Challenges and Opportunities for Soil Biodiversity in the Anthropocene

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Challenges and opportunities for soil biodiversity in the Anthropocene

Stefan Geisen[1], Diana H. Wall[2], Wim H. van der Putten[1,3]

[1] Department of Terrestrial Ecology, Netherlands Institute of Ecology, 6708 PB Wageningen, The Netherlands

[2] School of Global Environmental Sustainability and Department of Biology, Colorado State University, Fort Collins, 80523-1036 USA

[3] Laboratory of Nematology, Wageningen University & Research, PO Box 8123, 6700 ES, Wageningen, The Netherlands

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Biodiversity on Earth is strongly affected by human alterations of the environment. The majority of studies have considered aboveground biodiversity, however, little is known about how biodiversity changes belowground follow the same patterns as those aboveground. It has been established that communities of soil biota are substantially altered by human activities through soil sealing and agricultural land use intensification, by biological invasions, as well as through altered abiotic conditions as a result of climate change. Changes in soil biodiversity can alter ecosystem functions performed by the soil biota. Therefore, human-induced global changes have a feedback effect to the provisioning of ecosystem services via altered soil biodiversity. Here, we highlight the major phenomena that threaten soil biodiversity, and propose options to reverse the decline in soil biodiversity. We argue that it is essential to protect soil biodiversity as a rich reservoir and an insurance throughout the Anthropocene. Overall, we need to better understand the determinants of soil biodiversity, its functioning, plan to avoid further losses and restore soil biodiversity where possible. Safeguarding this rich biotic reservoir is essential for soil sustainability and, ultimately, the sustainability of human society.

Introduction

During the current Anthropocene a large fraction of the natural land has been turned into human-influenced biomes, which now represent about 75% of all land on Earth [1]. The rapidly increasing human population and the increasing ecological footprint per capita is further increasing the pressure on the remaining natural land. Along with that, climate is more rapidly changing than ever before, and extreme events including incidence and severity of drought and heavy storms are increasing, whereas invasions of introduced exotic organisms that can change entire ecosystems become more prevalent. These anthropogenic changes have profound implications for all types of biodiversity, which are decreasing at a rate 1000 times higher as before human presence [2]. Such biodiversity declines may be well illustrated by the fact that the global biomass of livestock has become more than ten times that of all wild mammals and birds together [3]. So far, the focus of diversity declines by scientific researchers and the concerned public focuses almost entirely on macroscopic plants and animals, both in water and on land [4, 5]. Far less is known about anthropogenic impacts on the diversity of microscopic organisms and those animals that are living hidden in soils, despite these organisms dominate the living biomass together with plants [3] as well as biodiversity on Earth.

While exact mechanisms often remain unknown [6], soil biodiversity plays a pivotal role in providing key ecosystem functions and services [7]. As such, a decrease in soil biodiversity is associated with a simultaneous decrease of several soil functions [8]. Knowledge on the composition and functions of soil biodiversity is increasing particularly due to new methods such as high throughput sequencing [9]. As we advance our understanding of soil biodiversity, are we missing something relevant? The simple answer is yes: soil biodiversity contains an unknown repertoire of biota that are directly involved in biochemical nutrient cycling such as in the global carbon cycle as well as in other ecosystem processes and services [10]. Thereby, soil biodiversity is directly involved in climate warming-related processes, such as such as controlling greenhouse gas emissions [7, 11], but soil biodiversity also contains some devastating plant and animal pests [12]. Human influences on the environment may, directly or indirectly, alter the physiological activity of the soil biota thereby enhancing their contributions to warming, pest outbreaks, and other alterations of soil-borne ecosystem services [7, 8]. Soil biodiversity offers major and nearly infinite opportunities such as serving as a reservoir of novel antibiotics, acting as biocontrol agents and biofertilizers and providing certain other ecosystem services. Knowledge on soil biodiversity needs to increase in order to enable using this immense biotic reservoir, and to mitigate negative anthropogenic changes that threaten belowground biodiversity. We argue that understanding, protecting and using soil biodiversity will be key challenges in order to maintain earth system functioning and to increase ecosystem health including soil, plants, animals and humans.

Soil biodiversity in a nutshell

Most of the carbon within biota on Earth is bound in plants (450 gigatons), whereas the second largest biotic carbon pool consists of soil biota, equaling roughly 92 gigatons when including subsoils [3]. This immense reservoir of carbon bound in soil biota prevents carbon from entering the atmosphere [11], but also supports long food chains, as a single gram of soil hosts millions of microbes and dozens of tiny invertebrate animals [7]. This diversity includes bacteria, fungi and their protist predators, and a wide range of animals that span in size from tens of micrometers in the case of nematodes to meters in the case of earthworms or mammals, such as foxes and badgers that spend part of their life in soils. Even the largest organism on earth, an *Armillaria* fungus, is purely soilborne: its size equals that of more than 1,000 football (both American football and soccer) fields [13]!

In terms of functioning, the soil community contains major decomposers, playing key roles in carbon and nutrient cycling, whereas pathogens, parasites, and mutualists directly control the performance of plants, and indirectly that of aboveground pests, pathogens and mutualists [7]. While understanding of soil biodiversity is increasing, most of its taxonomic diversity remains undescribed, while ecological functioning at high taxonomic resolution, such as at the species level, remains unknown for most soil organisms, particularly microorganisms (viruses, bacteria, fungi and protists) [6, 7]. Despite the functional importance of soil biodiversity to contribute to major soil functions and ecosystem services [8] – such as provisioning of clean drinking water, prevention of greenhouse gas production, control of diseases – soil organisms are insufficiently included in assessing soil quality, biodiversity declines and incorporated earth system models, in spite of their functional importance such as in controlling the global carbon cycle [10, 14]. Considering and integrating soil biodiversity into large-scale analyses and models will help to better understand the importance of soil biodiversity at a global scale.

Soil biodiversity is structured by physical and chemical soil properties, as well as by interactions with other soil and aboveground biota, including plants [7, 15]. Soil type, pH, carbon and nutrient contents and soil moisture, predominantly determine the structure of soil biodiversity both locally, regionally, and globally [16, 17]. However, also plants shape soil biodiversity and they often do that in a plant species-specific manner [18], while trophic, competitive, facilitative, and other types of interactions between soil organisms add further structuring elements to soil biodiversity as a whole [19, 20].

Anthropogenic impacts on soil biodiversity

The tight dependency of soil biodiversity to their surrounding abiotic and biotic environment makes the soil biota highly susceptible to anthropogenic changes [21, 22]. These changes are linked to the rapid growth of the human population, limiting the inhabitable soils beyond those that are life-hostile bare rock, and those in extremely hot deserts and cold polar regions. An increasing proportion of the land surface is sealed to expand cities and other infrastructure: every year in the European Union alone an amount of open soil with a surface as large as the city of Berlin is sealed [23]. In addition, land is being taken for mining activities to support us with energy and for agriculture to produce food, feed, and bioenergy (Figure 2). Just for food production, about 1 billion ha of land could be turned into agriculturally managed land by 2050 [24]. Furthermore, agricultural practices are being intensified to support the growing human population [24]. Intensified agriculture heavily depends on irrigation, the use of heavy machines and increased application rates of chemical fertilizers and pesticides. These factors cause habitat modifications that immediately change soil structure and physicochemical properties, which, together with changes in plant biodiversity, affect and commonly reduce soil biodiversity [25-27]. As such, microbial communities are becoming bacteria-dominated, whereas earthworms are killed and mycorrhizal fungi disrupted by soil tillage and other agricultural practices [28-30]. Land-use intensification of agricultural soil, pesticide use, such as neonicotinoids and glyphosate that can remain in soils for years and impact non-target organisms, all may affect soil biodiversity [31]. Common non-target effects are evident for neonicotinoids, as they are assumed to be causative agents of aboveground insect declines, but also can kill soil invertebrates including insects and earthworms [32, 33]. Pollution by heavy metals emerging from agricultural practices, as well as run-off pollution emerging from mining sites and melters, can kill microbial taxa and change the community composition of soil biodiversity [34].

Other anthropogenic impacts on soil biodiversity are associated with unintended changes of the environment, particularly the ongoing global climate change. Climate change involves various factors that affect soil biodiversity, including increases of extreme events such as drought and heavy rainfall, but also more continuous changes such as increases in CO_2 levels and temperature increases [21, 35, 36]. Extended periods of drought negatively impact most groups of soil life, for example by reducing the abundance and diversity of protists [37] and larger soil animals [38]. Heavy rain events are occurring increasingly. These events can promote the abundance and diversity of soil biota through increasing moisture levels [39], but waterlogging and increased soil erosion also reduces soil biodiversity [37, 38]. Increased atmospheric CO_2 levels can enhance microbial biomass by increasing plant production, but might reduce food web complexity, for example by a decrease in larger, omnivorous and predacious nematodes [36, 40]. Warming affects soil biodiversity, for example by promoting fungi over bacteria, which also affects the composition of higher trophic-level consumers [41]. Another unintended anthropogenic change that causes soil biodiversity declines is acid rain, resulting from increased sulphur dioxide and nitrogen oxide emissions, which change vegetation and soil chemistry [42-45]. Human-induced introductions of exotic plants, animals, and microbes change the composition and functioning of soil biota [46, 47]. A number of introduced exotic plant species become invasive, for example when released from specialized pathogens in their native range [48]. In turn, invasions of particularly soil-borne oomycetes or fungal species are considered the main source of emerging infectious diseases of plants [49].

Some of these anthropogenic changes might lead to extinctions of soil biota [50]. Certain phenomena belowground are comparable to those known for aboveground biota, such as that larger soil organisms face higher extinction risks over shorter periods of time and at local scales than smaller bodied organisms [51]. Likewise, larger organisms, for example top predators and earthworms, are impacted more strongly by changes in the soil environment than smaller-sized microbial taxa [52]. The negative effects on ecosystem engineers and controllers of entire food web structures may cause feedback loops that affect the entire soil biodiversity and, consequently, soil functioning. For example, a loss of soil biodiversity may lead to a reduction of soil multifunctionality [8]. One of the most obvious examples of biodiversity loss leading to reduced soil functioning is the reduction of earthworms through intensive agriculture that results in reduced water infiltration, thereby enhancing the risk of increased water erosion [27, 28]. However, it should be noted that the factor causing soil biodiversity loss also has a direct impact on soil functioning. In practice, these causes and consequences of soil biodiversity loss are so far difficult to translate to changes on soil and ecosystem functioning.

Newly emerging threats to soil biodiversity constantly appear (see also Box 1). Among those are diverse pharmaceuticals that spread into the environment, eventually being taken up and concentrated in soil organisms [53], which changes soil community composition and functioning [54]. Microplastics are hardly studied in soils to date [55], but are reported to negatively impact microarthropods [56] and earthworms [57]. All these examples show that many, if not most, environmental perturbations eventually affect and potentially threaten soil biodiversity and functioning of the entire soil community. Some of these changes may turn out to be irreversible or associated with efforts and costs to maintain soil biodiversity and ecosystem functioning. This reinforces the need to protect soils and their biodiversity and their functions, particularly those performed by soil organisms.

Possibilities to counteract soil biodiversity changes

Some of the anthropogenic changes affecting soil biodiversity can be easily reversed and soil biodiversity restored [12]. For example, in the case of soil sealing by pavement, opening up the surface and adding organic matter is an obvious starting point [23]. In many urban areas, pavement such as stones, concrete or asphalt can be (at least partially) removed from cities in order to green pavement, non-vegetated parts in gardens and parks. This will positively affect water infiltration after heavy rain events, control dust and provide a friendlier environment [23]. Also, green roofs can be constructed, gardens can be made more natural, such as by replacing monospecific ornamental plants with species rich flower mixtures – with plant species diversity being known to stimulate soil biodiversity that lead to increased soil functioning [58, 59]. These measures all promote soil biodiversity [60, 61] and aboveground biodiversity of plants, insects and birds [62, 63], overall leading to increase a variety of ecosystem functions [63, 64]. These examples show that even small changes, which often come at little monetary costs, may increase soil biodiversity and likewise also other ecosystem services.

Land managers and farmers can reduce their negative foot-print on soil biodiversity through increasing their efforts in ecologically intensifying agricultural practices [65]. Arable land margins with flower strips will influence the soil biodiversity underneath the strips with possibilities of enhancing the water quality of surface water by preventing fertilizer and pesticides to drift into the water [66, 97]. Reducing soil tillage may enhance soil organic matter, which positively affects soil carbon storage, soil drainage, nutrient provisioning and, possibly, crop sensitivity to extreme weather events [24, 65]. Organic agriculture may come at some cost of a reduced yield at the short-term, but through increases in the spatial homogeneity of soil biodiversity and soil functions might increase plant production over longer time spans [67].

Soil biodiversity only slowly recovers once industrial and agricultural sites are taken out of production, but without collaborative scientifically informed land management it takes decades or more to restore [68]. In those cases, restoration projects may be needed to increase soil biodiversity at for example abandoned mining sites, when agricultural fields are taken out of production, or to counteract global change-induced desertification. Microbial transplants together with seeding of target plant species might help speed up these processes [69, 70].

Other factors affecting soil biodiversity need to be regulated at larger levels, such as at a state and country level. Measures are already in place to control for the spread of invasive organism, which is often based on scientific guidance [71]. However, these should be expanded to international efforts to better identify and thereby prevent invasions of known and novel quarantine species that threaten native soil biodiversity [72]. The importance of invasions on soil biodiversity is illustrated by invasive earthworms that change soil biodiversity and soil systems by changing litter availability [73] and flatworms that feed on earthworms and thereby remove earthworm-performed functions in soils [74].

While there are many more options to mitigate soil biodiversity loss and even to restore soil biodiversity to some extent, the best option is to not destroy soil biodiversity in the first place. Soil biodiversity is not infinite and once species go extinct, these cannot be replaced. Even the previously assumed infinite diversity of bacteria seems limited – instead of trillions there are likely only millions of species [75], which illustrates the limitations of the reservoir of life in soils on earth.

Box 1: Anthropogenic (re-)generation of extinct biodiversity and evolution in soils with implication on humans

Human products might influence the evolution of life in soils. For example, antibiotics released into the environment, such as residing as a side-product in fertilizers, induce the production and transfer of antibiotic resistance genes between bacteria [76], including clinical pathogenic bacteria [77]. While species-definition issues in bacteria prevent an easy taxonomic delineation, these functionally new taxa might have direct implications on human health.

Alien organisms can find their way and survive in soils at least for some time. Especially through inputs from manure or waste, human-pathogenic microorganisms may enter soils and survive for weeks to years [78]. Life span of human pathogens can also increase if entering an intermediate host, such as soil protists, commonly coinciding with an increase in virulence of the pathogen [79]. Human pathogens also commonly settle on vegetative plant parts from where they can, in the case of crops that are consumed, infect humans [80]. Note, that here we do not highlight the many human pathogens that are common in soils, including the causative agents of Anthrax (by the bacterium *Bacillus anthracis*) and Botulinum toxin (BTX, by the bacterium *Clostridium botulinum*) [12]. Yet, if enriched by human practices, these soilborne organisms can survive and become a human threat even decades after enrichment [12, 81].

Ancient organisms may re-appear through climate change-induced thawing of permafrost. As a result, often viable microorganisms, mosses and nematodes some of which potentially represent human and animal pathogens, can survive and re-emerge after millennia [82,83].

Opportunities for soil biodiversity

The potential of soil biodiversity to increase soil functions can be exploited in an ecologically intensified and thereby a more sustainable type of agriculture [84]. Increased soil biodiversity makes soil productivity less dependent on external inputs including fertilizers and pesticides [85].

Cost reductions to buy and apply fertilizers and pesticides may be achieved through a more sustainable manner of soil biodiversity management, as soil biodiversity can act as biofertilizer by increasing nutrient turnover and as biocontrol by inhibiting pathogens. This would also result in decreased environmental pollution and insect die-off, while minimizing yield losses [83, 85]. With increased evidence pointing to negative side effects of many pesticides such as on reducing biodiversity [86, 87] that lead to banning their application, alternatives including the application of biocontrol agents are pivotal to sustain agricultural production. Many currently applied biocontrol agents against plant pathogens and plant pests are soil-borne and act in the plant's rhizosphere, such as plant growth-promoting rhizobacteria, biocontrol fungi and entomopathogenic nematodes [88]. As only a fraction of the soil biodiversity is currently known, there is a huge potential to find additional and potentially more efficient and pathogen-specific biocontrol agents [89]. Similarly, many so far unknown soil organisms contain a reservoir of genes of direct human interest, such as novel antibiotics that are potentially more effective than currently applied antibiotics [99, 91].

Soil biodiversity as a whole, or individual groups of soil biota, have been proposed to be reliable bioindicators for soil quality, as they quickly respond to changes and perturbations, such as induced by contaminants [10, 92]. The sheer diversity of life in soils might contain taxa or communities that are indicative for nearly all imaginable compounds, but their indication potential inherent within soil biodiversity has yet to be exploited [10]. Similarly, microorganisms and soil animals may actively contribute to the degradation of environmental pollutants and can actively be used for bioremediation of pesticides and other toxic or hardly degradable compounds [93, 94]. There is evidence that soil biodiversity can be applied to restore contaminated or degraded land [69].

Overall, soil biodiversity may help accomplishing many of the United Nations Sustainable Development Goals (SDGs). These SDGs have been proposed to help achieving a better and more sustainable future in order to decrease hunger, provide clean water, mitigate climate change and increase life in water and on land [12]. We yet have to fully exploit the potential of soil biodiversity as a sustainable resource to provide or assist in many ecosystem functions and services, such as using biocontrol agents to reduce pesticide-application, applying biodiversity monitoring to assess different facets of soil quality or to apply soil biota as biofertilizers instead of often environmentally unsustainable fertilization practices.

How much is soil biodiversity reduced in the Anthropocene?

As most of the biodiversity in soils has not yet been described, we cannot reliably assess the amount of soil biodiversity that has already been lost in the Anthropocene. As in better studied aboveground systems, anthropogenic impacts on and reduction of soil biodiversity will differ across spatial and temporal scales and between groups of organisms [95]. For example, human-induced invasions can lead to an increase in soil biodiversity at the short term, as not everything occurs everywhere, but can reduce biodiversity of native species on a longer term, as is illustrated for example by earthworm invasions in the US that reduce soil microarthropod diversity [73]. These changes can also feed back to aboveground changes, such as by reducing plant diversity

[73]. Yet, invasive earthworms might not always negatively affect overall biodiversity, as they can also increase local biodiversity [73].

Still, there is increasing evidence that soil biodiversity is decreasing in the Anthropocene [51]. Invasions that irreversibly reduce plant diversity especially at a global scale will likely reduce the diversity of strictly species-specific plant host-associated organisms. With increasing evidence that plant species host their own species-specific microbiomes [18], many plant-associated species will disappear as well when their host plant species go extinct. More research is needed in order to determine the magnitude of soil biodiversity declines. The potential of restoration efforts on soil biodiversity should be assessed in order to take effective counter measures for potential biodiversity declines. For example, the establishment of permanent cultures and conservation sites of unique ecosystems may help to protect local soil biodiversity wherever it is threatened to decline [96].

Summary

Soil biodiversity is threatened globally by human activities – in many intensively used soils but also all other soils that suffer from side-effects such as those induced by human-induced climate change. Ongoing depletion of soils places soil biodiversity under increasing pressure. This loss of soil biodiversity places essential ecosystem functions at risk, while these are naturally provided by soils when properly managed. If not functioning well, lost ecosystem services need to be compensated for by additional anthropogenic inputs, leading to a negative feedback loop that will disrupt the environment even further. A key to turn the negative into a positive feedback loop in the Anthropocene is likely hidden in a proper management of the soil biodiversity.

While research efforts are increasing, an even more complete understanding is needed on what (taxonomy and taxon) diversity is currently present in soils, what functions are performed by individual species or entire soil communities, how soil taxonomic and functional diversity is linked to ecosystem functioning and services, and how these will change. That approach may help to re-connect ecosystem services to soil biodiversity, thereby enhancing the sustainable provisioning of those services. We highlight some of the possibilities that soil biodiversity offers. For instance, soil biodiversity should be considered in soil quality investigations due to its multi-faceted diversity that can likely specifically detect any imbalances present in soils. Application of soil biodiversity as biofertilizers and biopesticides and in storing carbon is the next frontier in sustainable agriculture through the potential of reducing fertilizer and pesticide input. Targeted research in this direction is needed to evaluate and identify soil biota that can be used for these purposes, such as in the recently rapidly expanding field of (soil) microbiome research.

We believe that a better understanding of soil biodiversity and its integration into potential application such as in using soil biodiversity to increase soil functions will allow combining human needs with environmental sustainability, meaning to enable increasing human impact without the string of negative feedback effects as shown in Fig. 3. Therefore, soil biodiversity should become part of decision-making in order to make as much sustainable use as possible of the ecosystem services provided by the dark, but exciting world beneath our feet.

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Declaration of Interests

The authors declare no competing interests.

References

1. Ellis, E.C., and Ramankutty, N. (2008). Putting people in the map: anthropogenic biomes of the world. Frontiers in Ecology and the Environment *6*, 439-447.
2. Joppa, L.N., Connor, B., Visconti, P., Smith, C., Geldmann, J., Hoffmann, M., Watson, J.E.M., Butchart, S.H.M., Virah-Sawmy, M., Halpern, B.S., et al. (2016). Filling in biodiversity threat gaps. Science *352*, 416.
3. Bar-On, Y.M., Phillips, R., and Milo, R. (2018). The biomass distribution on Earth. Proceedings of the National Academy of Sciences *115*, 6506-6511.
4. Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., and Collen, B. (2014). Defaunation in the Anthropocene. *345*, 401-406.
5. Young, H.S., McCauley, D.J., Galetti, M., and Dirzo, R. (2016). Patterns, causes, and consequences of Anthropocene defaunation. Annual Review of Ecology, Evolution, and Systematics *47*, 333-358.
6. Wall, D.H., Bardgett, R.D., and Kelly, E. (2010). Biodiversity in the dark. Nature Geoscience *3*, 297.
7. Bardgett, R.D., and van der Putten, W.H. (2014). Belowground biodiversity and ecosystem functioning. Nature *515*, 505-511.
8. Wagg, C., Bender, S.F., Widmer, F., and van der Heijden, M.G.A. (2014). Soil biodiversity and soil community composition determine ecosystem multifunctionality. Proceedings of the National Academy of Sciences *111*, 5266-5270.
9. Geisen, S., Briones, M.J.I., Gan, H., Behan-Pelletier, V.M., Friman, V.P., De Groot, G.A., Hannula, S.E., Lindo, Z., Philippot, L., Tiunov, A.V., et al. (2019). A methodological framework to embrace soil biodiversity. Soil Biology and Biochemistry *in press*; doi.org/10.1016/j.soilbio.2019.107536.
10. Bünemann, E.K., Bongiorno, G., Bai, Z., Creamer, R.E., De Deyn, G., de Goede, R., Fleskens, L., Geissen, V., Kuyper, T.W., Mäder, P., et al. (2018). Soil quality – A critical review. Soil Biology and Biochemistry *120*, 105-125.
11. Singh, B.K., Bardgett, R.D., Smith, P., and Reay, D.S. (2010). Microorganisms and climate change: terrestrial feedbacks and mitigation options. Nat. Rev. Microbiol. *8*, 779-790.
12. Wall, D.H., Nielsen, U.N., and Six, J. (2015). Soil biodiversity and human health. Nature *528*, 69-76.
13. Ferguson, B., Dreisbach, T., Parks, C., Filip, G., and Schmitt, C. (2003). Coarse-scale population structure of pathogenic *Armillaria* species in a mixed-conifer forest in the Blue Mountains of northeast Oregon. J Canadian Journal of Forest Research *33*, 612-623.
14. Wieder, W.R., Allison, S.D., Davidson, E.A., Georgiou, K., Hararuk, O., He, Y., Hopkins, F., Luo, Y., Smith, M.J., Sulman, B., et al. (2015). Explicitly representing soil microbial processes in Earth system models. Global Biogeochemical Cycles *29*, 1782-1800.
15. Fierer, N. (2017). Embracing the unknown: disentangling the complexities of the soil microbiome. Nature Reviews Microbiology *15*, 579-590.
16. Delgado-Baquerizo, M., Oliverio, A.M., Brewer, T.E., Benavent-González, A., Eldridge, D.J., Bardgett, R.D., Maestre, F.T., Singh, B.K., and Fierer, N. (2018). A global atlas of the dominant bacteria found in soil. Science *359*, 320-325.
17. Tedersoo, L., Bahram, M., Põlme, S., Kõljalg, U., Yorou, N.S., Wijesundera, R., Ruiz, L.V., Vasco-Palacios, A.M., Thu, P.Q., Suija, A., et al. (2014). Fungal biogeography. Global diversity and geography of soil fungi. Science *346*, 1256688.

18. Berg, G., and Smalla, K. (2009). Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. FEMS Microbiol. Ecol. *68*, 1-13.

19. Bahram, M., Hildebrand, F., Forslund, S.K., Anderson, J.L., Soudzilovskaia, N.A., Bodegom, P.M., Bengtsson-Palme, J., Anslan, S., Coelho, L.P., Harend, H., et al. (2018). Structure and function of the global topsoil microbiome. Nature *560*, 233-237.

20. Thakur, M.P., and Geisen, S. (2019). Trophic regulations of the soil microbiome. Trends in microbiology.

21. de Vries, F.T., Liiri, M.E., Bjørnlund, L., Bowker, M.A., Christensen, S., Setala, H.M., and Bardgett, R.D. (2012). Land use alters the resistance and resilience of soil food webs to drought. Nat. Clim. Change *2*, 276-280.

22. Griffiths, B.S., and Philippot, L. (2013). Insights into the resistance and resilience of the soil microbial community. FEMS Microbiol. Rev. *37*, 112-129.

23. Scalenghe, R., and Marsan, F.A. (2009). The anthropogenic sealing of soils in urban areas. Landscape and Urban Planning *90*, 1-10.

24. Tilman, D., Balzer, C., Hill, J., and Befort, B.L. (2011). Global food demand and the sustainable intensification of agriculture. Proceedings of the National Academy of Sciences *108*, 20260.

25. Wardle, D.A., Bonner, K.I., Barker, G.M., Yeates, G.W., Nicholson, K.S., Bardgett, R.D., Watson, R.N., and Ghani, A. (1999). Plant removals in perennial grassland: Vegetation dynamics, decomposers, soil biodiversity, and ecosystem properties. Ecological Monographs *69*, 535-568.

26. Gardi, C., Jeffery, S., and Saltelli, A. (2013). An estimate of potential threats levels to soil biodiversity in EU. Global Change Biology *19*, 1538-1548.

27. Tsiafouli, M.A., Thébault, E., Sgardelis, S.P., de Ruiter, P.C., van der Putten, W.H., Birkhofer, K., Hemerik, L., de Vries, F.T., Bardgett, R.D., Brady, M.V., et al. (2015). Intensive agriculture reduces soil biodiversity across Europe. Global Change Biology *21*, 973-985.

28. Chan, K.Y. (2001). An overview of some tillage impacts on earthworm population abundance and diversity — implications for functioning in soils. Soil and Tillage Research *57*, 179-191.

29. Giller, K.E., Beare, M.H., Lavelle, P., Izac, A.M.N., and Swift, M.J. (1997). Agricultural intensification, soil biodiversity and agroecosystem function. Appl. Soil Ecol. *6*, 3-16.

30. Song, D., Pan, K., Tariq, A., Sun, F., Li, Z., Sun, X., Zhang, L., Olusanya, O.A., and Wu, X. (2017). Large-scale patterns of distribution and diversity of terrestrial nematodes. Applied Soil Ecology *114*, 161-169.

31. Bünemann, E.K., Schwenke, G.D., and Van Zwieten, L. (2006). Impact of agricultural inputs on soil organisms - a review. Soil Research *44*, 379-406.

32. Goulson, D. (2013). An overview of the environmental risks posed by neonicotinoid insecticides. Journal of Applied Ecology *50*, 977-987.

33. Pisa, L.W., Amaral-Rogers, V., Belzunces, L.P., Bonmatin, J.M., Downs, C.A., Goulson, D., Kreutzweiser, D.P., Krupke, C., Liess, M., McField, M., et al. (2015). Effects of neonicotinoids and fipronil on non-target invertebrates. Environmental Science and Pollution Research *22*, 68-102.

34. Giller, K.E., Witter, E., and McGrath, S.P. (1998). Toxicity of heavy metals to microorganisms and microbial processes in agricultural soils: a review. Soil Biology and Biochemistry *30*, 1389-1414.

35. Thakur, M.P., Del Real, I.M., Cesarz, S., Steinauer, K., Reich, P.B., Hobbie, S., Ciobanu, M., Rich, R., Worm, K., and Eisenhauer, N. (2019). Soil microbial, nematode, and enzymatic responses to elevated CO2, N fertilization, warming, and reduced precipitation. Soil Biology and Biochemistry *135*, 184-193.
36. Eisenhauer, N., Cesarz, S., Koller, R., Worm, K., and Reich, P.B. (2012). Global change belowground: impacts of elevated CO2, nitrogen, and summer drought on soil food webs and biodiversity. Global Change Biol. *18*, 435–447.
37. Geisen, S., Bandow, C., Römbke, J., and Bonkowski, M. (2014). Soil water availability strongly alters the community composition of soil protists. Pedobiologia *57*, 205–213.
38. Lindberg, N., Engtsson, J.B., and Persson, T. (2002). Effects of experimental irrigation and drought on the composition and diversity of soil fauna in a coniferous stand. Journal of Applied Ecology *39*, 924-936.
39. Clarholm, M. (1981). Protozoan grazing of bacteria in soil—impact and importance. Microb. Ecol. *7*, 343-350.
40. Niklaus, P., Alphei, J., Ebersberger, D., Kampichler, C., Kandeler, E., and Tscherko, D. (2003). Six years of in situ CO2 enrichment evoke changes in soil structure and soil biota of nutrient-poor grassland. Global Change Biology *9*, 585-600.
41. Briones, M.J.I., Ostle, N.J., McNamara, N.P., and Poskitt, J. (2009). Functional shifts of grassland soil communities in response to soil warming. Soil Biology and Biochemistry *41*, 315-322.
42. McCormick, J. (2013). Acid Earth: the global threat of acid pollution, (Routledge).
43. Reis, S., Grennfelt, P., Klimont, Z., Amann, M., ApSimon, H., Hettelingh, J.P., Holland, M., LeGall, A.C., Maas, R., Posch, M., et al. (2012). From acid rain to climate change. Science *338*, 1153.
44. Pennanen, T., Fritze, H., Vanhala, P., Kiikkilä, O., Neuvonen, S., and Bååth, E. (1998). Structure of a microbial community in soil after prolonged addition of low levels of simulated acid rain. Applied and Environmental Microbiology *64*, 2173.
45. Ruess, L., Sandbach, P., Cudlín, P., Dighton, J., and Crossley, A. (1996). Acid deposition in a spruce forest soil: effects on nematodes, mycorrhizas and fungal biomass. Pedobiologia *40*, 51-66.
46. Kourtev, P.S., Ehrenfeld, J.G., and Häggblom, M. (2002). Exotic plant species alter the microbial community structure and function in the soil. Ecology *83*, 3152-3166.
47. van der Putten, W.H., Klironomos, J.N., and Wardle, D.A. (2007). Microbial ecology of biological invasions. ISME J. *1*, 28-37.
48. van der Putten, W.H., Bardgett, R.D., Bever, J.D., Bezemer, T.M., Casper, B.B., Fukami, T., Kardol, P., Klironomos, J.N., Kulmatiski, A., Schweitzer, J.A., et al. (2013). Plant–soil feedbacks: the past, the present and future challenges. J. Ecol. *101*, 265-276.
49. Fisher, M.C., Henk, D.A., Briggs, C.J., Brownstein, J.S., Madoff, L.C., McCraw, S.L., and Gurr, S.J. (2012). Emerging fungal threats to animal, plant and ecosystem health. Nature *484*, 186-194.
50. Gaucher, E.A., Govindarajan, S., and Ganesh, O.K. (2008). Palaeotemperature trend for Precambrian life inferred from resurrected proteins. Nature *451*, 704.
51. Veresoglou, S.D., Halley, J.M., and Rillig, M.C. (2015). Extinction risk of soil biota. Nature Communications *6*, 8862.
52. Kladivko, E.J. (2001). Tillage systems and soil ecology. Soil and Tillage Research *61*, 61-76.
53. Kinney, C.A., Furlong, E.T., Kolpin, D.W., Burkhardt, M.R., Zaugg, S.D., Werner, S.L., Bossio, J.P., and Benotti, M.J. (2008). Bioaccumulation of pharmaceuticals and other

anthropogenic waste indicators in earthworms from agricultural soil amended with biosolid or swine manure. Environmental Science & Technology *42*, 1863-1870.

54. Wepking, C., Avera, B., Badgley, B., Barrett John, E., Franklin, J., Knowlton Katharine, F., Ray Partha, P., Smitherman, C., and Strickland Michael, S. (2017). Exposure to dairy manure leads to greater antibiotic resistance and increased mass-specific respiration in soil microbial communities. Proceedings of the Royal Society B: Biological Sciences *284*, 20162233.

55. Rillig, M. (2012). Microplastic in terrestrial ecosystems and the soil? Environmental Science & Technology *46*, 6453-6454.

56. Zhu, D., Chen, Q.-L., An, X.-L., Yang, X.-R., Christie, P., Ke, X., Wu, L.-H., and Zhu, Y.-G. (2018). Exposure of soil collembolans to microplastics perturbs their gut microbiota and alters their isotopic composition. Soil Biology and Biochemistry *116*, 302-310.

57. Huerta Lwanga, E., Gertsen, H., Gooren, H., Peters, P., Salánki, T., van der Ploeg, M., Besseling, E., Koelmans, A.A., and Geissen, V. (2016). Microplastics in the terrestrial ecosystem: implications for *Lumbricus terrestris* (Oligochaeta, Lumbricidae). Environmental Science & Technology *50*, 2685-2691.

58. Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., Fischer, M., Schulze, E.-D., Roscher, C., Weigelt, A., Allan, E., et al. (2010). Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature *468*, 553-556.

59. Brussaard, L., de Ruiter, P.C., and Brown, G.G. (2007). Soil biodiversity for agricultural sustainability. Agriculture, Ecosystems & Environment *121*, 233-244.

60. Schrader, S., and Böning, M. (2006). Soil formation on green roofs and its contribution to urban biodiversity with emphasis on Collembolans. Pedobiologia *50*, 347-356.

61. Rumble, H., and Gange, A.C. (2013). Soil microarthropod community dynamics in extensive green roofs. Ecological Engineering *57*, 197-204.

62. Lundholm, J.T. (2015). Green roof plant species diversity improves ecosystem multifunctionality. Journal of Applied Ecology *52*, 726-734.

63. Oberndorfer, E., Lundholm, J., Bass, B., Coffman, R.R., Doshi, H., Dunnett, N., Gaffin, S., Köhler, M., Liu, K.K.Y., and Rowe, B. (2007). Green roofs as urban ecosystems: ecological structures, functions, and services. BioScience *57*, 823-833.

64. Czemiel Berndtsson, J. (2010). Green roof performance towards management of runoff water quantity and quality: A review. Ecological Engineering *36*, 351-360.

65. Geertsema, W., Rossing, W.A.H., Landis, D.A., Bianchi, F.J.J.A., van Rijn, P.C.J., Schaminée, J.H.J., Tscharntke, T., and van der Werf, W. (2016). Actionable knowledge for ecological intensification of agriculture. Frontiers in Ecology and the Environment *14*, 209-216.

66. Marshall, E.J.P., and Moonen, A.C. (2002). Field margins in northern Europe: their functions and interactions with agriculture. Agriculture, Ecosystems & Environment *89*, 5-21.

67. Schrama, M., de Haan, J.J., Kroonen, M., Verstegen, H., and Van der Putten, W.H. (2018). Crop yield gap and stability in organic and conventional farming systems. Agriculture, Ecosystems & Environment *256*, 123-130.

68. Morriën, E., Hannula, S.E., Snoek, L.B., Helmsing, N.R., Zweers, H., de Hollander, M., Soto, R.L., Bouffaud, M.L., Buee, M., Dimmers, W., et al. (2017). Soil networks become more connected and take up more carbon as nature restoration progresses. Nature Communications *8*, 14349.

69. Wubs, E.R., van der Putten, W.H., Bosch, M., and Bezemer, T.M. (2016). Soil inoculation steers restoration of terrestrial ecosystems. Nat Plants *2*, 16107.

70. Requena, N., Perez-Solis, E., Azcón-Aguilar, C., Jeffries, P., and Barea, J.-M. (2001). Management of indigenous plant-microbe symbioses aids restoration of desertified ecosystems. Applied and Environmental Microbiology *67*, 495.
71. Lodge, D.M., Williams, S., MacIsaac, H.J., Hayes, K.R., Leung, B., Reichard, S., Mack, R.N., Moyle, P.B., Smith, M., Andow, D.A., et al. (2006). Biological invasions: recommendations for US policy and management. Ecological Applications *16*, 2035-2054.
72. Perrings, C., Dehnen-Schmutz, K., Touza, J., and Williamson, M. (2005). How to manage biological invasions under globalization. Trends in Ecology & Evolution *20*, 212-215.
73. Bohlen, P.J., Scheu, S., Hale, C.M., McLean, M.A., Migge, S., Groffman, P.M., and Parkinson, D. (2004). Non-native invasive earthworms as agents of change in northern temperate forests. Frontiers in Ecology and the Environment *2*, 427-435.
74. Boag, B., and Yeates, G.W. (2001). The potential impact of the New Zealand flatworm, a predator of earthworms, in Western Europe. Ecological Applications *11*, 1276-1286.
75. Louca, S., Mazel, F., Doebeli, M., and Parfrey, L.W. (2019). A census-based estimate of Earth's bacterial and archaeal diversity. PLOS Biology *17*, e3000106.
76. Heuer, H., Schmitt, H., and Smalla, K. (2011). Antibiotic resistance gene spread due to manure application on agricultural fields. Current Opinion in Microbiology *14*, 236-243.
77. Forsberg, K.J., Reyes, A., Wang, B., Selleck, E.M., Sommer, M.O.A., and Dantas, G. (2012). The Shared Antibiotic Resistome of Soil Bacteria and Human Pathogens. Science *337*, 1107-1111.
78. Nicholson, F.A., Groves, S.J., and Chambers, B.J. (2005). Pathogen survival during livestock manure storage and following land application. Bioresource Technology *96*, 135-143.
79. Greub, G., and Raoult, D. (2004). Microorganisms resistant to free-living amoebae. Clin. Microbiol. Rev. *17*, 413-433.
80. Berger, C.N., Sodha, S.V., Shaw, R.K., Griffin, P.M., Pink, D., Hand, P., and Frankel, G. (2010). Fresh fruit and vegetables as vehicles for the transmission of human pathogens. Environmental Microbiology *12*, 2385-2397.
81. Espelund, M., and Klaveness, D. (2014). Botulism outbreaks in natural environments – an update. Front. Microbiol. *5*.
82. Jansson, J.K., and Taş, N. (2014). The microbial ecology of permafrost. Nature Reviews Microbiology *12*, 414.
83. Shatilovich, A.V., Tchesunov, A.V., Neretina, T.V., Grabarnik, I.P., Gubin, S.V., Vishnivetskaya, T.A., Onstott, T.C., Rivkina, E.M. (2018) Viable nematodes from late pleistocene permafrost of the Kolyma river lowland. Doklady Biological Sciences *480*, 100-102.
84. Bender, S.F., Wagg, C., and van der Heijden, M.G. (2016). An underground revolution: biodiversity and soil ecological engineering for agricultural sustainability. Trends in Ecology & Evolution *31*, 440-452.
85. Maeder, P., Fliessbach, A., Dubois, D., Gunst, L., Fried, P., and Niggli, U. (2002). Soil fertility and biodiversity in organic farming. Science *296*, 1694.
86. Beketov, M.A., Kefford, B.J., Schäfer, R.B., and Liess, M. (2013). Pesticides reduce regional biodiversity of stream invertebrates. Proceedings of the National Academy of Sciences *110*, 11039.
87. Goulson, D., Nicholls, E., Botías, C., and Rotheray, E.L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science *347*, 1255957.

88. Compant, S., Duffy, B., Nowak, J., Clément, C., and Barka, E.A. (2005). Use of plant growth-promoting bacteria for biocontrol of plant diseases: principles, mechanisms of action, and future prospects. Applied and Environmental Microbiology *71*, 4951.
89. Beneduzi, A., Ambrosini, A., and Passaglia, L.M.P. (2012). Plant growth-promoting rhizobacteria (PGPR): their potential as antagonists and biocontrol agents. Genetics and Molecular Biology *35*, 1044-1051.
90. Riesenfeld, C.S., Goodman, R.M., and Handelsman, J. (2004). Uncultured soil bacteria are a reservoir of new antibiotic resistance genes. Environmental Microbiology *6*, 981-989.
91. Ling, L.L., Schneider, T., Peoples, A.J., Spoering, A.L., Engels, I., Conlon, B.P., Mueller, A., Schäberle, T.F., Hughes, D.E., Epstein, S., et al. (2015). A new antibiotic kills pathogens without detectable resistance. Nature *517*, 455.
92. Pulleman, M., Creamer, R., Hamer, U., Helder, J., Pelosi, C., Pérès, G., and Rutgers, M. (2012). Soil biodiversity, biological indicators and soil ecosystem services—an overview of European approaches. Current Opinion in Environmental Sustainability *4*, 529-538.
93. Haimi, J. (2000). Decomposer animals and bioremediation of soils. Environmental Pollution *107*, 233-238.
94. Gadd, G.M. (2010). Metals, minerals and microbes: geomicrobiology and bioremediation. *156*, 609-643.
95. McGill, B.J., Dornelas, M., Gotelli, N.J., and Magurran, A.E. (2015). Fifteen forms of biodiversity trend in the Anthropocene. Trends in Ecology & Evolution *30*, 104-113.
96. Cameron, E.K., Martins, I.S., Lavelle, P., Mathieu, J., Tedersoo, L., Bahram, M., Gottschall, F., Guerra, C.A., Hines, J., Patoine, G., et al. (2019). Global mismatches in aboveground and belowground biodiversity. Conservation Biology *in press*.
97. Upton, R.N., Bach, E.M., and Hofmockel, K.S. (2018). Belowground response of prairie restoration and resiliency to drought. Agriculture, Ecosystems & Environment *266*, 122-132.

Figure legends

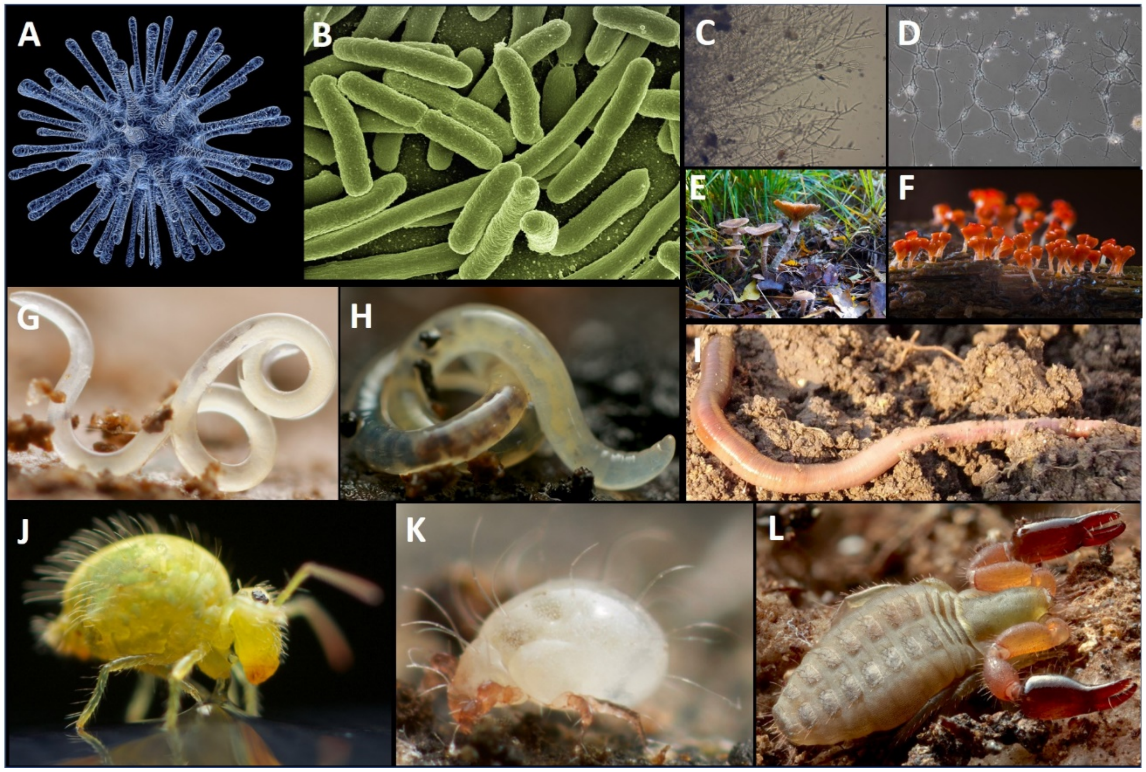

Figure 1. Overview of common organism groups living in soils including microorganisms (A-F) and animals (G-L). Thus far, only a tiny fraction of the immense morphological diversity of soil organisms is known, such as viruses (A) and bacteria (B). Many organisms that are more unrelated than for example humans and jellyfish can function in a similar way and even look alike as illustrated for fungal hyphae (C) and network-forming protist amoebae (D) as well as fruiting bodies of fungi (E) and protist slime molds (F). Soil animals are also morphologically diverse and include different types of worms with varying sizes, such as nematodes (grouped as microfauna; G), enchytraeids (mesofauna; H) and earthworms (macrofauna; I). The morphologically highly diverse microarthropods are morphologically far more diverse than worms and include such fascinating animals such as springtails (J), mites (K), and pseudoscorpions (L); note that sizes of the illustrated organisms vary profoundly and as such they inhabit different niches in soils [9]. © A-C, E-F, I: https://pixabay.com; D: Eckhard Völcker; G, H, J-L Andy Murray.

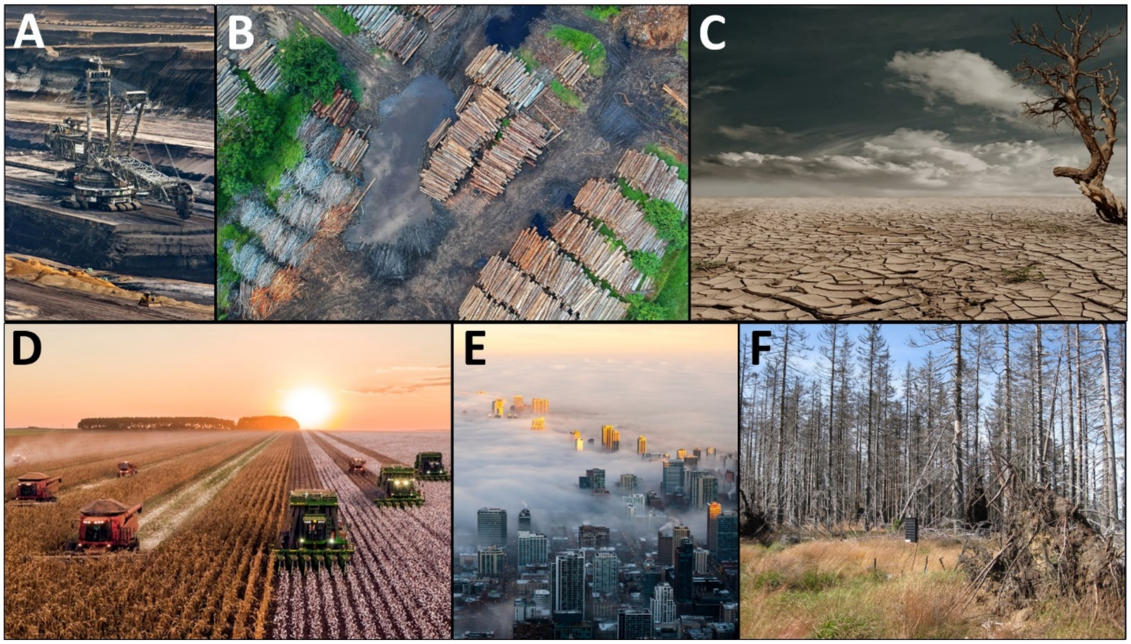

Figure 2. Overview of some major anthropogenic changes that immediately affect soil biodiversity. These can be divided into intentional changes to soils that unavoidably affect soil biodiversity including mining (A), deforestation (B), (agricultural) land use intensification (D) and sealing (E) and those that come along human-induced changes including pollution (E), changes in climate such as drought (C), acid rain or pathogen invasions (both can be represented by F). © A-B, D-E: https://www.pexels.com/; C: https://unsplash.com/; F: https://pixabay.com.

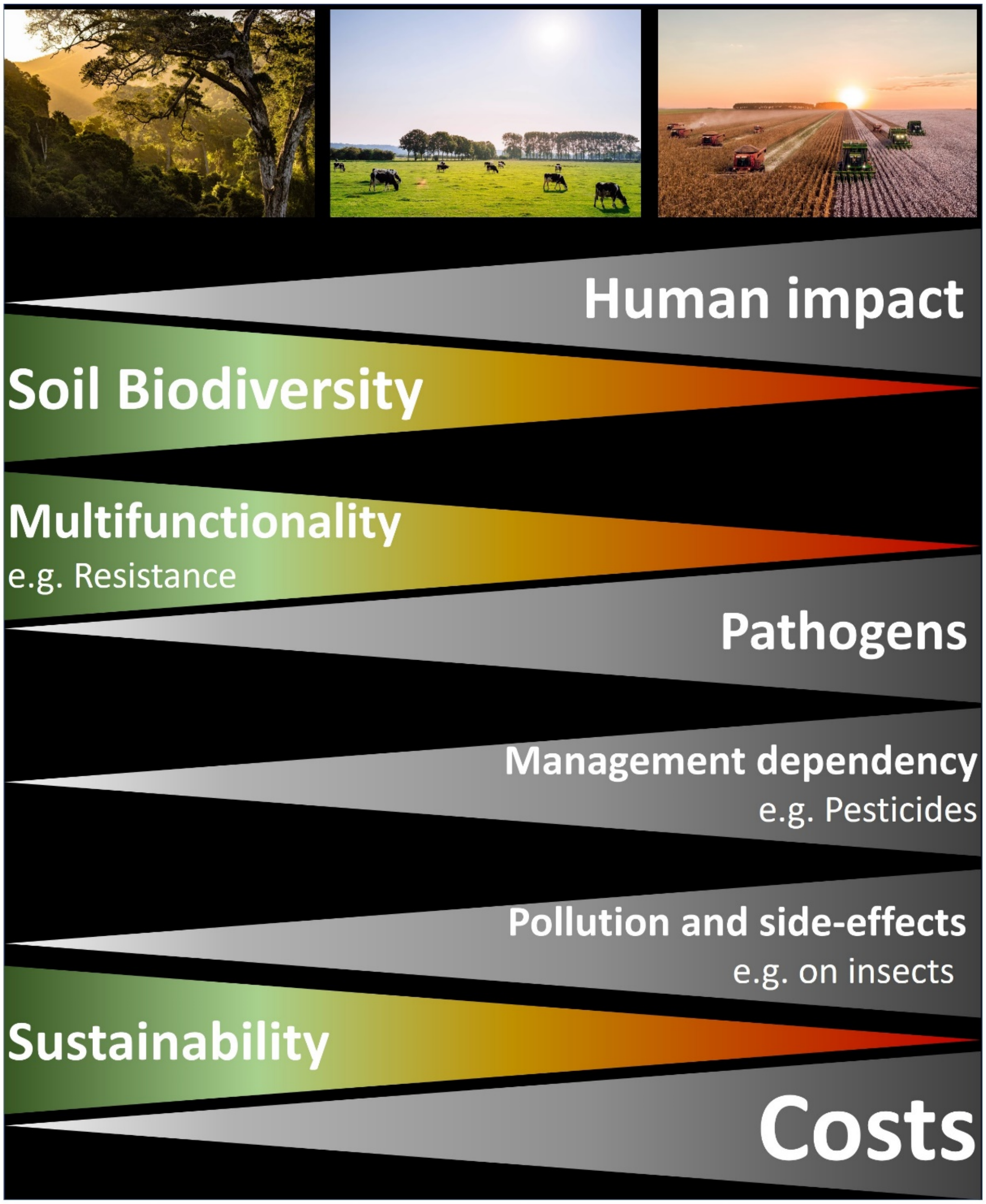

Figure 3. Anthropogenic changes, here exemplified as land use intensification, reduces soil biodiversity. This results in a decrease in soil functions and also increases the presence and effect-size of pathogens, leading to an increased need for management practices. As a side effect, pollution, such as through fertilizer leaching into the groundwater and pesticide-induced decrease of aboveground insects, threatens the environment. In the end, management costs increase and management becomes less sustainable as land-use intensification commonly begets increased management. By directly considering, managing and using soil biodiversity during land use intensification, we might mitigate this negative feedback loop.