Putting earthworm conservation on the map: Shortfalls and solutions for developing earthworm conservation

Sylvain Gérard, Thibaud Decaëns, Kevin R Butt, Maria J I Briones, Yvan Capowiez, Daniel Cluzeau, Kevin Hoeffner, Renée-Claire Le Bayon, Daniel F Marchán, Claire Marsden, et al.

▶ To cite this version:

Sylvain Gérard, Thibaud Decaëns, Kevin R Butt, Maria J I Briones, Yvan Capowiez, et al.. Putting earthworm conservation on the map: Shortfalls and solutions for developing earthworm conservation. Biological Conservation, 2024, 302, pp.110911. 10.1016/j.biocon.2024.110911 . hal-04818853

HAL Id: hal-04818853
https://hal.inrae.fr/hal-04818853v1

Submitted on 4 Dec 2024

Biological Conservation 302 (2025) 110911

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Perspective

Putting earthworm conservation on the map: Shortfalls and solutions for developing earthworm conservation

Sylvain Gérard [a,b,c,*], Thibaud Decaëns [b,c], Kevin R. Butt [c,d], Maria J.I. Briones [c,e], Yvan Capowiez [f], Daniel Cluzeau [c,g], Kevin Hoeffner [c,g], Renée-Claire Le Bayon [c,h], Daniel F. Marchán [i], Claire Marsden [a], Bart Muys [c,j], Céline Pelosi [c,f], Guénola Pérès [c,k], Helen R.P. Phillips [c,l], Luca Santini [c,m], Wilfried Thuiller [c,n], Mickaël Hedde [a,c]

[a] *Eco&Sols, INRAE, IRD, CIRAD, Institut Agro Montpellier, Campus La Gaillarde, Bâtiment 12, 2 place Viala, 34060 Cédex 2 Montpellier, France*
[b] *CEFE, Univ Montpellier, CNRS, EPHE, IRD, Univ Paul Valéry Montpellier 3, 1919, route de Mende, 34293 Cedex 5 Montpellier, France*
[c] *FRB-CESAB, 5 Rue de l'École de Médecine, 34070 Montpellier, France*
[d] *Ecological Engineering, University of Central Lancashire, Preston PR1 2HE, UK*
[e] *Departamento de Ecología y Biología Animal, Universidade de Vigo, 36310 Vigo, Spain*
[f] *INRAE, UMR EMMAH 1114 INRAE/Université d'Avignon, Bâtiment climat, Domaine Saint-Paul, Site Agroparc, 84914 Cédex 9 Avignon, France*
[g] *University of Rennes, CNRS, ECOBIO [(Ecosystèmes, Biodiversité, évolution)], UMR 6553, Avenue du Général Leclerc, Campus de Beaulieu, 35042 Rennes Cedex, France*
[h] *University of Neuchâtel, Institute of Biology, Functional Ecology Laboratory, Rue Emile-Argand 11, Neuchâtel, Switzerland*
[i] *Biodiversity, Ecology and Evolution Department, Faculty of Biology, Universidad Complutense de Madrid, Avda. de Séneca, 2 Ciudad Universitaria, 28040 Madrid, Spain*
[j] *Department of Earth & Environmental Sciences, Division of Forest, Nature and Landscape, KU Leuven, Celestijnenlaan 200E - box 2411, B-3001 Leuven, Belgium*
[k] *UMR SAS, Institut Agro Rennes-Angers, INRAE, 65 rue de Saint-Brieuc, CS 84215, 35042 Rennes Cedex, France*
[l] *Organismal and Evolutionary Biology, Faculty of Biological and Environmental Sciences, University of Helsinki, P.O. Box 4 (Yliopistonkatu 3), 00014, University of Helsinki, Finland*
[m] *Department of Biology and Biotechnologies 'Charles Darwin', Sapienza University of Rome, Viale Dell'Università 32, 00185 Rome, Italy*
[n] *Univ. Grenoble Alpes, Univ. Savoie Mont Blanc, CNRS, LECA, Laboratoire d'Ecologie Alpine, 38000 Grenoble, France*

ARTICLE INFO

Keywords:
Earthworm ecology
Monitoring
Metrics
Functional ecology
Spatial scales
Annelid

ABSTRACT

Earthworms are keystone organisms that influence both soil function and community assembly of other soil organisms. However, soils are increasingly threatened by global change, so there is an urgent need to consider earthworms in conservation strategies. Earthworm monitoring has been promoted in numerous European and country research programs, and the global interest in earthworm conservation is rising, resulting in a rapid increase in the availability of earthworm data. However, most research focuses on a limited number of local-scale indicators, mainly based on abundance, biomass, and species richness of assemblages along with Bouché's ecological categories. We argue that these metrics are insufficient to effectively address earthworm conservation issues. We suggest four ecological characteristics which may be more informative for the development of conservation plans. Measurement of how much a species is (i) rare or common, (ii) native/nonnative, endemic and invasive, (iii) a specialist or generalist, and (iv) a winner or loser in the Anthropocene are all promising tools to support earthworm diversity conservation. These metrics could also be applied to functional traits, but better definition of these traits is fundamental. Finally, we emphasize the need to broaden spatial scales in earthworm studies by analyzing alpha, beta and gamma components of diversity, as local diversity alone can be misleading.

---

* Corresponding author at: 18 Rue de Louvain, 34000 Montpellier, France.
E-mail address: sylvain.gerard@ens-paris-saclay.fr (S. Gérard).

https://doi.org/10.1016/j.biocon.2024.110911
Received 4 September 2024; Received in revised form 22 November 2024; Accepted 29 November 2024

1. Earthworms and conservation

1.1. Measures of global change imprints on earthworm are lacking

Soils are facing many threats from ongoing human activities (FAO et al., 2020). This is a major concern given that soils are home to 59 % of species on Earth (Anthony et al., 2023), which are essential for maintenance of key ecological processes, the function and stability of terrestrial ecosystems (Briones, 2018; Yang et al., 2018), in addition to provision of numerous ecosystem services (Pereira et al., 2018; Wall et al., 2012). Addressing soil biodiversity conservation should therefore be considered a top priority for policies and research. However, despite some noteworthy initiatives such as the EU Soil Strategy for 2030 (Panagos et al., 2022), soil organisms hardly capture attention and funding from policymakers (Zeiss et al., 2022), and are generally far less considered in conservation by comparison with aboveground biodiversity (Mammola et al., 2020; Phillips et al., 2022). This has led to insufficient protection of soil organisms and insufficient identification of soil biodiversity hotspots (Guerra et al., 2022).

Among soil animals, earthworms are probably the taxon that has received the most attention. Decades of research have shown their ecosystem engineering importance on soil functions (Blouin et al., 2013; Eisenhauer, 2010; Lavelle et al., 2006; Le Bayon et al., 2021; Vidal et al., 2023), and simultaneously as relevant indicators of soil quality (Al-Maliki et al., 2021; de Lima e Silva and Pelosi, 2024; Fründ et al., 2011). Earthworms are unique in that there is abundant information and recognition about their contribution to soil quality and their role as ecological indicators of it and providers of ecosystem services, but very little has been produced on their conservation, compared to other taxa (Fig. 1). This may be due to an overabundance of publications focusing on agricultural environments for this taxon (Fig. 1). Earthworm studies have inherited the tradition in soil biology to focus on functionality due to an overwhelming 'provider-perspective' (i.e., how soils provide benefits to human) (Phillips et al., 2020). They also suffer from being "non charismatic" taxa, for which it is more difficult to find intrinsic values or interest, and to express compassion or empathy (Miralles et al., 2019). Therefore, despite being under threat as part of soil biota, with documented human-induced extinctions, such as *Hypolimnus pedderensis* (Jamieson, 1974), which area has been flooded in 1972 for a hydroelectric power scheme (Blakemore, 2003), there is a critical lack of evidence on how they are responding to ongoing global change. This highlights a need to shift our focus on earthworms more towards a

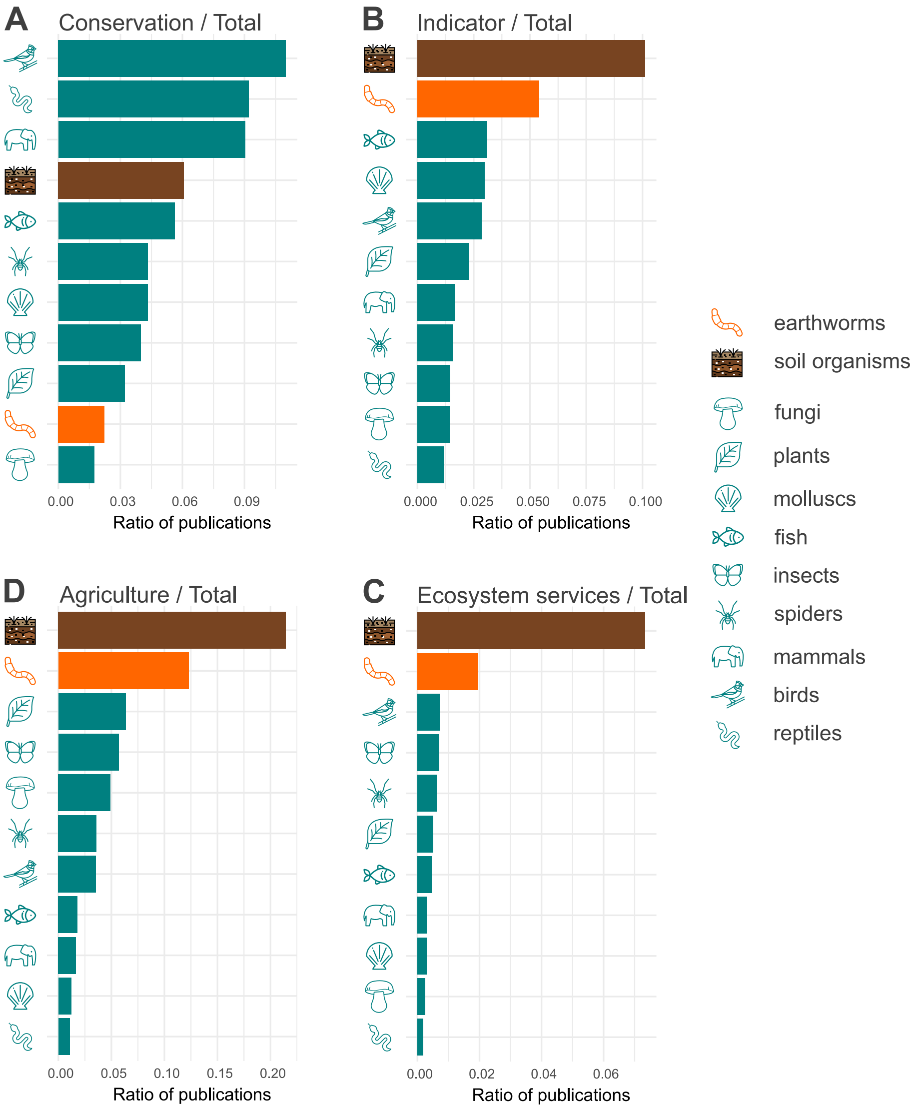

Fig. 1. Results of bibliometric analysis conducted on Web of Science for selected taxa and topics: Number of publications related to each taxon and (A) Conservation, (B) Indicator, (C) Ecosystem services, (D) Agriculture, divided by total number of publications related to each taxon. Details provided in Supplementary material. Data included herein are derived from Clarivate™ (Web of Science™). © Clarivate 2024. All rights reserved.

'nature for nature' perspective rather than a 'nature to society' approach (Pereira et al., 2020), and put this basic taxon in the foreground of conservation biology.

1.2. A rising interest and opportunities for earthworm conservation

There has been a recent and growing interest in understanding earthworm ecology and distribution in space and time. An increasing number of initiatives are underway to aggregate datasets of earthworm occurrences and species assemblages (species assemblage sensu Fauth et al. (1996)), reflecting a growing recognition of these organisms' key role in ecosystems (Table 1). In addition to data gathering initiatives, several projects aim to create new data to better understand the spatial and temporal distributions of earthworms. A number of citizen science programs have been launched, along with national soil monitoring programs (Table 1). However, these actions might lack historical data, underestimating the impacts of long-standing anthropic pressures (Mihoub et al., 2017). In France, the #Vers2022 program (Gérard et al., *submitted for publication*) has taken a unique opportunity to characterize long-term changes in earthworm assemblages and distribution, with a re-survey (after 50 years) of the seminal work of Marcel Bouché (Bouché, 1972).

The leverage of these existing or developing databases is promising for earthworm conservation. Recent studies have mapped present and future earthworm taxonomic and functional diversity (Fourcade and Vercauteren, 2022; Phillips et al., 2019; Salako et al., 2023; Zeiss et al., 2024), and have stressed the lack of protection status in areas with high local diversity (Zeiss et al., 2024). A strong emphasis has also been placed on earthworm invasions, especially in North America, highlighting the threat they pose to native soil communities (Mathieu et al., 2024). However, there is still substantial work to be undertaken. Only 6.7 % of earthworm species are assessed by the International Union for Conservation of Nature (IUCN) Red List (3612 out of a total of 5418 earthworm species (Brown et al., 2023)), including more than half (199) categorized as "Data Deficient" (Phillips et al., 2024). Earthworm data are limited in spatial and temporal coverage, and further affected by methodological variations that hamper comparability in space and time. Additionally, earthworms fall under heterogeneous taxonomic reference systems, which makes the task of integration and comparison particularly complex. This underlines the need for collaborative, standardized and comprehensive protocols (Ganault et al., 2024) to better assess earthworm conservation.

2. Commonly used assemblage indices are insufficient for earthworm protection

To date, the response of earthworm assemblages to environmental changes has been predominantly assessed through a limited number of indicators mostly based on total abundance, total biomass, species richness of communities and the relative abundance of ecological categories, as described by Bouché (1977). While the value of these indicators for informing the structure of assemblages has been largely documented, their relevance from a conservation perspective is questionable.

2.1. Abundance and biomass

Abundance (i.e., number of individuals) and biomass (i.e., total mass of individuals) are metrics that are easy to compute, as they require only simple identification, counting and weighing. Abundance is often used as a proxy for the state of a population and has therefore been frequently used in conservation (Callaghan et al., 2024; Dornelas et al., 2023). Yet, in the case of earthworms, abundance, despite sometimes used to detect changes at a species level (Szlávecz and Csuzdi, 2007), is generally applied, along with biomass, at the assemblage level (Bai et al., 2018; Barnes et al., 2023), and as an indicator of soil quality. However,

Table 1
Recent initiatives to improve accessible data on earthworm.

Type	Database name	Area	Description
Data gathering	Edaphobase	Germany	Data warehouse on soil organisms with data on taxonomy, zoogeography, and ecology (Burkhardt et al., 2014)
	Edaphobase 2.0	Europe	Data warehouse on soil organisms with data on taxonomy, zoogeography, and ecology (Russell et al., 2024)
	FaunaServices	South America	Soil fauna diversity linked to ecosystem services (Brown et al., 2024)
	EWINA (EarthWorms In North America)	North America	Database of native and alien earthworm species occurrences and introduction pathways of alien earthworm species (Mathieu et al., 2024)
	Soil BON Earthworm	World	Earthworm distribution, traits, and spatiotemporal diversity (Ganault et al., 2024)
	sOilFauna	World	Assessing the drivers of soil macrofauna communities and soil functioning (Mathieu et al., 2022)
	sWORM	World	Data on earthworm abundance, biomass, diversity and corresponding environmental properties (Phillips et al., 2021a)
	GloWorm	World	Compiling regional level data for large-scale distributions of native and non-native species (Phillips and Cameron, 2023)
	BETSI	World	Trait database for soil organisms (Joimel et al., 2021)
Monitoring scheme	National Earthworm Recording Scheme	UK	Better understanding of earthworm distribution and diversity through citizen science (Ashwood et al., 2024)
	Earthworm Downunder	Australia	Better understanding of earthworm distribution and diversity through citizen science (Baker et al., 1997)
	Earthworm Watch	UK	Better understanding of earthworm distribution and diversity through citizen science (Burton et al., 2024)
	OPVT (Participatory Earthworm Observatory)	France	Better understanding of earthworm distribution and diversity through citizen science (Guernion et al., 2017)
	RMQS-Biodiv (Network for Soil Quality Monitoring)	France	National monitoring program for monitoring earthworms (Imbert et al., 2023)
	NSMN (Netherlands Soil Quality Monitoring Network)	The Netherlands	National monitoring program for monitoring earthworms (Rutgers et al., 2009)

comparing abundances and biomasses is possible only if individuals exhibit similar probabilities of detectability across species, space, and time (Callaghan et al., 2024). Species detectability can vary between habitats (soils vs. microhabitats like deadwood (Zuo et al., 2023) and epiphytic soils (Dupont et al., 2023), or between soil layers (Capowiez et al., 2024)), or temporally (species surviving the dry season as a cocoon or in a resting state). Moreover, as earthworm ecological studies have shown (Dash and Senapati, 1980; Singh et al., 2021), abundance and biomass dynamics within assemblages can be driven by dominant species alone and be highly dependent on reproductive peaks or seasonal dynamics (Santini et al., 2017). Finally, as declines of one species can lead to increases in another (e.g., competitive release) and vice versa (e.g., invasive species), there may be no net decrease in assemblage-level abundance and biomass even though the assemblage composition changes (Santini et al., 2017).

2.2. *Species richness*

Species – or taxonomic – richness (i.e., the number of species – or taxa – in a given assemblage) is one of the most commonly used metrics in conservation as it brings useful information to help understand assembly rules in assemblages and is an indicator of conservation value (Meir et al., 2004). Species richness can be compared across locations, for similar sampling effort and within a clade, and has a strong value in assessing long-term diversity changes against historical data, typically local checklists (Blowes et al., 2024). However, this metric is not sufficient to evaluate many conservation issues. First, species richness does not inform turnover: species may be completely replaced, and richness would remain unaltered. Second, responding only to taxon colonization or extirpation, it does not allow detection of early warning signals which might anticipate changes at the assemblage level (Santini et al., 2017; Dornelas et al., 2023; Hillebrand et al., 2018). Third, species richness is a taxon-neutral metric, treating all species equivalently, hence hindering information about taxon proximity (functional, phylogenetic, and conservation values of species). Finally, taxonomic richness is highly dependent on a sampler's knowledge and how well the diversity is described. Earthworm species are still largely unknown, especially in tropical regions, but also within countries with an admitted well-known fauna such as France, where many species are still being described (Marchán et al., 2023a, 2023b). As taxonomic systems evolve regularly, even comparisons of historical taxonomic richness can become a challenging task (Carrasco, 2013), requiring particular care.

2.3. *Bouché's ecological categories*

Various attempts have been made to classify soil taxa according to how they affect, and are affected by, soil ecosystem functioning (Hedde et al., 2022). Such an accomplishment could help develop better conservation strategies for earthworms, as it would allow us to understand how soils are impacted by earthworm biodiversity changes. To date, Marcel Bouché's triangle classification (Bouché, 1977), has been used by an overwhelming majority of researchers. Relying on morpho-anatomical traits, he described three extreme types of evolutionary strategies (endogeic, epigeic and anecic; similar to Grime (1974) classification). Given that earthworm species appear relatively easy to categorize and these categories are reliable indicators of soil quality and functionality (Blouin et al., 2013), this classification seems relevant for conservation. Earthworm researchers frequently use this categorization for monitoring, focusing on the presence of a certain category or the relative abundance of each category in an assemblage. However, despite these advantages, Bouché's classification has some flaws in both its creation process and its applications. It was developed using a limited pool of species, without clear assignment rules and lacks experimental research support (Bottinelli and Capowiez, 2021). As a result, this classification has often been inappropriately used, such as through non-steady assignments or assignation to a distinct category instead of a position within a triangle or referring to "functional group" when they are not (Bottinelli et al., 2020; Bottinelli and Capowiez, 2021).

Commonly used assemblage metrics in earthworm research are simple ones and complement each other, but they lack subtlety in the understanding of biodiversity change mechanisms, and in particular, they neglect taxa identity. We argue that earthworm researchers should put a greater emphasis on earthworm conservation and use more conservation-related indices.

3. Proposal for a more informative and integrative set of indices for earthworm conservation monitoring

Here, we present four conservation aspects that we believe deserve greater emphasis, highlighted by advancements in existing earthworm research. Additionally, we describe metrics that can be applied in earthworm ecological studies.

3.1. *Rarity and commonness*

Rarity has always been an important topic in conservation ecology (Peters, 1987; Rabinowitz, 1981). Rare species, except for very emblematic ones (such as *Rhinoceros sondaicus* Desmarest, 1822), are less known but are of prime interest in conservation: they make up the majority of the world's species (Callaghan et al., 2023), they are more likely to be disrupted after a perturbation (Dopheide et al., 2020) and they are overall more endangered (Bland et al., 2015; Işik, 2011; Sykes et al., 2020). Rarity is dependent on population size, distribution extent and habitat specialization (Rabinowitz, 1981). In this way, rarity was assessed with categorical classification (Rabinowitz, 1981) and continuous metrics: Violle et al. (2017) at regional (restrictedness, based on geographical extent) or assemblage level (scarcity, based on abundance in the community) or Rose et al. (2023) with "rarity traits". The IUCN's "area of occupancy" (IUCN, 2024) could also be repurposed to measure rarity. Rarity assessment should also depend on the spatial scale under study, as species are not necessarily rare in every region they inhabit, just as species at global risk may not be locally prone to extinction (e.g., *Lynx lynx* Linnaeus, 1758 in Russia and Scandinavia, *Loxodonta africana* (Blumenbach, 1797) in Botswana). Finally, conserving rare and unique functional traits, as well as old, species-poor clades, should be of prime interest for conservation. This approach broadens the concept of rarity to include "functional rarity" and "phylogenetic rarity". These types of rarity are defined by a combination of taxonomic rarity and, respectively, functional, and phylogenetic originality (Pavoine et al., 2017; Violle et al., 2017).

The rarity of earthworm species has been poorly assessed, with few estimates (Maggia et al., 2021; Pérès et al., 2011). We do have indications that some species are rare, such as *Gatesona serninensis* (Bouché, 1972), which is known from only a single locality despite being in a well-sampled region, such as European France, and that some are common, such as *Pontoscolex corethrurus* (Müller, 1857), with a pantropical distribution (Fig. 2). However, earthworm species face a lack of data due to living in soils, an opaque environment, added to the difficulty of identification without costly magnifying instruments, which hinder the collection of additional data by citizens that could assist with rare species (Wilson et al., 2020). More data is therefore needed especially in less sampled regions, such as the tropics (Ganault et al., 2024), or in under sampled microenvironments, such as deadwood (Zuo et al., 2023), leading to species appearing rarer than they are (Ashwood et al., 2024). A significant effort to describe species new to science is also necessary, with the estimated number of species expected to be much higher than previously estimated (Decaëns et al., 2006; Goulpeau et al., 2024; Anthony et al., 2023).

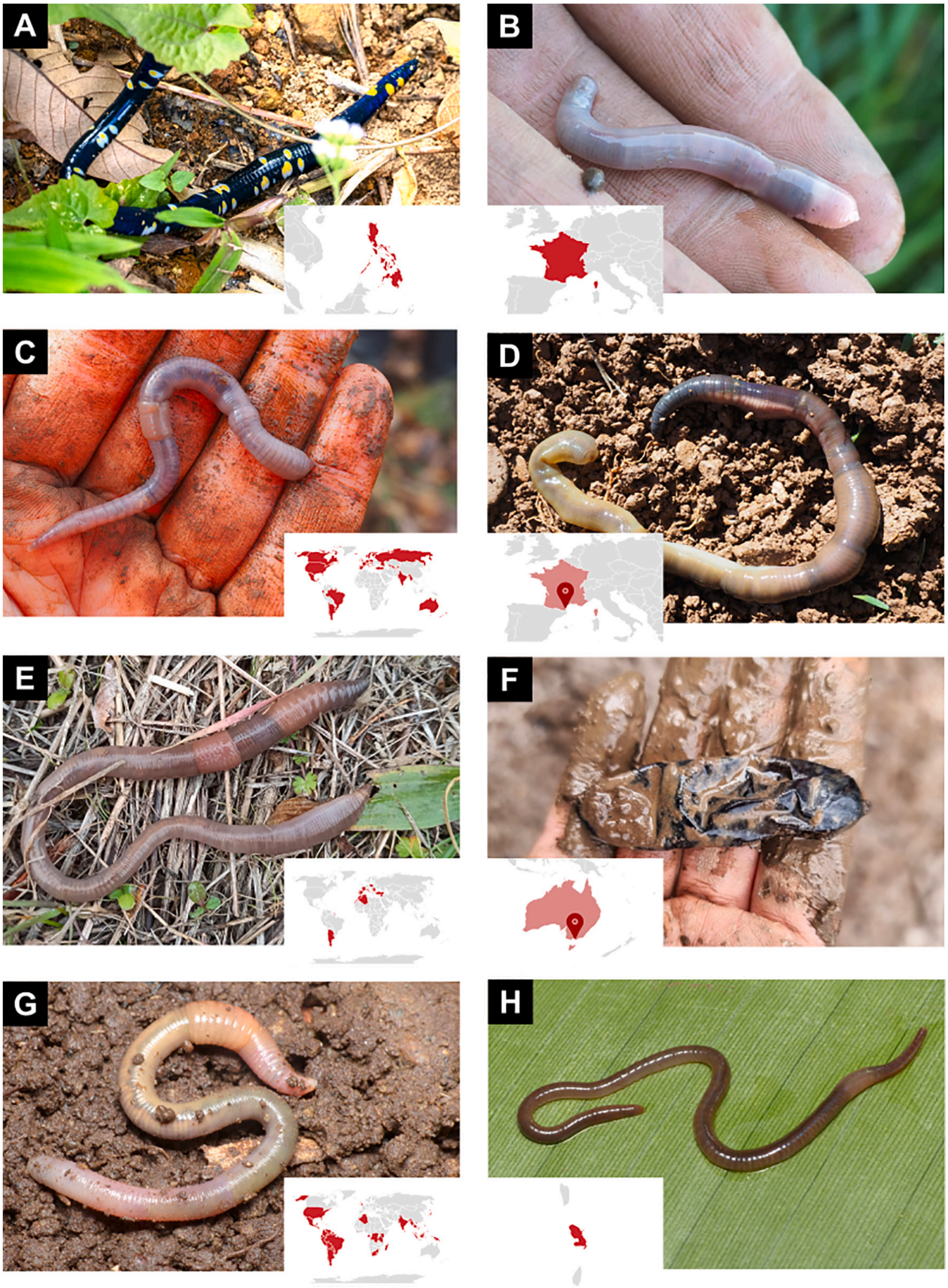

Fig. 2. Earthworm species illustrating conservation characteristics discussed in this work. A and B: Endemic species with the potential to become flagship species (A: "Fried Eggs Worm" *Archipheretima middletoni* James, 2009, endemic of the Philippines, B: *Avelona ligra* (Bouché, 1969), a bioluminescent species endemic to the Loire basin in France); C: *Octolasion cyaneum* (Savigny and Cuvier, 1826), a common species in temperate regions of the world; D: *Boucheona tenebrae* Marchán & Novo, 2023, a rare species known only from one locality in Southern France; E: *Octodrilus complanatus* (Dugès, 1828), a "winner" European species with an expanding range, notably on the island of Corsica (personal information); F: (Cocoon case of) *Megascolides australis* McCoy, 1878, a "loser" endemic species from Australia that is threatened and listed as "Endangered" in the IUCN Red List; G: *Pontoscolex corethrurus* (Müller, 1857), a species originating from Northern Amazonia invasive in many tropical regions; H: *Dichogaster* sp. Beddard, 1888, a "habitat-specialist" species living only in epiphytic soils of Bromeliads on the island of Martinique ("*Dichogaster* sp6" in Dupont et al., 2023). Red color on inserted maps: species distribution from Drilobase. Photographic credits: Forest Botial-Jarvis (A); corresponding author (B, C, D, E); iNaturalist user "gem_ash" (F); Mathieu Coulis (G, H). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.2. Nativeness, endemicity, invasiveness

The hypothesis that co-evolved communities are more stable because species are better adapted to one another makes the question of nativeness of particular interest in conservation ecology (Berthon et al., 2021). Endemic species, occurring only in a restricted area in their native region (Iannone et al., 2020), often bear significant heritage value due to their emblematic or symbolic nature for local people and society (e.g., “flagship” species), and their higher susceptibility to extinction (Işik, 2011). Integrated measures developed around nativeness and nonnativeness or endemism have mainly focused on evaluating how many native/nonnative/endemic taxa are present in a given region or assemblage (Hobohm and Tucker, 2014; Shipley and McGuire, 2022). However, the accuracy of these metrics depends on the amount of information available about each species to prevent misclassification of poorly sampled species as endemic. Additionally, these metrics are influenced by the varying definitions of nativeness (Lemoine and Svenning, 2022) and that endemism is highly scale- and time-dependent (Daru et al., 2020), and is a relative concept: one species may be considered endemic to a specific region or to an entire continent. Invasive species are also of prime interest for conservation ecologists because they can cause environmental harm (Iannone et al., 2020; Roy et al., 2023), and are listed as one of the five major threats to biodiversity (Roy et al., 2023). Invasiveness assessment is also complex, and often relies on expert opinion (Colautti et al., 2014), as one must know if the species is established (i.e., it is self-sustaining and able to reproduce without human intervention (Iannone et al., 2020)) and if it causes harm to native biota. Indeed, only a small proportion of nonnative species become invasive (Colautti et al., 2014; Williamson and Fitter, 1996), and invasiveness is variable within a species (Haubrock et al., 2024). Blackburn et al. (2011) developed a 10-category scheme spanning imported to invasive. Functional ecology has had a particular role with research aiming to identify the functional traits leading to invasiveness (Kaushik et al., 2022). However, care should be taken not to oppose endemism and invasiveness, as an endemic species in its native region can be invasive outside of it.

Numerous earthworm species have been described as endemic (Drilobase, http://taxo.drilobase.org/). Some endemic species are already well-highlighted, such as the 3-meter-long “Giant Gippsland Earthworm” (*Megascolides australis* McCoy, 1878), while others have the potential to gain similar attention, such as the “Fried Eggs Worm” (*Archipheretima middletoni* James, 2009) or *Avelona ligra* (Bouché, 1969), which glows in the dark (Fig. 2). Invasiveness in earthworm ecology has received stronger attention, but with a focus on Lumbricidae in North America (Eisenhauer et al., 2019b; Hendrix and James, 2004; Mathieu et al., 2024). Earthworm ecologists even have their own terminology, using “peregrine species”, often understood as a synonym for invasive, but this term lacks clarity. It was first mentioned in the early XX$_{th}$ century (Michaelsen, 1903), and Brown et al. (2006) later provided a proper definition. Thus, “peregrine” refers to species with high colonizing abilities, but is used for species in both their native or nonnative region. For the sake of clarity, we advocate the use of “native-peregrine” (colonizer in its native region) and “nonnative-peregrine” (colonizer in its nonnative region) instead. However, if nativeness and endemicity of earthworm have often been assessed, they are rarely considered within assemblage-scale studies. Despite promising, extensive studies on invasiveness, we recommend going further and considering nativeness and endemicity in earthworm ecology. The distribution of many earthworm species remains poorly understood; we therefore advocate the development of a comprehensive framework to classify species found in regions where they were previously unknown.

3.3. A specialist to generalist continuum

Specialists are defined as species with narrow environmental tolerance and resource selection, i.e., with a narrow niche (as opposed to generalists), with higher competitive abilities than generalist species within their optimal conditions (Futuyma and Moreno, 1988). Some refinements are often proposed, such as habitat specialist or diet specialist. Whether a species is specialist or generalist is of high conservation value because specialists are often more sensitive to disturbance (Devictor et al., 2008), and overall, more vulnerable to global change (Clavel et al., 2011; Morelli et al., 2020). For this reason, globally generalist species are increasing while specialist species are declining, leading to an overall biotic homogenization (Clavel et al., 2011). Specialization of a species can be assessed using its niche breath through different methods, whether we consider the Grinnellian or the Eltonian definition of the niche (Devictor et al., 2010). While taxa specialization can be estimated by quantifying their resource, habitat or interaction preferences (Devictor et al., 2010; Julliard et al., 2006), it requires a deep knowledge of their ecology and often relies on expert opinions. Specialization can be assessed using data of lesser quality, such as occurrence data, with the species specialization index (SSI) (Julliard et al., 2006) and its generalization to community, the community specialization index (CSI) (Devictor et al., 2008), or with species co-occurrence data (specialists co-occur with less species than generalists (Vimal and Devictor, 2015)). Functional traits can also be used to evaluate specialization, measuring how functionally distant a species is to others (Devictor et al., 2010).

Earthworm niches have been investigated using gradient analysis (Gabriac et al., 2023), Ecological Niche Modeling (ENM) and Species Distribution Modeling (SDM) (Fourcade and Vercauteren, 2022; Marchán et al., 2016), or isotopic niche assessment (Hsu et al., 2023). However, whether a single earthworm species is a generalist or specialist is rarely assessed by modeling. Notably, Hsu et al. (2023) showed that the jumping worm *Amynthas hilgendorfi* (Michaelsen, 1892) is a generalist species whereas *Lumbricus rubellus* (Hoffmeister, 1845) is a specialist.

3.4. Winners and losers

How species are affected by global change is pivotal for conservation strategies. McKinney and Lockwood (1999) defined “losers” as species that decline and “winners” as species that expand, due to human activities. These definitions can be applied to populations and be based on both changes in abundance or occupancy in a given area (Dornelas et al., 2019; Eichenberg et al., 2021; Criado et al., 2023), and should depend on the area under study. Interestingly, winners and losers can be native or nonnative (Tabarelli et al., 2012). Lists of threatened species, such as the IUCN Red List of Threatened Species (Bland et al., 2017), are perhaps the most common and easily accessible way of identifying losers for a species. However, a huge proportion of species are under-represented, especially invertebrates (Eisenhauer et al., 2019a; Mammola et al., 2020), and this list put the emphasis on threatened species, which can be species with very small populations, without necessarily showing declining trends, whereas species with declining trends may be considered as not endangered (McKinney and Lockwood, 1999). A more reliable way of addressing winners and losers rests on detecting the direction and the intensity of population or species trends over time (Wretenberg et al., 2006). Detecting winners and losers thus requires time-series, which are still mostly lacking for soil invertebrates. *Re*-surveys of historical data appear as a good strategy, with specific methods developed to identify species with significant gain or loss of abundance (Legendre, 2019). This assessment is based on species' responses to the environment and human activities, which means that it will be valid at a specific time and place. As a result, it is important to exercise caution when employing this as an indicator.

Currently, whether individual earthworm species are winners or losers is poorly known. Two extinctions have been documented—*Hypolimnus pedderensis* (Jamieson, 1974) and *Tokea orthostichon* (Schmarda, 1861) are both listed as ‘Extinct’ on the IUCN Red List. However, to date, too few earthworm species have been assessed for their conservation status (see Section 1.2), but recent initiatives could help address this (Cazalis et al., 2024). Germany recently paved the way with a Red List of all German species (Gruttke et al., 2016) categorizing all of their earthworm species into the IUCN categories. Pérès et al. (2011) used vulnerability traits, such as rarity and reproductive strategy, to assign a vulnerability index to species regarding soil pollutants. Mathieu and Jonathan Davies (2014) showed that Northern France was recolonized after the last glaciation by a reduced number of species that we propose could be called winners post-glaciation. In a more functional perspective, Fourcade and Vercauteren (2022) showed that heavily weighted earthworm species are predicted to benefit from future climate change, making heavy weight a “winner trait”.

The protection of earthworms would benefit from these metrics being more frequently measured at the species level (Fig. 2) and used as indicators in earthworm ecology. It would also be worthwhile to study closely the interactions with other species, as earthworms are a vital resource for many, particularly birds, and potential co-extinctions that could result from their decline. An important challenge still remains, as many earthworm species are still undiscovered, notably in tropical regions, and taxonomic inconsistencies persist. This can hinder the effective use of developed metrics and underscores the need for sustained, intensive research in this area.

4. A need to enlarge our spatial scales

Local, alpha diversity (i.e., at the assemblage scale) is one of the most explored facets of diversity in ecology. This allows for a detailed understanding of ecological mechanisms, but is not necessarily generalizable to larger scales. Data at local scales are often preferred because they are easier, quicker, and cheaper to analyze and monitor. However, focusing only on local diversity can be misleading in a conservation perspective. For example, the observed missing global net loss of local diversity actually hides a global homogenization of assemblages (Dornelas et al., 2023; Finderup Nielsen et al., 2019; McKinney and Lockwood, 1999). Moreover, metrics such as taxonomic richness or endemicity are highly dependent on the spatial scale (Chase et al., 2019; Daru et al., 2020; McGill et al., 2015). Local-scale-only results can lead to counter-intuitive interpretations for policymakers. Whittaker (1960) proposed breaking diversity down to its alpha (i.e., at the assemblage, local scale), gamma (i.e., regional) and beta (i.e., compositional change between assemblages) components. Beta diversity can also measure temporal change between assemblages, known as “temporal beta diversity”. These broadened scales of diversity are also suitable to functional or phylogenetic diversity (Chao et al., 2019, 2016). Further investigations into the gamma and beta components of earthworm diversity appear to be a tremendous untapped tool to assess earthworm biodiversity change.

Very few ecological earthworm studies have focused on more complex, beta and gamma scales. Mathieu and Jonathan Davies (2014), Maggia et al. (2021) and Goulpeau et al. (2024) analyzed patterns of alpha and beta diversity of earthworms, whereas Fourcade and Vercauteren (2022) and Wills and Abbott (2003) studied functional regional (gamma) diversity. The most encouraging work in this direction is that of Si-Moussi (2020) who analyzed alpha, beta and gamma components of taxonomic, functional and phylogenetic diversity of earthworms. Evidence has also shown that urban earthworm assemblages are undergoing homogenization (Tóth et al., 2020). With the increase of large earthworm data, an increasing number of studies have used continental or global scale data. However, they solely dealt with patterns of local diversity. Phillips et al. (2019) showed that temperate biomes have higher alpha diversity (i.e., local species richness) than those of the tropics. At a narrower European scale, Rutgers et al. (2016) and Zeiss et al. (2024) showed higher alpha diversity in Northern, Atlantic regions, despite Mediterranean regions being known for much higher regional diversity. These patterns can be explained by low alpha but high beta diversity in regions with high endemicity and regional richness in the world (Phillips et al., 2019), but also depend on the availability of data in these regions, and that they host many low occurrence taxa which are often excluded from modeling. Still, these results have sparked discussions (James et al., 2021; Phillips et al., 2021b) and can be misinterpreted by policymakers when building conservation strategies such as constantly choosing to protect a locally rich but regionally poor region over of a regionally rich but locally poor region. This underscores the need to expand the scales at which earthworm diversity is studied and reported.

5. Conclusions

While there have been notable successes in monitoring above-ground organisms for conservation purposes, soil fauna, particularly earthworms, still represent a mostly underexplored frontier. Public policies at the European level are now aware of the importance of valuing and protecting earthworms for the functions they perform. However, to date, existing monitoring initiatives have often failed to capture the dynamic complexity of these organisms. There is a recognized gap in our understanding of population dynamics and assemblage structures of earthworms at a global scale. However, rather than a limitation, this gap represents a promising avenue for development. The need for effective monitoring tools for soil fauna, similar to those employed for birds, plants, and mammals, is increasingly acknowledged. However, as we witness advancements in data acquisition and methodological approaches, there is a growing opportunity to transfer successful monitoring strategies from above-ground to below-ground organisms. This presents a significant area for future research in soil ecology, with the potential to enhance our understanding of earthworm ecology and contribute to effective soil conservation strategies.

CRediT authorship contribution statement

Sylvain Gérard: Writing – review & editing, Writing – original draft, Visualization, Data curation, Conceptualization. **Thibaud Decaëns:** Writing – review & editing, Writing – original draft, Supervision, Conceptualization. **Kevin R. Butt:** Writing – review & editing. **Maria J. I. Briones:** Writing – review & editing. **Yvan Capowiez:** Writing – review & editing. **Daniel Cluzeau:** Writing – review & editing. **Kevin Hoeffner:** Writing – review & editing. **Renée-Claire Le Bayon:** Writing – review & editing. **Daniel F. Marchán:** Writing – review & editing. **Claire Marsden:** Writing – review & editing. **Bart Muys:** Writing – review & editing. **Céline Pelosi:** Writing – review & editing. **Guénola Pérès:** Writing – review & editing. **Helen R.P. Phillips:** Writing – review & editing. **Luca Santini:** Writing – review & editing. **Wilfried Thuiller:** Writing – review & editing. **Mickaël Hedde:** Writing – review & editing, Writing – original draft, Supervision, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

To write this work, the authors used EditGPT (version 1.0.20) to improve English and to correct potential mistakes in a draft version of the manuscript. The modifications proposed were then reviewed, and the manuscript was rewritten with the help of all authors.

Declaration of competing interest

The authors declare no competing interest.

Acknowledgments

We would like to thank the FRB (Fondation pour la recherche sur la biodiversité) through the CESAB program, who offered ideal surroundings leading to this publication. We would also like to thank the Ecole Normale Paris-Saclay and INRAE department AgroEcoSystem for providing the corresponding author's PhD grant, and INRAE GloWorms. Finally, we are grateful to Vincent Devictor and Romy Zeiss for their insightful conversations and feedback on this work, and to Mathieu Coulis, Forest Botial-Jarvis, and iNat user "gem_ash" for providing valuable pictures for illustration. We have added references for all species cited in this work, as we believe that species descriptions should be treated like other research articles and appropriately cited.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110911.

Data availability

The authors have provided the data in the Supplementary Material.

References

Al-Maliki, S., Al-Taey, D.K.A., Al-Mammori, H.Z., 2021. Earthworms and eco-consequences: considerations to soil biological indicators and plant function: a review. Acta Ecol. Sin. 41, 512–523. https://doi.org/10.1016/j.chnaes.2021.02.003.

Anthony, M.A., Bender, S.F., van der Heijden, M.G.A., 2023. Enumerating soil biodiversity. Proc. Natl. Acad. Sci. 120, e2304663120. https://doi.org/10.1073/pnas.2304663120.

Ashwood, F., Brown, K.D., Sherlock, E., Keith, A.M., Forster, J., Butt, K.R., 2024. Earthworm records and habitat associations in the British Isles. Eur. J. Soil Biol. 122, 103642. https://doi.org/10.1016/j.ejsobi.2024.103642.

Bai, Z., Caspari, T., Gonzalez, M.R., Batjes, N.H., Mäder, P., Bünemann, E.K., de Goede, R., Brussaard, L., Xu, M., Ferreira, C.S.S., Reintam, E., Fan, H., Mihelič, R., Glavan, M., Tóth, Z., 2018. Effects of agricultural management practices on soil quality: a review of long-term experiments for Europe and China. Agric. Ecosyst. Environ. 265, 1–7. https://doi.org/10.1016/j.agee.2018.05.028.

Baker, G.H., Thumlert, T.A., Meisel, L.S., Carter, P.J., Kilpin, G.P., 1997. "Earthworms Downunder": a survey of the earthworm fauna of urban and agricultural soils in Australia. Soil Biology and Biochemistry, 5th International Symposium on Earthworm. Ecology 29, 589–597. https://doi.org/10.1016/S0038-0717(96)00184-8.

Barnes, A.E., Robinson, R.A., Pearce-Higgins, J.W., 2023. Collation of a century of soil invertebrate abundance data suggests long-term declines in earthworms but not tipulids. PloS One 18, e0282069. https://doi.org/10.1371/journal.pone.0282069.

Beddard, F.E., 1888. On certain points in the structure of Urochaeta, EP, and Dichogaster, nov. gen., with further remarks on the nephridia of earthworms. J. Cell Sci. 2, 235–282.

Berthon, K., Thomas, F., Bekessy, S., 2021. The role of 'nativeness' in urban greening to support animal biodiversity. Landsc. Urban Plan. 205, 103959. https://doi.org/10.1016/j.landurbplan.2020.103959.

Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarošík, V., Wilson, J. R.U., Richardson, D.M., 2011. A proposed unified framework for biological invasions. Trends Ecol. Evol. 26, 333–339. https://doi.org/10.1016/j.tree.2011.03.023.

Blakemore, R.J., 2003. Hypolimnus pedderensis. The IUCN Red List of Threatened Species 2003: e.T41254A10424837. https://doi.org/10.2305/IUCN.UK.2003.RLTS.T41254A10424837.en (Accessed on 22 November 2024).

Bland, L.M., Collen, B., Orme, C.D.L., Bielby, J., 2015. Predicting the conservation status of data-deficient species. Conserv. Biol. 29, 250–259. https://doi.org/10.1111/cobi.12372.

Bland, L.M., Keith, D., David, A., Miller, R.M., Murray, N.J., Rodríguez, J.P., 2017. Guidelines for the Application of IUCN Red List of Ecosystems Categories and Criteria, Version 1.1. International Union for the Conservation of Nature, Gland, Switzerland.

Blouin, M., Hodson, M.E., Delgado, E.A., Baker, G., Brussaard, L., Butt, K.R., Dai, J., Dendooven, L., Peres, G., Tondoh, J.E., Cluzeau, D., Brun, J.-J., 2013. A review of earthworm impact on soil function and ecosystem services. European J Soil Science 64, 161–182. https://doi.org/10.1111/ejss.12025.

Blowes, S.A., McGill, B., Brambilla, V., Chow, C.F.Y., Engel, T., Fontrodona-Eslava, A., Martins, I.S., McGlinn, D., Moyes, F., Sagouis, A., Shimadzu, H., van Klink, R., Xu, W.-B., Gotelli, N.J., Magurran, A., Dornelas, M., Chase, J.M., 2024. Synthesis reveals approximately balanced biotic differentiation and homogenization. Science. Advances 10, eadj9395. https://doi.org/10.1126/sciadv.adj9395.

Blumenbach, J.F., 1797. Handbuch der Naturgeschichte (Dieterich).

Bottinelli, N., Capowiez, Y., 2021. Earthworm ecological categories are not functional groups. Biol. Fertil. Soils 57, 329–331. https://doi.org/10.1007/s00374-020-01517-1.

Bottinelli, N., Hedde, M., Jouquet, P., Capowiez, Y., 2020. An explicit definition of earthworm ecological categories – Marcel Bouché's triangle revisited. Geoderma 372, 114361. https://doi.org/10.1016/j.geoderma.2020.114361.

Bouché, M.B., 1969. Observations sur les Lombricidés. VI. Une espèce psammophile du Val de Loire Octolasium ligrum sp. nov. (Oligochaeta, Lumbricidae). Rev. Ecol. Biol. Sol 6, 87–91.

Bouché, M.B., 1972. Lombriciens de France. In: Ecologie et Systématique. Ann. Zool. Ecol. Anim.. INRA Editions, Paris.

Bouché, M.B., 1977. Strategies lombriciennes. Ecol. Bull. 122–132.

Briones, M.J.I., 2018. The serendipitous value of soil Fauna in ecosystem functioning: the unexplained explained. Front. Environ. Sci. 6. https://doi.org/10.3389/fenvs.2018.00149.

Brown, G., Demetrio, W., Gabriac, et al., 2024. Soil macrofauna communities in Brazilian land-use systems. Biodiversity Data Journal 12, e115000. https://doi.org/10.3897/BDJ.12.e115000.

Brown, G.G., James, Samuel W., Pasini, A., Hunes, D.H., Benito, N.P., Martins, T., Sautter, K.D., 2006. Exotic, Peregrine, and invasive earthworms in Brazil: diversity, distribution, and effects on soils and plants. Carib. J. Sci. 42, 339–358.

Brown, G.G., James, S.W., Lapied, E., Decaëns, T., Reynolds, J.W., Misirlioğlu, M., Stojanović, M., Phillips, H., Cameron, E., 2023. A checklist of megadrile earthworm (Annelida: Clitellata) species and subspecies of the world. Zenodo.

Burkhardt, U., Russell, D.J., Decker, P., Döhler, M., Höfer, H., Lesch, S., Rick, S., Römbke, J., Trog, C., Vorwald, J., Wurst, E., Xylander, W.E.R., 2014. The Edaphobase project of GBIF-Germany—a new online soil-zoological data warehouse. In: Applied Soil Ecology, XVI International Colloquium on Soil Zoology & XIII International Colloquium on Apterygota, Coimbra, 2012 – Selected Papers, 83, pp. 3–12. https://doi.org/10.1016/j.apsoil.2014.03.021.

Burton, V.J., Jones, A.G., Robinson, L.D., Eggleton, P., Purvis, A., 2024. Earthworm Watch: insights into urban earthworm communities in the UK using citizen science. Eur. J. Soil Biol. 121, 103622. https://doi.org/10.1016/j.ejsobi.2024.103622.

Callaghan, C.T., Borda-de-Água, L., van Klink, R., Rozzi, R., Pereira, H.M., 2023. Unveiling global species abundance distributions. Nat Ecol Evol 7, 1600–1609. https://doi.org/10.1038/s41559-023-02173-y.

Callaghan, C.T., Santini, L., Spake, R., Bowler, D.E., 2024. Population abundance estimates in conservation and biodiversity research. Trends Ecol. Evol. 0. https://doi.org/10.1016/j.tree.2024.01.012.

Capowiez, Y., Marchán, D., Decaëns, T., Hedde, M., Bottinelli, N., 2024. Let earthworms be functional - definition of new functional groups based on their bioturbation behavior. Soil Biol. Biochem. 188, 109209. https://doi.org/10.1016/j.soilbio.2023.109209.

Carrasco, M.A., 2013. The impact of taxonomic bias when comparing past and present species diversity. Palaeogeography, Palaeoclimatology, Palaeoecology, Vertebrate palaeobiodiversity patterns and the impact of sampling bias 372, 130–137. https://doi.org/10.1016/j.palaeo.2012.06.010.

Cazalis, V., Di Marco, M., Zizka, et al., 2024. Accelerating and standardising IUCN Red List assessments with sRedList. Biol. Conserv. 298, 110761. https://doi.org/10.1016/j.biocon.2024.110761.

Chao, A., Chiu, C.-H., Jost, L., 2016. Phylogenetic diversity measures and their decomposition: a framework based on hill numbers. In: Pellens, R., Grandcolas, P. (Eds.), Biodiversity Conservation and Phylogenetic Systematics: Preserving our Evolutionary Heritage in an Extinction Crisis. Springer International Publishing, Cham, pp. 141–172. https://doi.org/10.1007/978-3-319-22461-9_8.

Chao, A., Chiu, C.-H., Villéger, S., Sun, I.-F., Thorn, S., Lin, Y.-C., Chiang, J.-M., Sherwin, W.B., 2019. An attribute-diversity approach to functional diversity, functional beta diversity, and related (dis)similarity measures. Ecological monographs 89, e01343. https://doi.org/10.1002/ecm.1343.

Chase, J.M., McGill, B.J., Thompson, et al., 2019. Species richness change across spatial scales. Oikos 128, 1079–1091. https://doi.org/10.1111/oik.05968.

Clavel, J., Julliard, R., Devictor, V., 2011. Worldwide decline of specialist species: toward a global functional homogenization? Front. Ecol. Environ. 9, 222–228. https://doi.org/10.1890/080216.

Colautti, R.I., Parker, J.D., Cadotte, M.W., Pysek, P., Brown, C.S., Sax, D.F., Richardson, D.M., 2014. Quantifying the invasiveness of species. Neobiota 21, 7–27. https://doi.org/10.3897/neobiota.21.5310.

Criado, M.G., Myers-Smith, I.H., Bjorkman, A.D., et al., 2023. Plant traits poorly predict winner and loser shrub species in a warming tundra biome. Nat. Commun. 14, 3837. https://doi.org/10.1038/s41467-023-39573-4.

Daru, B.H., Farooq, H., Antonelli, A., Faurby, S., 2020. Endemism patterns are scale dependent. Nat. Commun. 11, 2115. https://doi.org/10.1038/s41467-020-15921-6.

Dash, M.C., Senapati, B.K., 1980. Cocoon Morphology, Hatching and Emergence Pattern in Tropical Earthworms.

de Lima e Silva, C., Pelosi, C., 2024. Effects of glyphosate on earthworms: from fears to facts. Integr. Environ. Assess. Manag. 20, 1330–1336. https://doi.org/10.1002/ieam.4873.

Decaëns, T., Jiménez, J.J., Gioia, C., Measey, G.J., Lavelle, P., 2006. The values of soil animals for conservation biology. European Journal of Soil Biology, ICSZ 42, S23–S38. https://doi.org/10.1016/j.ejsobi.2006.07.001.

Desmarest, A.-G., 1822. Mammalogie: ou description des espèces de mammifères. Agasse.

Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, A., Couvet, D., 2008. Functional biotic homogenization of bird communities in disturbed landscapes. Glob. Ecol. Biogeogr. 17, 252–261. https://doi.org/10.1111/j.1466-8238.2007.00364.x.

Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P., Villéger, S., Mouquet, N., 2010. Defining and measuring ecological specialization. J. Appl. Ecol. 47, 15–25. https://doi.org/10.1111/j.1365-2664.2009.01744.x.

Dopheide, A., Makiola, A., Orwin, K.H., Holdaway, R.J., Wood, J.R., Dickie, I.A., 2020. Rarity is a more reliable indicator of land-use impacts on soil invertebrate communities than other diversity metrics. eLife 9, e52787. https://doi.org/10.7554/eLife.52787.

Dornelas, M., Gotelli, N.J., Shimadzu, H., Moyes, F., Magurran, A.E., McGill, B.J., 2019. A balance of winners and losers in the Anthropocene. Ecol. Lett. 22, 847–854. https://doi.org/10.1111/ele.13242.

Dornelas, M., Chase, J.M., Gotelli, N.J., Magurran, A.E., McGill, B.J., Antão, L.H., Blowes, S.A., Daskalova, G.N., Leung, B., Martins, I.S., Moyes, F., Myers-Smith, I.H., Thomas, C.D., Vellend, M., 2023. Looking back on biodiversity change: lessons for the road ahead. Philos. Trans. R. Soc., B 378, 20220199. https://doi.org/10.1098/rstb.2022.0199.

Dugès, A.-L., 1828. Recherches sur la circulation, la respiration et la reproduction des Annélides abranches. impr. C. Thuau.

Dupont, L., Brunet, C.-M., Fourcade, Y., James, S., Gabriac, Q., Coulis, M., 2023. Recording earthworm diversity on the tropical island of Martinique using DNA barcoding unveiled endemic species in bromeliad plants. Soil Biol. Biochem. 182, 109038. https://doi.org/10.1016/j.soilbio.2023.109038.

Eichenberg, D., Bowler, D.E., Bonn, A., Bruelheide, H., Grescho, V., Harter, D., Jandt, U., May, R., Winter, M., Jansen, F., 2021. Widespread decline in Central European plant diversity across six decades. Glob. Chang. Biol. 27, 1097–1110. https://doi.org/10.1111/gcb.15447.

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. https://doi.org/10.1016/j.pedobi.2010.04.003.

Eisenhauer, N., Bonn, A., A Guerra, C., 2019a. Recognizing the quiet extinction of invertebrates. Nat. Commun. 10, 50. https://doi.org/10.1038/s41467-018-07916-1.

Eisenhauer, N., Ferlian, O., Craven, D., Hines, J., Jochum, M., 2019b. Ecosystem responses to exotic earthworm invasion in northern North American forests. Research Ideas and Outcomes 5, e34564. https://doi.org/10.3897/rio.5.e34564.

FAO, ITPS, GSBI, CBD, 2020. State of Knowledge of Soil Biodiversity: Status, Challenges, and Potentialities. FAO, Rome. https://doi.org/10.4060/cb1928en.

Fauth, J.E., Bernardo, J., Camara, M., Resetarits, W.J., Van Buskirk, J., McCollum, S.A., 1996. Simplifying the jargon of community ecology: a conceptual approach. Am. Nat. 147, 282–286. https://doi.org/10.1086/285850.

Finderup Nielsen, T., Sand-Jensen, K., Dornelas, M., Bruun, H.H., 2019. More is less: net gain in species richness, but biotic homogenization over 140 years. Ecol. Lett. 22, 1650–1657. https://doi.org/10.1111/ele.13361.

Fourcade, Y., Vercauteren, M., 2022. Predicted changes in the functional structure of earthworm assemblages in France driven by climate change. Divers. Distrib. 28, 1050–1066. https://doi.org/10.1111/ddi.13505.

Fründ, H.-C., Graefe, U., Tischer, S., 2011. Earthworms as bioindicators of soil quality. In: Karaca, A. (Ed.), Biology of Earthworms. Springer, Berlin, Heidelberg, pp. 261–278. https://doi.org/10.1007/978-3-642-14636-7_16.

Futuyma, D.J., Moreno, G., 1988. The evolution of ecological specialization. Annu. Rev. Ecol. Evol. Syst. 19, 207–233. https://doi.org/10.1146/annurev.es.19.110188.001231.

Gabriac, Q., Ganault, P., Barois, I., Aranda-Delgado, E., Cimetière, E., Cortet, J., Gautier, M., Hedde, M., Marchán, D.F., Pimentel Reyes, J.C., Stokes, A., Decaëns, T., 2023. Environmental drivers of earthworm communities along an elevational gradient in the French Alps. Eur. J. Soil Biol. 116, 103477. https://doi.org/10.1016/j.ejsobi.2023.103477.

Ganault, P., Ristok, C., Phillips, H.R.P., Hedde, M., Capowiez, Y., Bottinelli, N., Decaëns, T., Marchan, D., Gérard, S., Mathieu, J., Potapov, A., Cameron, E.K., Brown, G., Bartz, M., Zeiss, R., Zi, Y., Tsiafouli, M., Russell, D.J., Guerra, C., Eisenhauer, N., 2024. Soil BON Earthworm - a global initiative on earthworm distribution, traits, and spatiotemporal diversity patterns. Soil Organisms 96. https://doi.org/10.25674/362.

Gérard, S., Decaëns, T., Marchán, D.F., et al. #Vers2022: 50-year resurvey data of French earthworm assemblages obtained after resampling Bouché's historical sites. *Submitted to publication.*

Grime, J.P., 1974. Vegetation classification by reference to strategies. Nature 250, 26–31. https://doi.org/10.1038/250026a0.

Gruttke, H., Binot-Hafke, M., Balzer, S., Haupt, H., Hofbauer, N., Ludwig, G., Matzke-Hajek, G., Ries, M., 2016. Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands, Band 4: Wirbellose Tiere (Teil 2). Münster (Landwirtschaftsverlag).–Naturschutz und Biologische Vielfalt 70, 598.

Goulpeau, A., Hedde, M., Ganault, P., Lapied, E., Maggia, M.-E., Marcon, E., Decaëns, T., 2024. Dissecting earthworm diversity in tropical rainforests. bioRxiv. https://doi.org/10.1101/2024.09.13.612984, 2024.09.13.612984.

Guernion, M., Hoeffner, K., Guillocheau, S., Hotte, H., Cylly, D., Piron, D., Cluzeau, D., Hervé, M., Nicolai, A., Pérès, G., 2017. When citizens and scientists work together: a french collaborative science network on earthworms communities distribution. In: EGU General Assembly Conference Abstracts, p. 13543.

Guerra, C.A., Berdugo, M., Eldridge, , et al.Delgado-Baquerizo, M., 2022. Global hotspots for soil nature conservation. Nature 610, 693–698. https://doi.org/10.1038/s41586-022-05292-x.

Haubrock, P.J., Soto, I., Ahmed, D.A., et al., 2024. Biological invasions are a population-level rather than a species-level phenomenon. Glob. Chang. Biol. 30, e17312. https://doi.org/10.1111/gcb.17312.

Hedde, M., Blight, O., Briones, M.J.I., et al., 2022. A common framework for developing robust soil fauna classifications. Geoderma 426, 116073. https://doi.org/10.1016/j.geoderma.2022.116073.

Hendrix, P., James, S., 2004. Invasion of Exotic Earthworms Into North America and Other Regions, pp. 75–88. https://doi.org/10.1201/9781420039719.ch5.

Hillebrand, H., Blasius, B., Borer, E.T., Chase, J.M., Downing, J.A., Eriksson, B.K., Filstrup, C.T., Harpole, W.S., Hodapp, D., Larsen, S., Lewandowska, A.M., Seabloom, E.W., Van de Waal, D.B., Ryabov, A.B., 2018. Biodiversity change is uncoupled from species richness trends: consequences for conservation and monitoring. J. Appl. Ecol. 55, 169–184. https://doi.org/10.1111/1365-2664.12959.

Hobohm, C., Tucker, C.M., 2014. How to quantify endemism. In: Hobohm, C. (Ed.), Endemism in Vascular Plants. Springer, Netherlands, Dordrecht, pp. 11–48. https://doi.org/10.1007/978-94-007-6913-7_2.

Hoffmeister, W., 1845. Die bis jetzt bekannten Arten aus der Familie der Regenwürmer. Als Grundlage zu einer Monographie dieser Familie. Braunschweig, Friedrich Vieweg und Sohn, 43pp.

Hsu, G.-C., Szlavecz, K., Csuzdi, C., Bernard, M., Chang, C.-H., 2023. Ecological groups and isotopic niches of earthworms. Applied Soil Ecology 181, 104655. https://doi.org/10.1016/j.apsoil.2022.104655.

Iannone, B., Carnevale, S., Main, M., Hill, J., McConnell, J., Johnson, S., Enloe, S., Andreu, M., Bell, E., Cuda, J., Baker, S., 2020. Invasive species terminology: standardizing for stakeholder education. The Journal of Extension 58. https://doi.org/10.34068/joe.58.03.27.

Imbert, C., Santorufo, L., Ortega, C., et al., 2023. Handbook to establish a large-scale soil biodiversity monitoring: the French experience of the RMQS-Biodiversity (No. EGU23-16392). Presented at the EGU23, Copernicus Meetings. https://doi.org/10.5194/egusphere-egu23-16392.

Işik, K., 2011. Rare and endemic species: why are they prone to extinction? Turk. J. Bot. 35, 411–417. https://doi.org/10.3906/bot-1012-90.

IUCN, 2024. The IUCN Red List of Threatened Species. Version 2024-1. URL. https://www.iucnredlist.org (accessed 10.7.24).

James, S.W., 2009. Revision of the earthworm genus Archipheretima Michaelsen (Clitellata: Megascolecidae), with descriptions of new species from Luzon and Catanduanes Islands. Philippines. Org. Divers. Evol. 9, 244–e1.

James, S.W., Csuzdi, C., Chang, C.-H., Aspe, N.M., Jiménez, J.J., Feijoo, A., Blouin, M., Lavelle, P., 2021. Comment on "Global distribution of earthworm diversity." Science 371, eabe4629. doi:https://doi.org/10.1126/science.abe4629.

Jamieson, B.G.M., 1974. The Indigenous Earthworms. Oligochaeta) of Tasmania, Megascolecidae.

Joimel, S., Nahmani, J., Hedde, M., Auclerc, A., Beaumelle, L., Bonfanti, J., Cortet, J., Ganault, P., Maunoury-Danger, F., Pey, B., 2021. A Large Database on Functional Traits for Soil Ecologists: BETSI, pp. 523–528.

Julliard, R., Clavel, J., Devictor, V., Jiguet, F., Couvet, D., 2006. Spatial segregation of specialists and generalists in bird communities. Ecol. Lett. 9, 1237–1244. https://doi.org/10.1111/j.1461-0248.2006.00977.x.

Kaushik, P., Pati, P.K., Khan, M.L., Khare, P.K., 2022. Plant functional traits best explain invasive species' performance within a dynamic ecosystem - a review. Trees, Forests and People 8, 100260. https://doi.org/10.1016/j.tfp.2022.100260.

Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P., Rossi, J.-P., 2006. Soil invertebrates and ecosystem services. European Journal of Soil Biology, ICSZ 42, S3–S15. https://doi.org/10.1016/j.ejsobi.2006.10.002.

Le Bayon, R.-C., Bullinger, G., Schomburg, A., Turberg, P., Brunner, P., Schlaepfer, R., Guenat, C., 2021. Earthworms, plants, and soils. In: Hydrogeology, Chemical Weathering, and Soil Formation. American Geophysical Union (AGU), pp. 81–103. https://doi.org/10.1002/9781119563952.ch4.

Legendre, P., 2019. A temporal beta-diversity index to identify sites that have changed in exceptional ways in space–time surveys. Ecol. Evol. 9, 3500–3514. https://doi.org/10.1002/ece3.4984.

Lemoine, R.T., Svenning, J.-C., 2022. Nativeness is not binary—a graduated terminology for native and non-native species in the Anthropocene. Restor. Ecol. 30, e13636. https://doi.org/10.1111/rec.13636.

Linnaeus, C. von, 1758. Systema Naturae per regna tria naturae. Secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio 1, 823.

Maggia, M.-E., Decaëns, T., Lapied, E., Dupont, L., Roy, V., Schimann, H., Orivel, J., Murienne, J., Baraloto, C., Cottenie, K., Steinke, D., 2021. At each site its diversity: DNA barcoding reveals remarkable earthworm diversity in neotropical rainforests of French Guiana. Applied Soil Ecology 164, 103932. https://doi.org/10.1016/j.apsoil.2021.103932.

Mammola, S., Riccardi, N., Prié, V., Correia, R., Cardoso, P., Lopes-Lima, M., Sousa, R., 2020. Towards a taxonomically unbiased European Union biodiversity strategy for 2030. Proc. R. Soc. B Biol. Sci. 287, 20202166. https://doi.org/10.1098/rspb.2020.2166.

Marchán, D.F., Refoyo, P., Fernández, R., Novo, M., de Sosa, I., Díaz Cosín, D.J., 2016. Macroecological inferences on soil fauna through comparative niche modeling: the case of Hormogastridae (Annelida, Oligochaeta). Eur. J. Soil Biol. 75, 115–122. https://doi.org/10.1016/j.ejsobi.2016.05.003.

Marchán, D.F., Novo, M., Domínguez, J., Da Silva, A., Martínez, A., Gerard, S., Hedde, M., Decaëns, T., 2023a. The best is yet to come: six new species within a large-bodied earthworm genus (Scherotheca, Lumbricidae) in a densely sampled region (south-western France). Zool. J. Linn. Soc. 198, 802–820. https://doi.org/10.1093/zoolinnean/zlad002.

Marchán, D.F., Novo, M., Domínguez, J., Sánchez, N., Decaëns, T., 2023b. Contribution to the knowledge of the genus Boucheona (Oligochaeta, Hormogastridae) in France with a newly described species and a redescribed species. Zootaxa 5255, 68–81. https://doi.org/10.11646/zootaxa.5255.1.11.

Mathieu, J., Jonathan Davies, T., 2014. Glaciation as an historical filter of below-ground biodiversity. J. Biogeogr. 41, 1204–1214. https://doi.org/10.1111/jbi.12284.

Mathieu, J., Antunes, A.C., Barot, S., et al., 2022. sOilFauna - a global synthesis effort on the drivers of soil macrofauna communities and functioning: WORKSHOP REPORT. Soil Organisms 94, 111–126. https://doi.org/10.25674/so94iss2id282.

Mathieu, J., Reynolds, J.W., Fragoso, C., Hadly, E., 2024. Multiple invasion routes have led to the pervasive introduction of earthworms in North America. Nat Ecol Evol 8, 489–499. https://doi.org/10.1038/s41559-023-02310-7.

McCoy, F., 1878. Megascolides australis (McCoy). The Giant Earth-Worm. In: Prodomus to the Zoology of Victoria, 1, pp. 21–25.

McGill, B.J., Dornelas, M., Gotelli, N.J., Magurran, A.E., 2015. Fifteen forms of biodiversity trend in the Anthropocene. Trends Ecol. Evol. 30, 104–113. https://doi.org/10.1016/j.tree.2014.11.006.

McKinney, M.L., Lockwood, J.L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol. Evol. 14, 450–453. https://doi.org/10.1016/S0169-5347(99)01679-1.

Meir, E., Andelman, S., Possingham, H.P., 2004. Does conservation planning matter in a dynamic and uncertain world? Ecol. Lett. 7, 615–622. https://doi.org/10.1111/j.1461-0248.2004.00624.x.

Michaelsen, W., 1892. Terricolen der Berliner Zoologischen Sammlung. II. Arch. Für Naturgeschichte 58, 209–261. https://doi.org/10.5962/bhl.part.8321.

Michaelsen, W., 1903. Die geographische Verbreitung der Oligochaeten. R. Friedländer, Berlin. https://doi.org/10.5962/bhl.title.11667.

Mihoub, J.-B., Henle, K., Titeux, N., Brotons, L., Brummitt, N.A., Schmeller, D.S., 2017. Setting temporal baselines for biodiversity: the limits of available monitoring data for capturing the full impact of anthropogenic pressures. Sci. Rep. 7, 41591. https://doi.org/10.1038/srep41591.

Miralles, A., Raymond, M., Lecointre, G., 2019. Empathy and compassion toward other species decrease with evolutionary divergence time. Sci. Rep. 9, 19555. https://doi.org/10.1038/s41598-019-56006-9.

Morelli, F., Benedetti, Y., Callaghan, C.T., 2020. Ecological specialization and population trends in European breeding birds. Global Ecology and Conservation 22, e00996. https://doi.org/10.1016/j.gecco.2020.e00996.

Müller, F., 1857. Description of a new species of Earth-worm (Lumbricus corethrurus). Ann. Mag. Nat. Hist. 20, 13–15. https://doi.org/10.1080/00222935709487865.

Panagos, P., Montanarella, L., Barbero, M., Schneegans, A., Aguglia, L., Jones, A., 2022. Soil priorities in the European Union. Geoderma Reg. 29, e00510. https://doi.org/10.1016/j.geodrs.2022.e00510.

Pavoine, S., Bonsall, M.B., Dupaix, A., Jacob, U., Ricotta, C., 2017. From phylogenetic to functional originality: guide through indices and new developments. Ecol. Indic. 82, 196–205. https://doi.org/10.1016/j.ecolind.2017.06.056.

Pereira, L.M., Davies, K.K., den Belder, E., et al., 2020. Developing multiscale and integrative nature–people scenarios using the Nature Futures Framework. People and Nature 2, 1172–1195. https://doi.org/10.1002/pan3.10146.

Pereira, P., Bogunovic, I., Muñoz-Rojas, M., Brevik, E.C., 2018. Soil ecosystem services, sustainability, valuation and management. Current Opinion in Environmental Science & Health, Sustainable soil management and land restoration 5, 7–13. https://doi.org/10.1016/j.coesh.2017.12.003.

Pérès, G., Vandenbulcke, F., Guernion, M., Hedde, M., Beguiristain, T., Douay, F., Houot, S., Piron, D., Richard, A., Bispo, A., Grand, C., Galsomies, L., Cluzeau, D., 2011. Earthworm indicators as tools for soil monitoring, characterization and risk assessment. An example from the national Bioindicator programme (France). In: Pedobiologia, 9th International Symposium on Earthworm EcologyXalapa, Veracruz, Mexico, 5th–10th September 2010, 54, pp. S77–S87. https://doi.org/10.1016/j.pedobi.2011.09.015.

Peters, R.L., 1987. Conservation biology: the science of scarcity and diversity. Ecol. Restor. 5, 23–24. https://doi.org/10.3368/er.5.1.23.

Phillips, H.R.P., Cameron, E.K., 2023. The GloWorm Project: Compiling regional level data to understand large-scale distributions of native and non-native species. https://doi.org/10.5281/zenodo.10409014.

Phillips, H.R.P., Guerra, C.A., Bartz, M.L.C., et al., 2019. Global distribution of earthworm diversity. Science 366, 480–485. https://doi.org/10.1126/science.aax4851.

Phillips, H.R.P., Beaumelle, L., Eisenhauer, N., Hines, J., Smith, L.C., 2020. Lessons from the WBF2020: extrinsic and intrinsic value of soil organisms. Soil Org 92, 121–127. https://doi.org/10.25674/so92iss2pp121.

Phillips, H.R.P., Bach, E.M., Bartz, M.L.C., et al., 2021a. Global data on earthworm abundance, biomass, diversity and corresponding environmental properties. Sci Data 8, 136. https://doi.org/10.1038/s41597-021-00912-z.

Phillips, H.R.P., Briones, M.J.I., Brown, G.G., Decaëns, T., Cameron, E., Eisenhauer, N., 2021b. Response to Comment on "Global distribution of earthworm diversity." Science 371, eabe4744. doi:https://doi.org/10.1126/science.abe4744.

Phillips, H.R.P., Cameron, E., Eisenhauer, N., 2022. Illuminating biodiversity changes in the 'Black Box.' Research Ideas and Outcomes 8, e87143. doi:https://doi.org/10.3897/rio.8.e87143.

Phillips, H.R.P., Brown, G.G., James, S.W., Mathieu, J., Reynolds, J.W., Dharmasiri, M.E., Singer, C.L., Briones, M.J.I., Proctor, H.C., Cameron, E.K., 2024. The applicability of Regional Red List assessments for soil invertebrates: First assessment of five native earthworm species in Canada. https://doi.org/10.1101/2024.08.23.608777.

Rabinowitz, D., 1981. Seven forms of rarity. In: The Biological Aspects of Rare Plant Conservation. Wiley, pp. 205–217.

Rose, M.B., Velazco, S.J.E., Regan, H.M., Franklin, J., 2023. Rarity, geography, and plant exposure to global change in the California Floristic Province. Glob. Ecol. Biogeogr. 32, 218–232. https://doi.org/10.1111/geb.13618.

Roy, H.E., Pauchard, A., Stoett, P., Truong, T.R., 2023. IPBES Invasive Alien Species Assessment: Summary for Policymakers.

Russell, D.J., Naudts, E., Soudzilovskaia, N.A., et al., 2024. Edaphobase 2.0: advanced international data warehouse for collating and using soil biodiversity datasets. Appl. Soil Ecol. 204, 105710. https://doi.org/10.1016/j.apsoil.2024.105710.

Rutgers, M., Schouten, A.J., Bloem, J., Van Eekeren, N., De Goede, R.G.M., Jagersop Akkerhuis, G.a.J.M, Van der Wal, A., Mulder, C., Brussaard, L., Breure, A.M., 2009. Biological measurements in a nationwide soil monitoring network. Eur. J. Soil Sci. 60, 820–832. https://doi.org/10.1111/j.1365-2389.2009.01163.x.

Rutgers, M., Orgiazzi, A., Gardi, C., et al., 2016. Mapping earthworm communities in Europe. Applied Soil Ecology, Soil biodiversity and ecosystem functions across Europe: A transect covering variations in bio-geographical zones, land use and soil properties 97, 98–111. https://doi.org/10.1016/j.apsoil.2015.08.015.

Salako, G., Russell, D.J., Stucke, A., Eberhardt, E., 2023. Assessment of multiple model algorithms to predict earthworm geographic distribution range and biodiversity in Germany: implications for soil-monitoring and species-conservation needs. Biodivers. Conserv. 32, 2365–2394. https://doi.org/10.1007/s10531-023-02608-9.

Santini, L., Belmaker, J., Costello, M.J., Pereira, H.M., Rossberg, A.G., Schipper, A.M., Ceaușu, S., Dornelas, M., Hilbers, J.P., Hortal, J., Huijbregts, M.A.J., Navarro, L.M., Schiffers, K.H., Visconti, P., Rondinini, C., 2017. Assessing the suitability of diversity metrics to detect biodiversity change. Biological Conservation, SI:Measures of biodiversity 213, 341–350. https://doi.org/10.1016/j.biocon.2016.08.024.

Savigny, J.-C., Cuvier, G., 1826. Analyse des travaux de l'Académie royale des Sciences pendant l'année 1821, partie physique [Zoology from p. 172]. In: Mémoires de l'Académie (Royale) Des Sciences de l'Institut (Imperial) de France, pp. 176–184.

Schmarda, L.K., 1861. Neue Wirbellose Thiere Gesammelt auf einer Reise um die Erde. Vol. vol. 1(2). 212pp. Verlag von Wilhelm Engelmann, Leipzig.

Shipley, B.R., McGuire, J.L., 2022. Interpreting and integrating multiple endemism metrics to identify hotspots for conservation priorities. Biol. Conserv. 265, 109403. https://doi.org/10.1016/j.biocon.2021.109403.

Si-Moussi, S., 2020. Apports de la fouille de données à la modélisation des communautés écologiques (These de doctorat). SupAgro, Montpellier.

Singh, J., Cameron, E., Reitz, T., Schädler, M., Eisenhauer, N., 2021. Grassland management effects on earthworm communities under ambient and future climatic conditions. Eur. J. Soil Sci. 72, 343–355. https://doi.org/10.1111/ejss.12942.

Sykes, L., Santini, L., Etard, A., Newbold, T., 2020. Effects of rarity form on species' responses to land use. Conserv. Biol. 34, 688–696. https://doi.org/10.1111/cobi.13419.

Szlávecz, K., Csuzdi, C., 2007. Land use change affects earthworm communities in eastern Maryland, USA. Eur. J. Soil Biol. 43, S79–S85. https://doi.org/10.1016/j.ejsobi.2007.08.008.

Tabarelli, M., Peres, C.A., Melo, F.P.L., 2012. The 'few winners and many losers' paradigm revisited: emerging prospects for tropical forest biodiversity. Biol. Conserv. 155, 136–140. https://doi.org/10.1016/j.biocon.2012.06.020.

Tóth, Z., Szlavecz, K., Epp Schmidt, D.J., Hornung, E., Setälä, H., Yesilonis, I.D., Kotze, D.J., Dombos, M., Pouyat, R., Mishra, S., Cilliers, S., Yarwood, S., Csuzdi, C., 2020. Earthworm assemblages in urban habitats across biogeographical regions. Appl. Soil Ecol. 151, 103530. https://doi.org/10.1016/j.apsoil.2020.103530.

Vidal, A., Blouin, M., Lubbers, I., Capowiez, Y., Sanchez-Hernandez, J.C., Calogiuri, T., van Groenigen, J.W., 2023. Chapter one - the role of earthworms in agronomy: Consensus, novel insights and remaining challenges. In: Sparks, D.L. (Ed.), Advances in Agronomy. Academic Press, pp. 1–78. https://doi.org/10.1016/bs.agron.2023.05.001.

Vimal, R., Devictor, V., 2015. Building relevant ecological indicators with basic data: species and community specialization indices derived from atlas data. Ecol. Indic. 50, 1–7. https://doi.org/10.1016/j.ecolind.2014.10.024.

Violle, C., Thuiller, W., Mouquet, N., Munoz, F., Kraft, N.J.B., Cadotte, M.W., Livingstone, S.W., Mouillot, D., 2017. Functional rarity: the ecology of outliers. Trends Ecol. Evol. 32, 356–367. https://doi.org/10.1016/j.tree.2017.02.002.

Wall, D.H., Bardgett, R.D., Behan-Pelletier, V., Herrick, J.E., Jones, T.H., Six, J., Strong, D.R., Putten, W.H. van der, Ritz, K., 2012. Soil Ecology and Ecosystem Services. OUP Oxford.

Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological monographs 30, 279–338. https://doi.org/10.2307/1943563.

Williamson, M., Fitter, A., 1996. The varying success of invaders. Ecology 77, 1661–1666. https://doi.org/10.2307/2265769.

Wills, A., Abbott, I., 2003. Landscape-scale species richness of earthworms in the Porongurup Range, Western Australia: influence of aspect, soil fertility, and vegetation type. Biol. Fertil. Soils 39, 94–102. https://doi.org/10.1007/s00374-003-0683-5.

Wilson, J.S., Pan, A.D., General, D.E.M., Koch, J.B., 2020. More eyes on the prize: an observation of a very rare, threatened species of Philippine Bumble bee, Bombus irisanensis, on iNaturalist and the importance of citizen science in conservation biology. J. Insect Conserv. 24, 727–729. https://doi.org/10.1007/s10841-020-00233-3.

Wretenberg, J., Lindström, Å., Svensson, S., Thierfelder, T., Pärt, T., 2006. Population trends of farmland birds in Sweden and England: similar trends but different patterns of agricultural intensification. J. Appl. Ecol. 43, 1110–1120. https://doi.org/10.1111/j.1365-2664.2006.01216.x.

Yang, G., Wagg, C., Veresoglou, S.D., Hempel, S., Rillig, M.C., 2018. How soil biota drive ecosystem stability. Trends Plant Sci. 23, 1057–1067. https://doi.org/10.1016/j.tplants.2018.09.007.

Zeiss, R., Eisenhauer, N., Orgiazzi, A., Rillig, M., Buscot, F., Jones, A., Lehmann, A., Reitz, T., Smith, L., Guerra, C.A., 2022. Challenges of and opportunities for protecting European soil biodiversity. Conserv. Biol. 36, e13930. https://doi.org/10.1111/cobi.13930.

Zeiss, R., Briones, M.J.I., Mathieu, J., Lomba, A., Dahlke, J., Heptner, L.-F., Salako, G., Eisenhauer, N., Guerra, C.A., 2024. Effects of climate on the distribution and conservation of commonly observed European earthworms. Conserv. Biol. 38, e14187. https://doi.org/10.1111/cobi.14187.

Zuo, J., Muys, B., Berg, M.P., Hefting, M.M., van Logtestijn, R.S.P., van Hal, J., Cornelissen, J.H.C., 2023. Earthworms are not just "earth" worms: multiple drivers to large diversity in deadwood. For. Ecol. Manag. 530, 120746. https://doi.org/10.1016/j.foreco.2022.120746.