focus of discussion.

Gaps and inconsistencies in our taxonomic knowledge will also complicate attempts to link databases. Recent discoveries of high amounts of cryptic species diversity detected using DNA barcodes (King et al., 2008), as well as high levels of endemism and undescribed species in inter-tropical areas (Lavelle and Lapiéd, 2003), suggest that the taxonomic deficit for earthworms may be larger than previously thought (Decaëns et al., 2013). Several cases of cryptic diversity have already been documented for some of the most common European species (*Allolobophora chlorotica*—King et al., 2008; *Lumbricus terrestris*/*Lumbricus herculeus*—James et al., 2010; *Aporrectodea caliginosa*—Perez-Losada et al., 2009; *Aporrectodea rosea*, *Lumbricus rubellus*—Porco et al., 2013). These species complexes have been the subject of several hundreds of scientific publications where the information gathered was assigned to a single species name. Moreover, these morphologically undetectable entities are possibly associated with different biological and ecological traits (James et al., 2010), which has consequences for our knowledge of the taxonomical nomenclature, the species distribution, the actual global diversity, and even their phylogenetic relationships (reviewed in Porco et al., 2012a,b). To fully rectify this situation, a massive barcoding effort of the specimens from previous studies would be required, but this would be expensive and is not possible for many studies for which samples are no longer available or were poorly preserved. However, we strongly suggest that future studies incorporate systematic DNA barcoding of specimens to avoid this issue.

4.3. Summary and future steps

Despite a long list of global databases containing information on earthworms, the data provided in each of those databases is not yet suitable to explore the questions earthworm scientists are most interested in. Further, knowledge within that community about the existence of those databases is generally low. Also, the existing databases have been developed to answer certain research questions and thus data structure is very heterogeneous and not straightforward to combine for global synthesis work. The present paper provides a summary of the existing databases, research interests, data required by scientists to address their research questions, and gaps in data coverage to guide future research activities. The high number of participants joining the 'Earthworm Database Workshop' at ISEE 10 (~40% of all conference attendees), the lively discussion during the workshop, and the wide variety of research questions asked on the questionnaires indicate that there is great demand by earthworm scientists to assemble information on earthworm abundances, biomasses, traits, genetics, and taxonomy in a global database. As this cannot be realized as a side project of a few individuals only, a working group has been initiated to examine the potential for fundraising and/or identifying other existing databases (e.g., Drilobase) providing the infrastructure to contain the different types of data wanted by the scientific community.

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References

- Bardgett, R.D., 2002. Causes and consequences of biological diversity in soil. *Zoology* 105, 367–375. doi:http://dx.doi.org/10.1078/0944-2006-00072.
- Brown, G.G., 1995. How do earthworms affect microfloral and faunal community diversity. *Plant Soil* 170, 209–231. doi:http://dx.doi.org/10.1007/BF02183068.
- Decaëns, T., 2010. Macroecological patterns in soil communities. *Glob. Ecol. Biogeogr.* 19, 287–302. doi:http://dx.doi.org/10.1111/j.1466-8238.2009.00517.x.
- Decaëns, T., Porco, D., Rougerie, R., Brown, G.G., James, S.W., 2013. Potential of DNA barcoding for earthworm research in taxonomy and ecology. *Appl. Soil Ecol.* 65, 35–42. doi:http://dx.doi.org/10.1016/j.apsoil.2013.01.001.
- Edwards, C.A., 2004. *Earthworm Ecology*. CRC Press, Boca Raton, FL.
- Eisenhauer, N., 2010. The action of an animal ecosystem engineer: Identification of the main mechanisms of earthworm impacts on soil microarthropods. *Pedobiologia* 53, 343–352. doi:http://dx.doi.org/10.1016/j.pedobi.2010.04.003.
- James, S.W., Porco, D., Decaëns, T., Richard, B., Rougerie, R., Erseus, C., 2010. DNA barcoding reveals cryptic diversity in *Lumbricus terrestris* L., 1758 (Clitellata): resurrection of *L. herculeus* (Savigny, 1826). *PLoS One* 5, e15629. doi:http://dx.doi.org/10.1371/journal.pone.0015629.
- King, R.A., Tibble, A.L., Symondson, W.O.C., 2008. Opening a can of worms: unprecedented sympatric cryptic diversity within British lumbricid earthworms. *Mol. Ecol.* 17, 4684–4698. doi:http://dx.doi.org/10.1111/j.1365-294X.2008.03931.x.
- Lavelle, P., Bignell, D., Lepage, M., Wolters, V., Roger, P., Ineson, P., Heal, O.W., Dhillon, S., 1997. Soil function in a changing world: the role of invertebrate ecosystem engineers. *Eur. J. Soil Biol.* 33, 159–193.
- Lavelle, P., Lapiéd, E., 2003. Endangered earthworms of Amazonia: an homage to Gilberto Righi: the 7th international symposium on earthworm ecology-Cardiff-Wales-2002. *Pedobiologia* 47, 419–427. doi:http://dx.doi.org/10.1078/0031-4056-00207.
- Lubbers, I.M., van Groenigen, K.J., Fonte, S.J., Six, J., Brussaard, L., van Groenigen, J.W., 2013. Greenhouse-gas emissions from soils increased by earthworms. *Nat. Clim. Change* 3, 187–194. doi:http://dx.doi.org/10.1038/NCLIMATE1692.
- Nielsen, U.N., Ayres, E., Wall, D.H., Li, G., Bardgett, R.D., Wu, T., Garey, J.R., 2014. Global-scale patterns of assemblage structure of soil nematodes in relation to climate and ecosystem properties. *Glob. Ecol. Biogeogr.* 23, 968–978. doi:http://dx.doi.org/10.1111/geb.12177.
- Perez-Losada, M., Ricoy, M., Marshall, J.C., Dominguez, J., 2009. Phylogenetic assessment of the earthworm *Aporrectodea caliginosa* species complex (Oligochaeta: Lumbricidae) based on mitochondrial and nuclear DNA sequences. *Mol. Phylogenet. Evol.* 52, 293–302.
- Pey, B., Nahmani, J., Auclerc, A., Capowicz, Z., Cluzeau, D., Cortet, J., Decaëns, T., Deharveng, L., Dubs, F., Joimel, S., Briard, C., Grumiaux, F., Laporte, M.-A., Pasquet, A., Pelosi, C., Pernin, C., Ponge, J.-F., Salmon, S., Santorufó, L., Hedde, M., 2014. Current use of and future needs for soil invertebrate functional traits in community ecology. *Basic Appl. Ecol.* 15, 194–206. doi:http://dx.doi.org/10.1016/j.baec.2014.03.007.
- Porco, D., Bedos, A., Greenslade, P., Janion, C., Skarżyński, D., Stevens, M.I., et al., 2012a. Challenging species delimitation in Collembola: cryptic diversity among common springtails unveiled by DNA barcoding. *Invert. Syst.* 26, 470–477.
- Porco, D., Potapov, M., Bedos, A., Busmachu, G., Weiner, W.M., Hamra-Kroua, S., Deharveng, L., 2012b. Cryptic diversity in the ubiquitous species *Parisotoma notabilis* (Collembola, Isotomidae): a long-used chimeric species? *PLoS One* 7, e46056. doi:http://dx.doi.org/10.1371/journal.pone.0046056.
- Porco, D., Decaëns, T., Deharveng, L., James, S., Skarżyński, D., Erséus, C., Butt, K.R., Richard, B., Hebert, P.D.N., 2013. Biological invasions in soil: DNA barcoding as a monitoring tool in a multiple taxa survey targeting European earthworms and springtails in North America. *Biol. Invasions* 15, 899–910.
- Powell, J.R., Craven, D., Eisenhauer, N., 2014. Recent trends and future strategies in soil ecological research-Integrative approaches at Pedobiologia. *Pedobiologia* 57, 1–3. doi:http://dx.doi.org/10.1016/j.pedobi.2014.01.001.
- Rutgers, M., Orgiazzi, A., Gardi, C., Römcke, J., Jänsch, S., Keith, A.M., Neilson, R., Boag, B., Schmidt, O., Murchie, A.K., Blackshaw, R.P., Pérès, G., Cluzeau, D., Guernion, M., Briones, M.J.L., Rodeiro, J., Piñeiro, R., Díaz Cosín, D.J., Sousa, J.P., Suhadolc, M., Kos, I., et al., 2016. Mapping earthworm communities in Europe. *Appl. Soil Ecol.* 97, 98–111. doi:http://dx.doi.org/10.1016/j.apsoil.2015.08.015.
- Scheu, S., 2003. Effects of earthworms on plant growth: patterns and perspectives: the 7th international symposium on earthworm ecology-Cardiff-Wales-2002. *Pedobiologia* 47, 846–856. doi:http://dx.doi.org/10.1078/0031-4056-00270.
- Van Groenigen, J.W., Lubbers, I.M., Vos, H.M.J., Brown, G.G., De Deyn, G.B., van Groenigen, K.J., 2014. Earthworms increase plant production: a meta-analysis. *Sci. Rep.* 4 doi:http://dx.doi.org/10.1038/srep06365.
- Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., Putten van der, W.H., Wall, D.H., 2004. Ecological linkages between aboveground and belowground biota. *Science* 304, 1629–1633. doi:http://dx.doi.org/10.1126/science.1094875.