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Sustainable measures for the protection and restoration of soil biodiversity in Germany

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Abstract

Soils are habitat for the majority of terrestrial life and soil biodiversity plays a crucial role in providing important ecosystem services. However, soil biodiversity is under threat and measures need to be taken to protect and restore it, but conservation so far usually focuses on the protection of attractive or endangered aboveground species. Furthermore, the small size of soil organisms and the considerable taxonomic expertise required for their identification result in a poor consideration of soil biodiversity when evaluating conservation measures. In this review, we compile the available knowledge on the effectiveness of conservation and restoration measures for soil biodiversity in Germany. We provide information on the following habitats: forests, inland wetlands (peatlands and floodplains), coastal sites, and urban areas; and on aboveground as well as belowground soil micro-, meso-, and macrofauna, as well as (to a lesser extent) soil microorganisms. Repeated measures, like management of forest sites are mainly applied in economically utilized areas, with soil biodiversity benefitting from reduced land-use intensity and the creation of a more natural environment. In strongly degraded landscapes (e.g., dried wetlands), an initial impulse measure is usually needed to restore natural conditions, with subsequent conservation management afterwards. In general, habitat heterogeneity is an important factor for increasing soil biodiversity not only above- but also belowground. Its positive effects apply at landscape scale by providing diverse environmental conditions and stepstone habitats, as well as at the small scale with many microhabitats at a few square meters. The main goal of protection and restoration measures must not be to maximize the number of species in a given area, but to establish a habitat-specific species community.

Keywords German Biodiversity Assessment | Collembola | Oribatida | Carabidae | Araneae

1 Introduction

Biodiversity loss is one of the most relevant and pressing topics in our present world. However, our knowledge on the biodiversity of soil organisms is still fragmentary, which is in strong contrast to the fact that close to 60 % of species worldwide are directly connected to soil as a habitat (Anthony et al. 2023). Therefore, a group of 22 German soil biodiversity scientists came together as part of the recent German Biodiversity Assessment (the so-called "Faktencheck Artenvielfalt"; Wirth et al. 2024) covering the status and temporal trends of

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soil biodiversity, drivers of soil biodiversity change, and soil-related ecosystem services in Germany (for more details see Eisenhauer et al. 2024). The reviewed literature included a set of >5,500 scientific papers (indexed in Web of Science, search by 31 July 2023) and grey literature reports e.g., degree theses and final project reports by governmental and non-governmental organizations (done via manual search). Here, we present an overview of sustainable protection and restoration measures of soil biodiversity from this national report, divided according to habitat type. Although we focus on Germany, the results within the habitat types can certainly be transferred to other countries located in temperate climate zones. Above that, Germany is a good starting point for such a review, because several long-term studies on the effects of different kinds of soil protection measures have been performed here in recent years. For instance, in large size biodiversity experiments manipulating aboveground biodiversity like the Jena experiment (Roscher et al. 2004, Eisenhauer 2024), or the Biodiversity Exploratories project that addresses effects of land use on soil organism populations (e.g., Fischer et al. 2010, Erdmann et al. 2012, Pollierer & Scheu 2017).

When evaluating soil biodiversity, it should be noted that species numbers and abundances depend heavily on the habitat type and vary between taxa (Toschki et al. 2021, Hohberg et al. 2025). In particular, there are clear differences between forests and open land. While Oribatida, Collembola, and Chilopoda reach the highest species numbers in forests, Diplopoda, Lumbricidae, and Enchytraeidae tend to be most species-rich in extensively used grassland and forests. Enchytraeidae are sometimes even (more) species-rich in arable land (Toschki et al. 2021). When comparing different forest types, the diversity of most organism groups is higher in deciduous and mixed forests, whereas abundances of Oribatida, Collembola, Diplopoda, and Enchytraeidae are particularly high in spruce forests (Eisenhauer et al. 2024). However, a high number of species is not necessarily an indicator of near-natural conditions. Special habitats like floodplains, bogs, and salt marshes for instance support a small number of highly specialized species, which means that not only species numbers but also species identity needs to be considered (Lehmitz 2014).

Nature conservation measures are seldom applied for the sake of soil biodiversity, but usually for the protection of landscape as well as attractive or endangered aboveground species, or for the restoration of ecosystem services, e.g. flood prevention (Kleemann et al. 2025). Soil biodiversity can only indirectly benefit from these measures and is usually not considered in the evaluation of conservation projects, also because their extremely high diversity and heterogeneous distribution in space and time makes their assessment difficult and time-consuming (Goldmann et al. 2016, Goldmann et al. 2020). Evidence for the strength and direction of effects of conservation measures on soil organisms is therefore scattered and mainly restricted to ecosystems in economically utilized areas, i.e., forests and agricultural soils (see Doms-Grimm 2024), in which soil biodiversity is expected to influence yield or other ecosystem services.

In the present publication, we aim to sum up the results from a systematic review about existing knowledge on effects of protection measures on different soil organism groups in forests, inland wetlands, coastal soils, and urban areas in Germany. A summary of relevant measures and their effect on soil biodiversity is given in Table 1. Agricultural land is considered in a

Table 1. Overview of sustainable measures for soil fauna protection.

Habitats	Measure	Description	Impact on soil biodiversity
all	Establishment of nature conservation areas; improvement of degraded soils	reduction of land-use intensity, restoration of near-natural environmental, and particularly soil conditions	Conservation and protection of existing soils and soil biodiversity, promotion of biodiversity in degraded soils
all	Increasing small-scale heterogeneity	Reduce area covered by uniform land-use types, create structural elements, increase local plant biodiversity	Increasing biodiversity through an increase in microhabitats (= ecological niches), diversification of food resources and microclimate, improved dispersal through stepping stone habitats
all	Reduced land-use intensity	Reduction in use of fertilizer, pesticides, heavy machinery, grazing pressure; reduced harvest frequency/intensity	Conservation and protection of existing soils and soil biodiversity, reduction of soil compaction, pollution and physical impairment
all	Increased plant/crop diversity	In open land: crop rotation, mixed crops and catch crops, field margins, hedge rows, fallow land; In forest: transition from monocultures to mixed forest, agro-forest systems Urban area: reduced mowing frequency in urban greenspace (parks etc.)	Increased food diversity (root exudates, litter, seeds) and increased number of microhabitats

Table 1 continued.

Habitats	Measure	Description	Impact on soil biodiversity
all	Promotion of native plant species	Removal of invasive plant species, planting/ sowing of native trees, shrubs, herbs	Increased adaptation of soil fauna to native plant-based food sources and consequently improved decomposition
forest	Reduction in use (and individual weight) of heavy machinery	Use of smaller vehicles, reduction in weight per unit area (e.g., via caterpillar vehicles)	Reduced soil compaction
forest	Diversification of tree age within individual stands	Preserving old tree stands (> 180 years), promotion of stands of different age at the landscape level	Increased number of microhabitats, diversification of herb layer and micro climate via dense and sparse patches, promotion of species with low dispersal abilities
forest	Adaptation of timber harvest system	Single-stem or group harvest instead of clearcutting, preservation of old habitat trees	Preservation of microhabitats, habitat structure, stepping stone habitats
forest	Dead wood retention	Retention of dead wood in different decay stages and from different tree species; Retention of individual wind thrown tree stems (also in managed forests)	Increase of availability and diversity of food sources; increase in number of hiding places and nesting space; increased moisture
floodplains	Re-connection of fossil floodplain to river flood regime	Relocation of embankments, removal of bank enforcements and river straightening measures, re-connection of oxbow lakes	Increased temporal and spatial heterogeneity increase microhabitat number; reduction of velocity
floodplains	(Re) establishment of floodplain habitats	Establishment of sand banks, dunes, peninsulas	Increased number of typical habitats for specialized species
peatlands	Rewetting	Removal of drainage systems (pipes, pumps, ditches), raising of ground water level to 10 cm below soil surface	Changes in community composition: promotion of specialized species, reduction of generalists
peatlands	Promotion of peatland vegetation	Inoculation of peat moss, allocation of cuttings from other peatlands	Accelerated establishment of peatland typical environment
peatlands	Top soil removal	Uppermost soil incl. vegetation is removed	Reduction in nutrient availability promotes specialized flora and fauna; reduction of non-peatland species in soil seed bank
peatlands	Removal of tree and shrub saplings	Removal of tree and shrub saplings	Reduction of shadow, competition and water drainage by woody vegetation promotes peatland typical environment
peatlands	Low-intensity mowing or grazing	Grazing by water tolerant livestock (e.g., water buffalo)	Supports peatland-specific vegetation through suppression of trees and shrubs
coastal sites	Restoration of salt marshes	Relocation of embankments provides space for natural establishment of salt marsh vegetation	Changes in community composition: promotion of specialized halophilic species, reduction of generalists
coastal sites	Protection and conservation of dunes	Prohibition to enter dunes, establishing of typical vegetation (e.g., European beachgrass)	Reduction of erosion
coastal sites	Moderate grazing	Reduction of grazing intensity by sheep / cattle	Reduced trampling and erosion, reduced dominance of grazing tolerant herbs
urban area	Implementation of allotment gardens and urban gardening space in urban planning	Active promotion of green spaces under low-intensity use but high plant diversity	Establishment of small scale, heterogeneous habitats, stepping stone habitats
urban area	Unsealing of soil surfaces	Removal of concrete surfaces from squares, yards, pathways and entrances; Replacement of asphalt with grass pavers, removal of gravel gardens	Establishment of habitats for soil organisms
urban area	Remediation of former landfills	Active planting of vegetation in parallel to natural succession	Establishment of habitats for soil organisms
urban area	Green roofs, planted substrate-filled, vertical modules at walls	Creation of green space on non-used private and public area	Establishment of habitats for soil organisms, stepping stone habitats

separate article in the present issue (Filser et al. 2025). Since appropriate measures differ between habitats, our review is separated into single sections focusing on forests, inland wetlands, coastal soils, and urban areas, respectively. Further, we divide biodiversity protection measures into environment-related measures, and actor-related measures that aim to change the actions of actors by providing information and enacting laws, permissions and financial incentives. Here, our main focus is on the environment-related measures, because they affect soil biodiversity directly. For a discussion of actor-related measures see last paragraph.

Environment-related conservation measures can be classified into three categories:

- Impulse: One-time interventions, such as rewetting of peatlands, implemented to address specific environmental issues and change environmental conditions in the long term.
- Management: Ongoing or periodic interventions, including practices like forest thinning, aiming at maintaining long-term ecological health and integrated into routine land-use activities.
- Protected Areas: Designated regions, such as nature reserves or national parks, where human activities are restricted to preserve biodiversity and protect ecosystems from external pressures. Unfortunately, we are not aware of any studies in Germany assessing the effects of the establishment of protected areas on soil biodiversity.

2 Forests

Forests fulfil many important soil-related ecosystem services such as carbon storage, provision of drinking water, and nutrient supply (FAO et al. 2020, Wagg et al. 2014). Around 32 % (11.5 Mio ha) of the German area is covered by forests (BMEL 2024). After the last ice age, the forests of Central Europe were naturally characterised by beech-dominated deciduous forests. However, centuries of human management have changed them considerably, and beech trees have largely been replaced by faster-growing, non-native tree species, often in monoculture. Today, climatic changes require forest conversion towards more site-appropriate and climate-resilient (mixed) forests. The fourth National Forest Inventory in 2024 confirmed a mixed forest share of 79 % in German forests, with an upward trend (BMEL 2024).

Changes in tree species identity or in the number of co-occurring tree species (e.g., during forest conversion from monoculture to mixed forest) have both direct and indirect effects on soil organisms. For example, the composition of tree species affects nutrient supply for soil animals via the chemical composition of litter, while at the same time root morphology, root exudates and associated mycorrhiza vary (Hölscher et al. 2002, Lang et al. 2011, Prada-Salcedo et al. 2021). Several studies revealed that species number and tree identity do not significantly affect species numbers or abundances of different soil organism groups, but their species composition (Cesarz et al. 2013, Hofmann et al. 2023, Penone et al. 2019, Pollierer et al. 2021, Richter et al. 2023, Russell & Gergocs 2019, Salamon & Alphei 2009, Salamon & Wolters 2009). For example, Collembola density and species richness exhibited hardly any differences between beech forests, spruce forests and mixed stands of the same age (Salamon & Alphei 2009). However, the proportion of fungivorous Collembola was higher in mixed stands due to higher fungal biomass, while more epedaphic and herbivorous Collembola species were found in spruce forests. A meta-analysis of springtail communities in German deciduous, coniferous forests and mixed forests also showed that forest conversion had little impact on species abundance and species number (Russell & Gergocs 2019). Instead, the species composition changed gradually from deciduous to mixed to coniferous forests. The same is true for soil nematode communities. While ash trees mainly promote bacterivorous nematodes, abundances of fungivores increased under beech (Cesarz et al. 2013). In a comparison of four transitional stages from pure coniferous forest of the same age to mixed stands of *Fagus sylvatica*, *Abies alba* and *Picea abies* of different ages, forest conversion mainly influenced the proportion of different nematode feeding types (Salamon & Wolters 2009). In a recent metabarcoding study on the effect of tree species on the fungal community in soil and on the bark of trees, tree species explained only 1–3 % of variances in species numbers, but had a major effect on species composition (Hofmann et al. 2023). Only a few fungal species occurred on all tree species but in high abundances.

The effects of identity and diversity of tree species and stand age on various groups of organisms were also investigated within Germany's probably most extensive long-term monitoring program, the Biodiversity Exploratories (Fischer et al. 2010). Comparing the effects of forest management in three different regions of Germany confirmed that for most taxa forest type had only a minor influence on the abundance and diversity of soil organisms, but did have an impact on species composition. For example, forest type explained only 4 and 8 % of variances in nematode biomass in the litter layer and mineral soil, respectively. However, the community composition (at family level) changed with forest type (Richter et al. 2023). Similarly, species numbers of Collembola differed only marginally between forest types (Pollierer & Scheu 2017). However, a study at the level of trophic groups showed that macrofauna herbivores were most diverse in unmanaged forests and that predatory macrofauna was the only group directly negatively affected by forest management intensity (Pollierer et al. 2021). Considering various correlated factors separately rather than management type as a whole, revealed that canopy cover significantly affected 13 groups of plants, animals, fungi, and bacteria (Penone et al. 2019). With increasing canopy cover, the number and abundance of species decreased, while the proportion of specialized forest species increased (Penone et al. 2019). Canopy cover and the correlated development of shrub and herb layer change the availability and diversity of basal resources of the soil food web (e.g., leaf litter; Eisenhauer et al. 2011, Gilliam 2007). Ganault et al. (2021) show a higher number of species of macrofauna in mixed forests with lower canopy cover compared to pure coniferous forest stands. In general, the response of belowground groups (fungi, bacteria) to forest characteristics may be lower than that of aboveground groups, but the admixing of oaks (here: *Quercus robur* and *Q. petraea*) benefits above- as well as belowground groups (Penone et al. 2019).

The presence of deadwood is of particular importance for soil biodiversity in forests. Deadwood offers a high number of microhabitats, stores rainwater, provides food as well as breeding habitats and hiding places. It has been shown to support the biodiversity of various beetle families (Brunet & Isacsson 2009, Jabin et al. 2004, Seibold et al. 2016), snails (Kappes 2005, Kappes 2006), Diptera, Hymenoptera, Isopoda, Chilopoda, and Diplopoda (Jabin et al. 2007, Stokland et al. 2012, Topp et al. 2006). In particular, fungi decomposing deadwood (often basidiomycetes; Heilmann-Clausen & Christensen 2003, 2004) are both food and habitat for soil organisms (Maraun et al. 2014, Matthewman & Pielou 1971, Minnich et al. 2021, Nazari et al. 2023). A high diversity of deadwood increases the diversity of associated organisms (Penone et al. 2019, Seibold et al. 2016). Another important factor is the degree of decomposition of the deadwood. For example, species richness of beetles and fungi is highest at intermediate decomposition levels (Brunet & Isacsson 2009, Heilmann-Clausen & Christensen 2003, 2004), whereas snails are most diverse at high decomposition levels (Kappes et al. 2009, Müller et al. 2005). Overall, Brunet et al. (2010) conclude in their review that a quantity of at least 20 m³ per ha of deadwood is necessary to maintain a high level of biodiversity in managed beech forests. On average, German forests contain 29 m³ of deadwood per ha, although there are significant differences between the individual federal states (BMEL 2024). Aiming for a mosaic of deadwood of different tree species in different states of decomposition is therefore the best way to promote soil biodiversity.

Overall, a wide range of management measures can be implemented in forests to promote soil biodiversity. In addition to the retention of deadwood, a heterogeneous structure can be achieved by allowing trees of different ages to grow together, by varying degrees of canopy closure in order to support thermophilic species in open areas and to enable the development of a distinct herb layer. Much of this heterogeneity develops automatically in protected areas e.g., through wind throw. However, soil biodiversity can also be promoted in managed forests by favoring single-stem or group harvesting over clear-cutting. Even in clear-cuts, the situation can be significantly improved by retaining individual trees or groups of trees, especially for species of soil arthropods and snails that depend on deadwood. The preservation of trees can be focused on economically less valuable but biologically richer trees. Forest edges are particularly suitable for the preservation of habitat trees such as old beech trees with broad crowns and many microhabitats. Individual trees that have fallen due to windthrow should also remain in managed forests. Further, the reduction of machine weight for timber harvesters can reduce soil compaction (Ampoorter et al. 2007) and therefore improve soil pore size and habitable space for different soil fauna taxa (Beylich et al. 2010).

At the landscape level, forests should be (and already are) specifically converted to more site-appropriate and climate-stable forests. Integrative approaches that strive for a balance between production and conservation goals promote mixed forests of beech and spruce, pine or oak. These mixed forests are more similar to natural vegetation and less susceptible to disturbance than monocultures. In terms of their economic value, they lie between pure coniferous and pure beech forests.

3 Inland wetlands

Wetlands are a unique habitat type at the interface of aquatic and terrestrial conditions. Wetland soils such as those of floodplains and peatlands have a strong potential for carbon storage. Peatlands for instance cover 5% of the total land area of Germany, but their share in stored carbon is about fivefold this value (Tegetmeyer et al. 2021, Jacobs et al. 2018). However, while wetland soils are effective carbon sinks when water saturated, in dry condition they become a carbon source (Li et al. 2024). Therefore, rewetting of floodplains and peatlands is one of the most effective climate protection measures. In addition, restoration of wetland habitats offers great potential for the conservation of above- and belowground biodiversity, since intact floodplains comprise a wide variety of habitats: forests and open land, sandbanks, dunes, islands and peninsulas. Differences in topology, i.e., the presence of knolls and depressions, resulting in differences in soil moisture, grain size, and organic matter content, further increase small-scale habitat heterogeneity and therefore the biodiversity of soil organisms (Bonn et al. 2002, Lessel et al. 2011, Plum & Filser 2005, Russell & Griegel 2006). Occasional flooding events cause moderate disturbance to the floodplain, enhance connectivity within the ecosystem, and increase nutrient and organic matter content of floodplain soils (Tockner et al. 2010, Ward et al. 1999). Furthermore, they provide niche space for a number of endangered, flooding-adapted soil fauna species (Russell et al. 2002, Gruppe et al. 2017, Rumm et al. 2016), while generalist species are increasingly found in the non-flooded part behind an embankment (fossil floodplain) (Scheunemann et al. unpublished, BUND 2023). Similarly, intact peatlands often harbour only low numbers, but sometimes high densities, of species that are restricted to this type of habitat (BMU & BfN 2021, Markkula 1986, Standen & Latter 1977), whereas drained peatlands are characterized by a large number of generalist species (Lehmitz 2014). The diversity and species composition of soil fauna therefore provide valuable information about peatland conditions, in particular when different soil fauna groups are investigated in parallel (Balkenhol et al. 2018, Gałka et al. 2017, Haase & Balkenhol 2015, Lehmitz et al. 2020).

In many European countries, peatlands and floodplains are under threat. Around 94% of peatlands in Germany are currently drained and account for more than 7% of the country's total greenhouse gas emissions (UBA 2023). The condition of the majority of floodplain soils in Germany is categorized as highly unnatural with soils under agricultural use for grazing, mowing, crop production, or forestry. In over 80% of German river courses, natural flooding is prevented by embankment and river straightening (BMU & BfN 2021). These measures have reduced the area affected by active flooding to less than 10% of its initial size (BMU & BfN 2021). Canalization and embankment severely restrict dynamic biophysical processes and feedback mechanisms over broad spatial and temporal scales. The restoration of wetland soils, i.e., the water-saturated status and hydrodynamics, often requires strong initial impulse measures followed by long-term management.

In order to restore floodplain landscapes to a near-natural character, usually an initial, large-scale restoration measure is needed to allow a natural flooding regime of the river. This may include the relocation of embankments and removal of bank stabilization and river straightening measures. A natural flooding regime is of crucial importance for the establishment of a floodplain-typical population structure and species composition of soil organisms (Lessel et al. 2011, Russell et al. 2002). For aboveground organisms, artificial flooding in e.g., polders, basically fulfills the same purpose as natural flooding. This has been shown for ground beetles and spiders in the Weser, Elbe and Oder floodplain, as well as for Collembola in the floodplains of Oder and Rhine (Bonn et al. 2002, Lessel et al. 2011, Russell & Griegel 2006).

After embankment removal or relocation, the next flood event directly affects the soil fauna with immense ecological changes from inundation by seepage water to natural flooding. Snails for example react very quickly to the new conditions by a rapid conversion of the species community to floodplain-typical representatives (Rumm et al. 2016). Other impulse measures carried out during floodplain restoration are removal of bank stabilization and/or river straightening measures, and creation of additional habitats such as islands or sandbanks. The latter increases habitat heterogeneity for above- and belowground soil organisms and is considered very beneficial for biodiversity. Next to costly measures such as the reconnection of oxbow lakes and the removal of river straightening, even the comparatively inexpensive removal of bank reinforcements can lead to an increase in soil biodiversity due to changes in current velocity with subsequent natural creation of e.g., sandbanks as habitat for specialist Carabidae or other soil animals (Günther & Assmann 2005).

To achieve initial rewetting in peatlands, drainage must be stopped by switching off pumps and closing drainage pipes and ditches. Adjusting the groundwater table to approx. 10 cm below soil surface is essential for the regeneration of peat mosses and soil microorganisms (van Dijk et al. 2009, Gałka et al. 2017). At the beginning, rewetting leads to a decline in biodiversity and density of soil organisms that are adapted to the drained situation (Ausden et al. 2001, Bobuľská et al. 2020; van Dijk et al. 2009, Gruppe et al. 2017). After that, more specialized epigeic animal groups like spiders and Carabidae may colonize rewetted peatlands quickly, thereby increasing species numbers again (Gruppe et al. 2017, Gaudig & Krebs 2016). They often arrive from very small intact peatland areas in the vicinity, which are therefore worth preserving despite their often small size (Buchholz 2016, van Dijk et al. 2009, Gałka et al. 201, Gaudig & Krebs 2016). In general, the restoration of a typical peatland composition of soil fauna and soil microbiome can only be achieved in the long term (Emsens et al. 2020, Silvan et al. 2000). Since peat moss grows very slowly and the active migration capacity of many soil animals is low, even 15 years after peatland restoration the entire species diversity of e.g., Staphylinidae has not recovered (Hoffmann et al. 2018). The immigration of smaller and less mobile taxa from soil meso- and microfauna might take even longer, but studies on that topic are rare. Only after 70 years of natural regeneration, the Collembola community of a peatland in northern Poland was fully restored (Sławski et al. 2022).

Among periodic management measures in peatlands, the regular removal of woody vegetation is most important as it promotes typical peatland vegetation that is vulnerable to shading, competition and increased soil water drainage by trees and shrubs. Grazing by sheep or water buffalo can help to keep peatlands permanently open (Succow Foundation 2023, EU Life Project Schreiadler 2023), while mowing may remove nutrients if e.g., dense stands of reeds have formed due to nitrogen pollution. Mowing is most beneficial for rove beetle diversity (Staphylinidae) when applied once per year in summer, while mowing during winter destroys hibernation sites of specialized species, and results in reduced densities (Hoffmann et al. 2016). Topsoil removal is another possibility to reduce nutrient stocks and increase water level (Huth et al. 2019, Zak et al. 2018).

4 Coastal soils

At the German coasts of the Baltic and North Sea, sand dunes serve as habitat for a whole range of belowground specialists of soil fauna e.g., bizarrely shaped mites and Collembola (Salmane & Spungis 2009), or the wolf spider *Arctosa perita* (Bonte et al. 2000). Established coastal protection measures like the planting of European beachgrass (*Ammophila arenaria)* contribute to preserving sand dunes as habitats for these soil organisms. Similarly, the North Sea salt marshes vegetated by halophytes are inhabited by specialized soil fauna species that are adapted to flooding and salinity. However, successful salt marsh establishment depends on the seed bank of the restored area or the proximity to existing salt marshes (Bernhardt & Koch 2003, Erfanzadeh et al. 2010), and restored saltmarshes do not achieve the species diversity of natural salt marshes in the short term. The formation and preservation of existing salt marshes depends on the area of appropriate hydrology (Wolters et al. 2005, Wanner 2009). Studies on the diversity and density of aboveground soil animals (spiders, Carabidae) show that with restoration of hydrology and salinity, salt marsh vegetation as well as soil fauna communities change towards higher proportions of salt-tolerant and hygrophilous species (Seiberling et al. 2023, Seiberling & Stock 2009). However, smaller dike openings, e.g., through slices, often do not restore the entire hydrology and therefore do not prevent the dominance of highly competitive generalist species (Seiberling & Stock 2009).

In the long term, reduction of land-use intensity is an effective management measure to protect existing salt marsh vegetation and soil biodiversity since e.g., reduced stocking decreases soil compaction and supply of detritus and nutrients (Andresen et al. 1990, Neuhaus, Stelter & Kiehl 1999, Seiberling & Stock 2009). Further, reduced erosion caused by trampling of livestock has a very positive effect on the sedimentation rate and thus the vegetation of salt marshes (Wanner 2009, Wolters et al. 2005). However, complete abandonment of grazing can result in detrimental loss of biodiversity by establishment of *Elymus athericus* (sea couch grass) monocultures (Pétillon et al. 2005, Nolte et al. 2019). Although it is part of the native vegetation in late successional stages, this grass can lead to a strong reduction of the spider diversity when becoming dominant (Valéry et al. 2004). Moderate grazing or mowing is the only effective management measure against the spread of *E. athericus* (Pétillon et al. 2005).

5 Urban areas

Around 14% of the German territory (5 million hectares) are covered by urban areas i.e., settlement and transportation areas (BBSR 2023). Urban soils can be considered extreme habitats, and are characterized by high levels of pollution, compaction, and high temperature in summer. This results in urban soil fauna communities consisting of species that are resistant to pollutants and drought, but that are less specialized in other respects (Dijck et al. 2023, Pétremand et al. 2018). In general, soil-dwelling (endogeic) and less mobile groups of soil fauna (e.g., Lumbricidae) decrease in species numbers with increasing urbanization, while mobile generalists (e.g., Isopoda, Diplopoda), sometimes show increased densities (Szabó et al. 2023). For example, urban vegetable gardens provide habitat for the local species pool of Collembola populations, although the proportion of generalists in the communities is high (Joimel et al. 2019). Further, with small-scale differences in terrain structure, soil texture and cultivation mode, private and allotment gardens can have a positive impact on functional and species biodiversity, while sustainable practice can even strengthen soil multifunctionality (Tresch et al. 2019). The same is true for parks and cemeteries, where small-scale measures such as fallow land, dead wood, natural tree regeneration, reduction of ivy to encourage other plants, but also leaving ivy cover in other places, and tolerating vegetation on walls and other human structures enhance biodiversity (Buchholz et al. 2018, Kowarik et al. 2016).

In urban green spaces, increased plant biodiversity has a positive effect on the biodiversity of soil fauna and thus on the multifunctionality and carbon storage capacity of urban soils (Schittko et al. 2022). In parks and lawns, this can be achieved through management changes like reduced mowing frequency, either by omitting parts of the lawn area or by reducing the frequency of mowing (Chollet et al. 2018, Proske et al. 2022). Lawns mowed once or twice a year showed 30 % higher plant species richness within 6 years than those mowed 6-12 times a year (Sehrt et al. 2020, Unterweger 2018). Through feedback effects from aboveground on belowground living organisms (e.g., through predator-prey relationships), soil biodiversity benefits from reduced mowing intensity as well (Buchholz et al. 2018, Egerer & Philpott 2022). Targeted planting or sowing of native wildflowers increases soil biodiversity as well. Replacement of exotic small shrubs with native flowers in roadside green spaces increased the abundances of aboveground soil invertebrates (Collembola, Isopoda, Opilionida, ground-hunting spiders) by up to 260 % within two years, while reducing maintenance cost by 60–80 % (Mody et al. 2020). In urban parks, native tree species should be planted preferably, because e.g., the non-native American red oak (*Quercus robur*) reduces the proportion of specialized forest species in the Oribatid community and slows down litter decomposition (Kohyt & Skubała 2020).

Sealed soil surfaces are a characteristic of urban areas, with the covered soil being lost for soil biodiversity and functions. However, soil multifunctionality is partly restored within a few years after unsealing, with microbial activity and biomass being similar to that of agricultural soils after only two years (Renella 2020). Soil meso- and macrofauna colonize unsealed urban soils within time frames similar to that of green roof colonization (see below), with naturally developing ruderal herbal vegetation enhancing successful revitalization of soil and soil fauna biodiversity in the long term. Sown grass cover, on the other hand, only increases population density of soil animal groups during early successional stages (Renella 2020, Koehler 2000, Koehler & Müller 2003). Renaturation of the recently fashionable gravel gardens falls under the topic of unsealing as well, with positive effects on aboveground biodiversity (Ferber 2021) likely reflecting benefits for belowground biodiversity.

Roof surfaces covered by substrate and plants, i.e., green roofs, can help in increasing ecosystem services like water retention and evaporation, as well as (soil) biodiversity in urban habitats. Extensive green roofs, consisting of a thin layer of substrate (< 20 cm) and grasses or stonecrop species (*Sedum* spp.) are exposed to drought during summer and freezing in winter, strongly limiting the soil animal population density and diversity (Buttschardt 2001, Knapp, et al. 2019, Rumble & Gange 2017). For example, neither Oligochaeta (Lumbricidae and Enchytraeidae), nor Isopoda or Myriapoda were able to colonize extensive green roofs in Karlsruhe. In contrast, Collembola and oribatid mites represented the main parts of the soil animal food web, although with significantly lower overall densities and in different proportions as compared to a nearby forest soil (Buttschardt 2001). In addition, life cycles of soil animals inhabiting the green roofs were shifted towards higher densities in early spring due to restricted times of favourable conditions (i.e., drought in summer, freezing in winter; Buttschardt 2001). Still, extensive green roofs can make a relevant contribution to soil biodiversity in cities, especially with increasing age: Collembola population density and community structure change towards more specialized species within the first ten years after establishment (Schrader & Böning 2006). Increasing food availability by initial inoculation of green roofs with e.g., saprotrophic *Trichoderma* sp. can further increase the abundance of Collembola and other fungivorous microarthropods (John et al. 2017), while inoculation with bacterial cultures seems to have a negative effect in the long term (Rumble & Gange 2017). In contrast, intensive green roofs are similar to roof gardens with flowerbeds, perennials and shrubs. The thick substrate layer (> 30 cm) promotes a higher biodiversity of spiders, bees and beetles (Fründ 1996, Madre et al. 2013, but see also Dijck et al. 2023), as well as earthworms (epigeics and endogeics only, no deep burrowers; Schrader & Steiner 2002). Soil animals probably colonize green roofs by wind transport and by clinging to the feet of birds (Joimel et al. 2018, Lehmitz et al. 2011). Further, the original planting substrate as well as compost applications can also promote soil fauna in green roofs (Joimel et al. 2018, 2022). Still, green roofs only harbor a very small section of the local fauna, usually mainly generalist species, in low densities (Fründ 1996, Schrader & Steiner 2002), but they can provide stepping stone habitats and connect biotopes, and have therefore become an indispensable part of urban planning.

6 Actor-related measures

Measures influencing the actors who live and operate in the relevant habitats can indirectly affect soil biodiversity. They can be divided into legal provisions (regulatory instruments), financial support for desired measures (incentive-based, financial instruments) and knowledge transfer or environmental education (informational instruments).

Currently, soil biodiversity is only indirectly taken into account in legislation. Legal provisions include the establishment and maintenance of protected areas e.g., Natura 2000-areas or FFH-areas, as well as national and European laws. At European level, the EU Biodiversity Strategy and EU Soil Strategy for 2030, and the upcoming Soil Monitoring and Resilience Directive are most important for the restoration of ecosystems and enhancing biodiversity across Europe (European Commission 2023). Further, implementation of conservation measures in agricultural and forest ecosystems is also guided by the EU's Common Agricultural Policy (CAP) (European Commission 2020). On a national level, laws for protection and restoration of soils, as well as the Federal Nature Conservation Act provide a legal framework for soil protection, sustainable land use, and biodiversity conservation. In addition, federal and states' forest acts guide reforestation measures and sustainable forest management, while the Water Framework Directive and Flood Risk Management Guideline focus on measures like rewetting of floodplains or coastal sites.

Financial support is a very effective instrument for steering and promoting protective measures. In terms of incentive-based financial instruments for promoting biodiversity, a number of funding programs for active restoration as well as restoration research are available at federal and state level, as well as internationally (e.g., EcoSchemes). However, none of these programmes are specifically aimed at promoting soil biodiversity, and their time limitations hamper the establishment of long-term measures.

Knowledge transfer on the importance of healthy soils and soil biodiversity is a key factor in promoting the sustainable use of soil. The most important informational instrument is environmental education that often targets children and young people (Xylander & Glante 2025). Federal programs include financial support of courses on nature experience and learning locations. Furthermore, community gardens, urban gardening, and school gardens can impressively demonstrate e.g., soil biodiversity in compost heaps along with the process of material decomposition and humus formation. Exhibitions in natural history museums can raise the visitors' awareness of soil biodiversity, too. The travelling exhibition 'The Thin Skin of the Earth - Our Soils' by the Senckenberg Museum of Natural History Görlitz, for example, has recorded more than one million visitors, and is accompanied by modern formats such as the virtual reality application 'Adventure Soil Life' (Baber et al. 2019) or smartphone apps like BODENTIERhoch4 (Neu et al. 2022). Targeting a more specialized audience, information events and counseling agencies for regional farmers and foresters can contribute to the promotion of soil biodiversity, for example by demonstrating the positive effects of establishing flower field margins in the Baden-Württemberg Network of Demonstration Farms for the Promotion of Biodiversity.

7 Conclusion

Measures to conserve and protect soil biodiversity differ greatly depending on the habitat that is to be restored. Overall, in highly managed habitats (agriculture, forests) a change in management is usually sufficient to improve soil biodiversity, whereas in wetlands an initial impulse measure (e.g., rewetting) is required, followed by subsequent management. In the short term, the initial stimulus often decreases species richness by decreasing numbers of generalist species, while in the long term, colonization of the habitat by more habitat-specific species results in a "better" ecological stage of the respective area.

Given the low dispersal abilities of soil organisms, a close proximity and connection of different near-natural habitat types harbors the highest potential for soil biodiversity at the landscape scale. At the smaller scale, a variety of abiotic factors (soil moisture, acidity, humus content, etc.) and microhabitats (deadwood, plant diversity, depressions, etc.) promote soil biodiversity the most. Still, legislation that stipulates the protection of soil fauna, financial support for targeted impulse and management measures, and raising awareness for soils and their ecosystem services are further important instruments for advancing the protection of soil biodiversity.

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