SOIL ORGANISMS 97 (0) · 2025

Online First
https://doi.org/10.25674/449

Status and trends in soil biodiversity – a national survey of Germany

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Received 20 January 2025 | Accepted 21 March 2025 | Published online 16 June 2025

* This paper is part of the special collection 'Faktencheck Artenvielfalt'

Abstract

Soils are among the habitats with the most species-rich communities on our planet. However, knowledge about soil biodiversity status and trends varies by organism group and this also applies to Germany. For soil microorganisms and microfauna, only a fraction of the expected number of species has been described so far. For most groups of soil mesofauna, including collembolans, oribatid mites, and enchytraeids, checklists exist, but yet undescribed and cryptic species are to be expected, and data on the distribution and trends of taxa are missing. Larger animals belonging to the soil macrofauna, including earthworms, millipedes, centipedes, ants, isopods, ground beetles, and spiders, are better studied, and checklists and Red Lists exist in Germany. However, even in these rather well-studied groups, genetic information is limited and population trends for species remain largely unknown due to the lack of long-term, large-scale monitoring programs. Only few soil animal groups have been sufficiently studied to allow conclusions on their regional distribution and the degree of endemism or the distribution of possible neobiota.

At the national, European, and global scale, data on soil biodiversity in space and time is very patchy and inconsistent. We therefore also lack baseline values to record and assess potential changes that are currently taking place. Moreover, soils are heterogeneous, varying spatially and temporally, and soil biodiversity distribution is influenced by the dynamics of resources and habitat characteristics. Spatial variation in the presence of soil animals depends on microhabitat structure, animal body size, animal mobility, and dispersal. At small scales, the physical structure and pore space of the soil play an essential role for soil organisms and their interactions. At larger scales, different habitat types contribute to soil biodiversity, with geological substrate playing a key role. Compared to aboveground communities, soil biota are more buffered against climatic fluctuations and climate change effects are thus likely to be less pronounced and delayed. Even in a rather well-studied country like Germany, our understanding of the status and trends of soil biodiversity is still scarce, and we urgently need research initiatives of taxonomists, soil ecologists, data scientists, and molecular biologists who would jointly discover and monitor soil biodiversity, and predict possible spatio-temporal changes and their consequences.

Keywords Biodiversity trend | biodiversity change | Red lists | spatial biodiversity distribution | soil animals | soil fauna | soil microorganisms

* Christian Wirth, Helge Bruelheide, Nina Farwig, Jori Maylin Marx, Josef Settele (eds.): Faktencheck Artenvielfalt. oekom verlag, 2024. (ISBN: 978-3-98726-095-7, https://doi.org/10.14512/9783987263361)

Background

Above-ground, Germany faces dramatic losses of species diversity e.g., in several insect taxa that became well known around the world (Hallmann et al. 2017, Seibold et al. 2019). However, it is currently unknown what is happening below-ground, since soil organisms are usually ignored in biodiversity assessments and reports (Phillips et al. 2017, Guerra et al. 2021a). This represents a drastic bias in our picture of actual biodiversity, because soils are among the habitats with the most species-rich invertebrate communities on our planet (Eisenhauer & Hines 2021; Anthony et al. 2023). Soils are estimated to hold ~59% of the global biodiversity (Anthony et al. 2023), with thousands of microorganisms and tiny animals fulfilling important ecosystem functions and services, such as nutrient cycling, carbon sequestration, food production, and water regulation (Bardgett & van der Putten 2014; Eisenhauer & Hines 2021; Kleemann et al., 2025 This issue). Recording the status and recognizing trends in species composition in soil is therefore a particularly important task (Guerra et al. 2021a). However, the high level of species richness together with the cryptic nature of soil and the small body size of its inhabitants is at the same time the reason why soil biodiversity data is still very incomplete at national to global scales. Monitoring species composition and trends is time-consuming, needs expert knowledge and a combination of different techniques. On a large scale, monitoring programs for a few selected taxa have recently become possible through the use of molecular methods. Still, taxonomic expertise and traditional morphology-based analysis of communities remain essential for most groups of soil organisms. Using Germany as an example, we here summarize what is presently known about the status and trends of soil biodiversity at a national level and the measures that are undertaken in order to increase this knowledge.

Number and identity of soil-dwelling taxa occurring in Germany

The availability of data regarding species inventories in soil varies by organism group, and our knowledge gaps generally increase with decreasing body size and increasing biodiversity of the group (Table 1). For soil microflora and microfauna, only a fraction of the expected number of species has been described and genetically characterized so far (Origiazzi et al. 2016). For instance, for bacteria, archaea, fungi, protozoa, algae, and nematodes, we expect a high number of yet undescribed species, and we are still far from having a complete species list for Germany.

While comprehensive data on the diversity and variability of soil prokaryote communities, i.e. **bacteria and archaea,** is not yet available for Germany, monitoring projects have been realized in the USA, China, France, and England in recent years. They used PCR-based DNA analysis, which provide valuable information as indicators of diversity, but only allow limited conclusions to be drawn about biomass and changes in activities or ecological functions. New methods based on metagenome analyses provide more detailed functional (potential) data, but only quantitatively dominant taxa can be recorded (Jansson & Hofmockel 2018). However, the less dominant taxa provide important ecosystem services, such as nitrification in the nitrogen cycle, which would be overlooked in this way (Jousset et al. 2017). A combination of PCR-dependent and -independent DNA analyses is therefore ideal for monitoring. In order to facilitate comparability between different monitoring programs, it will be further necessary to develop standardized protocols for soil sampling, storage, DNA extraction, and sequence analyses (Finn et al. 2023).

The occurrence and distribution of phytopathogenic **fungi** is recorded, for example, for important cereal diseases by plant protection services at state level. Comparable information at the national level is, however, not available for saprotrophic or mycorrhizal fungi as well as for a large number of free-living fungi without any host relationship. Information on temporal changes in the diversity of macrofungi can possibly be obtained via Citizen Science and the German Society for Mycology (www.dgfm-ev.de), e.g. regarding edible mushrooms.

For unicellular **green algae** and **cyanobacteria**, we have neither species inventories nor systematic studies on temporal changes in their species composition for Germany. The knowledge gap is in striking contrast to the great importance of green algae and cyanobacteria as primary producers, nitrogen fixers, carbon stores, and food sources in the soil energy and nutrient balance as well as in soil food webs, where they live in near-surface layers with on average 5.5 million cells per gram of soil (Jassey et al. 2022; O. Schmidt et al. 2016).

Protists is a collective term for all unicellular eukaryotic microorganisms that are not plants, animals, or fungi; it thus is a paraphyletic group. The level of knowledge about their diversity and their contribution to the biotic communities in soils is also very limited. New sequence-based studies provide first insights into the great variety and diversity of protists in soils (Bonkowski et al. 2019). They point out that microscope-based studies only cover a small proportion of protists and provide a limited picture of their community

Table 1. State of knowledge on the species occurrence of important soil organism groups in Germany, sorted by increasing body size and degree of coverage.

Organim Group	Number of species known in Germany	Reference	Degree of coverage	Red List
Viruses	?	-	insufficient	-
Bacteria, Cyanobacteria, Archaea	?	-	insufficient	-
Algae (e.g. green algae)	?	-	insufficient	-
Protists	?	-	insufficient	-
Fungi	?	-	insufficient	-
Actinedid mites (Endeo- & Prostigmata)	?	-	insufficient	-
Nematodes (Nematoda)	ca. 2.000	Sturhan & Hohberg 2016	very incomplete	-
Rotifers (Rotifera)	ca. 300	M. Devetter, pers. reference, estimated from well-studied Czech Republic	very incomplete	-
Tardigrades (Tardigrada)	91	Bingemer & Hohberg 2017 Schuster & Schill 2024	very incomplete	-
Predatory mites (Mesostigmata)	ca. 900	A. Christian, pers. reference	incomplete	-
Collembolans (Collembola)	525	www.edaphobase.org	incomplete	-
Oribatid mites (Oribatida)	560	Weigmann et al. 2015	incomplete	in progress
Enchytraeids (Enchytraeidae)	152	www.edaphobase.org Schmelz & Collado 2010	incomplete	-
Proturans (Protura)	41	Balkenhol & Szeptycki 2003	incomplete	-
Diplurans (Diplura)	26	Christian 2003, Spelda 2025	incomplete	-
Rove Beetles (Staphylinidae)	1.479	J. Schmidt et al. 2021	incomplete	BFN2021/5
Ground Beetles (Carabidae)	582	J. Schmidt et al. 2016	good	BFN2016/4
Spiders (Araneae)	992	Blick et al. 2016	good	BFN2016/4
Woodlice (Oniscidea)	49	Grünwald 2016	good	BFN2016/4
Ants (Formicidae)	116	Seifert 2011	good	BFN2011/3
Pauropods (Pauropoda)	36	Voigtländer et al. 2016	good	-
Symphylans (Symphyla)	18	Voigtländer et al. 2016	good	-
Centipedes (Chilopoda)	56	Decker et al. 2016	good	BFN2016/4
Millipedes (Diplopoda)	118	Reip et al. 2016	good	BFN2016/4
Earthworms (Lumbricidae)	49	Lehmitz et al. 2016, Graefe et al. 2019	good	BFN2016/4

structure. Microscopic studies are mainly limited to the Ciliata and testate amoebae (Wanner et al. 2008, Wanner & Xylander, 2003). Sequence-based methods, however, indicate that other protist groups, especially Cercozoa and Amoebozoa, dominate in soils and account for the majority of the diversity. Parasitic protists from the Alveolata group, which have been little studied to date, are also of high diversity (Nguyen et al. 2021).

Nematodes are usually well described and monitored for economically important plant parasitic species, but much less regarding free-living nematodes. The latter make up by far the largest fraction of nematodes in soils, both in terms of numbers and species richness. The entire group of soil nematodes are comparatively well studied in some European countries i.e., The Netherlands and Hungary, and it has been roughly estimated that a minimum of 2000 species are likely to occur in Germany (Sturhan & Hohberg 2016). Of these, only 608 species are currently reported and documented in the Edaphobase database for soil biodiversity (www.edaphobase.org) (Russell et al. 2024). The discrepancy is due to the comparatively low number of studies in Germany, a knowledge gap that, in view of the considerable importance of nematodes for virtually all ecosystem processes in soils, especially for nutrient cycling and plant growth needs to be addressed and filled with data in the near future in a combined effort by taxonomists (description of unknown species) and ecologists (monitoring programs) (Gebremikael et al. 2016; van den Hoogen et al. 2019; Topalović & Geisen 2023).

Collembolans with 525 species, **oribatid mites** with 560 species, and **enchytraeids** with 152 species are comparatively well studied in Germany. They are involved in the decomposition of soil organic matter, and enchytraeids in particular play a decisive role in nutrient cycling and soil formation in particular in soils where earthworms are absent (Düker 2003; Römbke 1997). National species catalogues exist for each of the three groups. However, these are certainly not complete, because, firstly, some regions and habitat types in Germany, e.g. urban areas, have hardly been studied to date. Secondly, molecular biological studies show that morphological species identification often fails to recognise cryptic species (Escher et al. 2022, Schmelz et al. 2017). And thirdly, even for morphologically recognisable species, there are too few species recorded compared to other countries (e.g., Potapov et al. 2023). A large study conducted in four federal states in Germany at 36 sites and twelve different habitat types (Toschki et al. 2021) reported 101 enchytraeid species, of which as many as a quarter had not yet been described before. Notably, for each of the three mesofauna groups large-scale monitoring campaigns are lacking but are needed in order to complete the species lists for Germany and at the same time to determine the distribution of the species, their habitat requirements, and extinction risk.

Predatory mites are the most important group of predatory mesofauna in soils. Their diversity is generally well recorded in Germany, with a total of around 900 species. However, as is the case with springtails and oribatid mites, there are probably additional cryptic species. However, molecular studies on the diversity of predatory mites, which could provide information on the existence of cryptic species, are lacking. Predatory mite communities differ greatly between different habitats and are therefore also suitable bioindicators. Other important predatory soil dwellers are **staphylinid beetles**. With around 1500 species they are significantly more diverse than carabid beetles in Germany and this also applies globally (J. Schmidt et al. 2021). In most staphylinid species both larvae and adults live in the pore space system of soils. For this reason and due to their usually smaller body size and higher species richness, they are much less well studied than carabid beetles. Molecular studies that could facilitate and accelerate the assessment of their species diversity are lacking entirely.

Well-studied groups include **earthworms, millipedes, centipedes, pauropods, symphylans, ants, isopods, carabid beetles,** and **spiders**, for which there are checklists and Red Lists in Germany. However, even in these groups genetic information is limited and population trends for species remain unknown due to the lack of long-term, large-scale monitoring programs (Phillips et al. 2017).

Regional distribution and endemism

Only few soil animal groups have been sufficiently studied to allow conclusions on their (supra) regional distribution and the degree of endemism. One notable exception is the largest earthworm native to Germany, the giant earthworm (*Lumbricus badensis*). The representatives of this species grow up to 50 cm long, making them comparatively conspicuous, and they have so far only been found in the southern Black Forest (Lehmitz et al. 2016). The six endemic species within the millipedes, *Glomeris malmivaga*, *Pyrgocyphosoma titianum*, *Rhymogona serrata*, *R. verhoeffi*, *R. wehrana,* and *Xylophageuma vomrathi* have also all been reported from Baden-Württemberg, four of them from the Black Forest (Reip et al. 2016). There are two local endemics of ground beetles in the south-west German highlands, *Nebria praegensis* and *Oreonebria boschi* (J. Schmidt et al. 2016). Of the two endemic spider species, only

Centromerus piccolo, also known as the dwarf moss weaver, is associated with the soil and has so far only been reported from the Lower Rhine and Saxony-Anhalt (Blick et al. 2016). Endemism in soil meso- and microfauna as well as soil microorganisms is still poorly understood due to the lack of data on the distribution of species.

For the same reasons, information on threats to biodiversity in soils is very biased towards a few taxa that are elaborately listed by species experts in the Red Lists, i.e. ants, spiders, carabid beetles, earthworms, myriapods, or used as bioindicators in current monitoring programs of the federal states e.g., some earthworm species, springtails, and soil microbial biomass. Rather alarming examples in Germany are ants and carabid beetles: of the 108 and 582 species in Germany, respectively, 1 and 25 species are considered extinct or lost, 61 and 269 species (56% and 46 %) are included in the Red List, and a further 18 ant and 57 carabid species in the Early Warning List (J. Schmidt et al. 2016). For representatives of the soil meso- and microfauna, the present data basis is too limited to derive changes in their distribution or even predict the degree of endangerment.

Neobiota and invasive species in German soil

We have very limited knowledge on Neobiota and invasive species in soil as well as their impacts on ecosystems. The few known cases are primarily plant and animal pathogens and fruiting body-forming fungi. For example, the tree-damaging fungus *Diplodia pinea* is spreading with climate change in Germany. Another fungal species, the 'salamander plague' *Batrachochytrium salamandrivorans* (Chytridiomycota) that was initially introduced from Asia, has now been detected in some German forest soils, where it may eradicate entire populations of salamanders (Dalbeck et al. 2018). Similar to the oomycete *Phytophtora infestans*, which was brought to Europe from North America and led to the total collapse of the potato harvest and a major famine in Ireland in 1845, potato pests are still arriving in Europe today. For example, a tropical bacterium *Ralstonia solanacearum*, which now survives relatively well in our soils due to the milder winters caused by climate change (Julius Kühn-Institut 2024).

Moreover, the invasion of the nematode *Meloidogyne chitwoodi,* which is a root infesting parasite of many crops (e.g., tomatoes and potatoes), has been detected in Germany in recent years (BVL 2014). Another invasive species is the 4 - 5 cm large flatworm *Obama nungara*, a predator of earthworms; originating from South America, it is spreading rapidly in Europe since 2008 and was detected in a soil sample in Regensburg in 2021 (Kutschera & Ehnes 2021).

By contrast, there is very little information on soil organisms introduced into Germany that do not cause immediate economic or ecological damage. Exceptions are invasive species that are already well established or occur in particular high densities e.g., the thermophilic chilopods, *Cryptops anomalans* and *Lamycetes emarginatus*, the woodlouse *Armadillidium nasatum*, and a collembolan species originating from the USA, *Desoria trispinata* (Decker et al. 2016; Grünwald 2016; Roithmeier et al. 2018).

Soil biodiversity in space and their temporal trends

We have very patchy and inconsistent data on soil biodiversity in space and time, both on national and also on European and global scale (Guerra et al. 2021a, 2024). Soils are very heterogeneous substrates and vary greatly both spatially and temporally. Soil biodiversity distribution is controlled by the spatial and temporal dynamics of resources and habitat characteristics (Bluhm et al. 2019; Pollierer et al. 2007). Usually, most of the biomass and diversity of soil organisms is concentrated in the layers a few centimetres below the surface, where oxygen and organic substrates are available, while in agricultural fields soil organisms may be distributed over the entire plough horizon or are even more numerous in deeper layers, depending on the agricultural practices and environmental conditions (Filser & Fromm 1995). The horizontal variation in the composition and diversity of soil fauna depends strongly on the structure, size, and distribution of microhabitats: On a small scale, the physical structure and pore space of the soil play an essential role for many soil organisms and their interactions (Erktan et al. 2020; Vos et al. 2013); on a larger spatial scale, in particular different habitat types contribute to the diversity of soil organisms (Toschki et al. 2021). However, data from the Biodiversity Exploratories suggest that the drivers of soil biodiversity differ across spatial scales and taxonomic groups (Le Provost et al. 2021).

An important factor that contributes to the spatial variation in the composition and diversity of soil organisms is the geological substrate of the soil. German soils are characterized by a very heterogenous pattern of geological substrate with small parts of the landscape showing an acidic upper soil layer with a pH <5 or calcareous soils with pH >7 (Scherstjanol et al. 2021).

Soil animal communities in calcareous soils differ fundamentally from those in acidic soils. The pH value of the soil also characterizes the composition of soil microorganisms and important macro-decomposers such as earthworms, woodlice, and millipedes are dependent on the availability of calcium and occur in low diversity and density in acidic soils (Schaefer 1991). For the turnover of the species composition of soil fauna on a large spatial scale (e.g., Germany or Europe), the active dispersal potential of soil animals is typically lower than the passive dispersal potential, i.e. transport by wind (Lehmitz et al. 2011), water currents (Schuppenhauer et al. 2019), and phoresis on larger animals (Türke et al. 2018). Humans contribute to the homogenization of soil animal communities worldwide (Banerjee et al. 2024; Delgado-Baquerizo et al. 2021). Compared to biotic communities above the soil, soil biota is more strongly buffered by the soil against fluctuations in climatic factors. High temperatures in summer and the associated loss of soil moisture are probably more important for soil biodiversity than low temperatures in winter (Junggebauer et al. 2024; Phillips et al. 2024).

The diversity and composition of soil animal communities generally changes considerably following major disturbances or interventions (Dunger et al. 2001; Scheu & Schulz 1996; Phillips et al. 2024). Different groups of soil organisms reach their maximum diversity and highest densities in very different habitats e.g., testate amoebae and some groups of nematodes in acidic forests, while it is alkaline mixed forests for most groups of macrofauna. Sometimes we find spatial patterns that are still unresolved, such as the clear east-west distribution of two closely related species of millipedes in Germany (Fig. 1). Due to insufficient data, we currently only have a very limited understanding of the spatio-temporal dynamics of soil organisms. We also lack baseline values to record and assess potential changes that are currently taking place. A national assessment of soil biodiversity is a complex endeavour, but fundamental to understand the current state and trends of soil biodiversity (Guerra et al. 2024).

In contrast to the above-ground fauna, for which dramatic decline in species and biomass has been documented in some cases in recent years (Hallmann et al. 2017; Seibold et al. 2019), there is no sufficient data on temporal trends in the abundance and diversity of soil animals. One exception is carabid beetles, which are easy to detect using pitfall traps, where a drastic decline in diversity has been documented in northern Germany (Homburg et al. 2019) and in England (Brooks et al. 2012). However, since carabid beetles live primarily on the soil surface, these results are not transferable to species that live in the soil. In addition, studies with pitfall traps only allow very limited insight into quantitative changes in the structure of animal communities.

As part of the Biodiversity Exploratories (https://www.biodiversity-exploratories.de), a DFG-funded infrastructure priority program for functional biodiversity research, quantitative studies are being carried out on the basis of heat-extracted soil animals in beech forests of different ages and in coniferous forests. Over a period of twelve years, these studies showed no consistent trend of changes in the density and diversity for a broad spectrum of soil arthropods (Junggebauer et al. 2024; M. Pollierer pers. comm.). In arable land, however, many studies have shown that intensification of agriculture is linked to a decrease in the density and diversity of soil organisms (Phillips et al. 2024). It is therefore very likely that soil biodiversity in open land habitats has decreased as a result of intensified land use in recent decades. This assumption is confirmed by recent experimental studies, which show that the biodiversity of soil fauna decreases with intensification of land use (Phillips et al. 2024; Yin et al. 2019; Yin et al. 2020).

In addition to changes in land-use intensity, the influence of changes in crops, fallow periods after harvesting and crop rotation on soil biodiversity has also been documented, showing that the density of soil animals is particularly low in maize fields (Scheunemann et al. 2015; Filser et al., 2025, this issue). However, there is no convincing documentation of these processes on larger spatial scales.

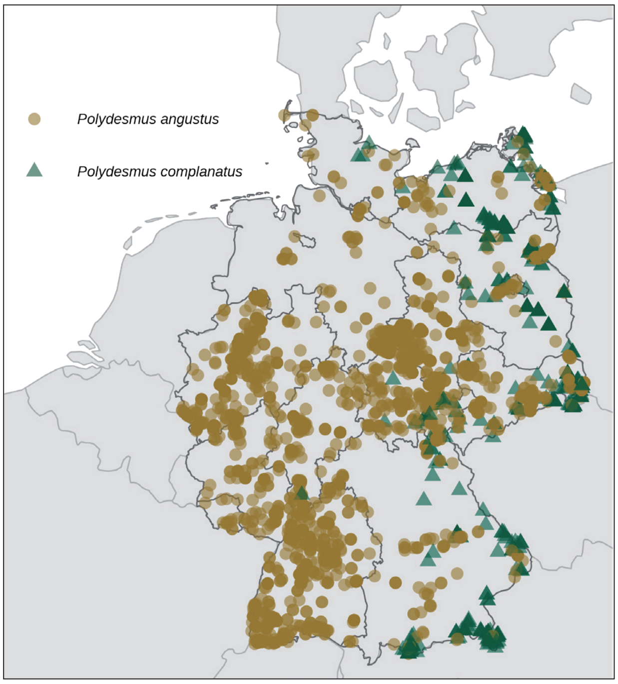

Figure 1. Distribution of two millipede species *Polydesmus angustus* and *Polydesmus complanatus* in Germany, based on data from Edaphobase (www.edaphobase.org, Russell et al. 2024).

The Hohenheim Climate Change Experiment (klimawandel.uni-hohenheim.de) gives an idea of the trends in soil biodiversity to be expected under climate change scenarios. In this large-scale field experiment, global warming and increasing drought were simulated on arable land. Both climate change drivers primarily affected the composition of the species communities in the short term (2 years), while species diversity remained unchanged, at least in the short term, compared to the reference areas not exposed to climate change (Guo et al. 2021; Siebert et al. 2019). Many factors influencing soil biodiversity have only been studied in isolation, and there is a lack of information on the interactions of co-occurring factors that can have synergistic effects on soil organisms and functions (Rillig et al. 2019; Beaumelle et al. 2023). The limited information existing so far suggests non-additive (i.e., synergistic) effects of different global change drivers on soil biodiversity (Rillig et al. 2019; Ni et al. 2025).

Present and next steps

Research and monitoring initiatives, such as Soil BON (global, https://monitor.soilbon.org/; Guerra et al. 2021b) and Unknown Germany (national, www.unknown-Germany.org), are currently developing research communities and launching projects to promote species discovery and the assessment of soil biodiversity status and trends. The National Soil Monitoring Centre, founded in December 2024, is currently preparing the nationwide baseline survey of soil biodiversity and the establishment of a long-term monitoring program. Future monitoring and the evaluation of future trends in soil biodiversity will then be realised on this baseline survey. Looking back in time, trends over the last 25 to 45 years will be determined by large-scale resampling of soils where nematodes, collembolans, oribatid mites, and enchytraeids were studied on species level in the 1980s and 1990s in a project funded by the Leibniz Association called TrenDiv, which will start in 2025.

AI-based modelling methods will make it possible to close current gaps from existing distribution data and area-wide environmental data, identify drivers, predict future changes, and also validate these calculations. A good example is the global trend analysis by Patoine et al. (2022), which modelled the spatio-temporal change in soil microbial biomass for the years 1992 to 2013 based on a large data synthesis. A spatially better resolved analysis for Germany is still pending. For many soil organism groups, however, the data basis for this still needs to be increased to a minimum, as AI-based modelling can only be as good as its data basis.

Databases such as Edaphobase, which currently hosts around 480,000 data sets, bundle all available data on the occurrence of invertebrates in soil (national, European, global) together with their habitat requirements and make them openly accessible for comprehensive evaluations, modelling, and predictions (Russell et al. 2024, www.edaphobase.org). Imaging, machine learning, and robotics increase and accelerate sample throughput.

Large project approaches such as the German Barcode of Life and Translational Biodiversity Genomics, in close collaboration with taxon experts, are developing the necessary genomic resources, laboratory and bioinformatic tools, and are establishing the routines and species-specific sequence libraries to enable the use of molecular techniques (metabarcoding, metagenomics) for large monitoring campaigns recording species inventories of soil organism communities in the future (Geiger et al. 2016, Lehmitz & Decker 2017, Schenk et al. 2017, Wesener et al. 2016, Collins et al. 2023, A. Schmidt et al. 2022).

Another crucial need is to counteract the current loss of taxonomic expertise on soil biodiversity. To reverse this trend, the scientific community needs to invest in capacity building. Online and in-person teaching programs are developed at national, European, and global level, e.g. the SoilMATs - Soil Meiofauna Advanced Taxonomy school within the EU TETTRIs initiative of the Consortium of European Taxonomic Facilities (CETAF), to attract and train young researcher in taxonomy, phylogeny, and ecology in particular of understudied soil micro- and mesofauna groups (https://cetaf.org/dest/soilmats-soil-meiofauna-advanced-taxonomy-school/). The establishment of taxonomists, the continuation of the above-mentioned and other urgently needed initiatives, and the decoding of knowledge gaps are only possible if the appropriate resources are provided by funding bodies.

Acknowledgments

We acknowledge funding by the German Federal Ministry of Education and Research within the Research Initiative for the Conservation of Biodiversity (FedA) under the funding code 16LC2001B and by the German Research Foundation (Deutsche Forschungsgemeinschaft, DFG; FZT 118, 202548816; Ei 862/29-1).

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