

## The threat-work: a network of potential threats to soil biodiversity

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### Abstract

Soils are estimated to contain more than half of the biodiversity on our planet, encompassing a rich spectrum of genes, organisms and functions that play a crucial role in many ecological processes, such as nutrient cycling, organic matter decomposition, and the creation of a well-structured soil matrix. However, soils encounter many threats that significantly challenge their functionality and biodiversity. The FAO Report on the State of Knowledge of Soil Biodiversity identified 12 primary threats to soil and soil biodiversity, highlighting regional and unique ecozonal perspectives. Most threats to soil come from anthropogenic land use activities and management practices associated with intensive agriculture, livestock, forestry, and other resource extraction activities, as well as industrial activities, infrastructure and urbanization, which vary in strength across various regions and ecozones. However, these threats are highly interconnected and often culminate in losses to soil organic matter (SOM) and soil organic carbon (SOC) — also considered a threat itself — that drives changes in physical, chemical and biological attributes of the soil environment that lead to soil biodiversity loss. We conceptualize these interlinked threats as a threat network or ‘threat-work’, where the loss of SOM plays a pivotal role. Addressing this threat-work requires a mechanistic understanding of how soil biodiversity loss occurs across diverse landscapes and ecozones. SOM is essential for creating a favorable environment for soil biodiversity by enhancing nutrient availability, water retention, and soil structure. Losses in SOM, closely tied to the mechanisms of soil biodiversity loss, alter physical, chemical, and biological soil attributes, leading to biodiversity decline. Such knowledge can identify priority areas for restoration and inform best practices to conserve soil biodiversity. Protecting and enhancing SOM is central to these efforts. By disentangling the drivers of soil biodiversity loss and their interactions within this threat network, we can develop holistic strategies to mitigate soil biodiversity loss, safeguard soil health, and ensure the sustainability of soil ecosystems globally.

**Keywords:** soil organic matter, soil structure, best practices, conservation, soil nutrients.

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## 1. Introduction

Soils are estimated to contain more than half the biodiversity of our planet (Anthony et al. 2023), encompassing a rich spectrum of genes, organisms and functions that play a crucial role in many ecological processes such as nutrient cycling, organic matter decomposition, and the creation of a well-structured soil matrix (Coleman 2008, Wan et al. 2022, Wu et al. 2024). Recognizing the critical functionality of soil biodiversity has spurred interest in understanding the intricate relationships between soil organisms and their roles in sustaining ecosystem functions (Cadel et al. 2023). Herewith, soil biodiversity has emerged as a central topic in scientific research (Wall et al. 2012, Wagg et al. 2014, Delgado-Baquerizo et al. 2020, Philippot et al. 2024). Concomitant is a noticeable shift from localized studies that quantify soil biodiversity to a broader exploration of theories and fundamentals on a global scale (Adhikari & Hartemink 2016, Orgiazzi et al. 2016a). This shift in focus reflects a growing awareness of the crucial contributions of soil biodiversity to global processes, such as nutrient cycling, carbon sequestration, primary productivity and overall ecosystem resilience (Coleman 2008).

Soil biodiversity, like all global biodiversity, is facing severe declines, and a comprehensive review of the interactive effects of multiple threats and stressors is warranted (Jeffery & Gardi 2010, Gardi et al. 2013, Geisen et al. 2019, Rillig et al. 2019, Tibbett et al. 2020, Guerra et al. 2020a, Barreto & Lindo 2022, Guerra et al. 2022). Declines in soil biodiversity come from a multitude of threats and stressors that present significant challenges to their functionality and biodiversity (Blankinship et al. 2011, Lindo 2015). In this context, threats are defined as factors, conditions or environmental trends with potentially negative impacts on ecosystem components (e.g., the well-being of a species, population, community or ecosystem), while stressors are defined as specific processes that harm ecosystem components, causing lethal or sublethal negative effects on the ecosystem components. The effects of threats or stressors may be acute, while some may be more chronic. Either can carry legacy effects that create time lags or feedback (e.g., Rousk et al. 2013), making a thorough understanding to prevent or ameliorate these threats and stressors difficult.

The FAO Report on the Status of Soil Biodiversity (FAO et al. 2020) outlined 12 primary threats to soil biodiversity (Table 1; Figure 1). Although these threats may differ among various regions in the world, the majority of them predominantly stem from anthropogenic land use activities and management practices, such as intensive agriculture, livestock farming, ranching,

forestry, deforestation, resource extraction activities such as mining, and oil and gas exploration, and industrial activities, infrastructure and urbanization (Gregory et al. 2015, Orgiazzi et al. 2016b). These landscape-level human-induced activities degrade soil and disrupt the soil's physical, chemical and biological characteristics that are critical for maintaining soil biodiversity. Physical disruptions to soil structure include compaction, soil sealing and erosion (Gardi et al. 2013) that result in the loss of pore space, diminished oxygen availability, altered soil temperature, and hinder the movement of air, water and nutrients. Chemical alterations in soil arise from direct applications of substances like chemical fertilizers, pesticides, and pollutants (Biswas et al. 2018), as well as indirect consequences of other activities and management practices that can shift soil pH, ion concentrations, nutrient availability, metals and/or salts, or redox potential (Semple et al. 2003). Reductions in bioregulation and biocontrol manifest through the introduction of invasive species (Gardi et al. 2013), shifts in the dominance of certain species like pests and pathogens, and losses in key species that maintain stability in soil food webs (de Castro et al. 2021), multifunctionality (Wagg et al. 2014), and mutualistic relationships.

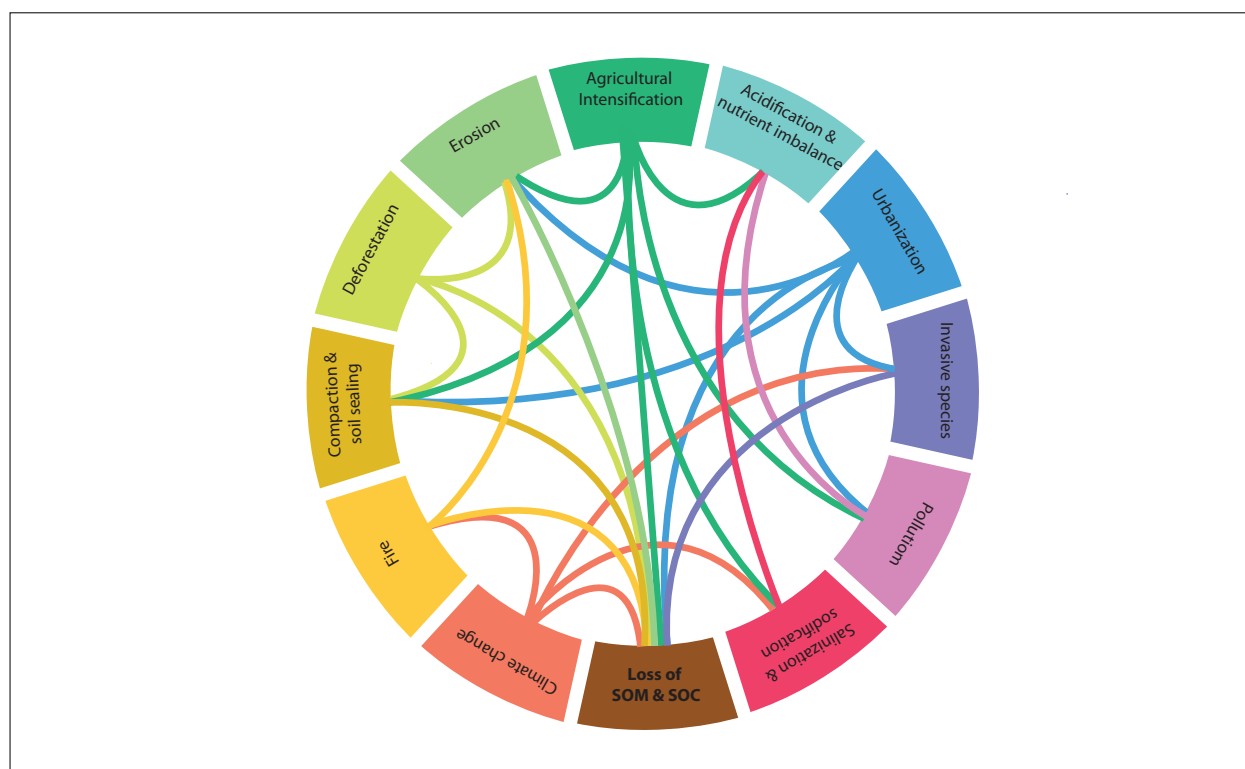
The most substantial indicator of degraded soil, and a common result of most threats is the loss of soil organic matter (SOM) (Figure 1) (Jeffery et al. 2010). Soil organic matter plays a pivotal role in maintaining soil physical properties, while SOM decomposition by microorganisms, and faecal pellet formation by soil fauna in particular (McGill & Spence 1985) contributes to the formation of stable soil aggregates, fostering a well-structured soil matrix (Oades 1984). The depletion of SOM also leads to the loss of essential components such as carbon and nutrients (Johnston et al. 2009), along with adverse effects on moisture-holding capacity and soil structure (Li et al. 2018). Soil organic matter forms an important resource basis for the soil food web (Hunt et al. 1987), and the trophic interactions among soil organisms, in particular the soil fauna, are recognized as important components in the cycling of materials, carbon and nutrients in soils (Barreto et al. 2024). The relationship between soil biodiversity and SOM is intimately linked (de Vries and Caruso 2016); not only does SOM form the basis of food webs, but recent studies have indicated that a large percentage of SOM is soil organism necromass (Wang et al. 2021), and the loss of SOM may be indicative of a negative feedback loop in this relationship (Camenzind et al. 2023). The loss of SOM can have additional feedback effects on physical, chemical and other biological attributes of the soil environment, further exacerbating negative impacts on soil biodiversity.

**Table 1.** The main threats to soil biodiversity, as outlined by the UN-FAO report on the Status of Soil Biodiversity (2020), are linked to specific stressors and the mechanisms of soil biodiversity loss.

Threat as outlined by UN-FAO	Stressor	Mechanism
Deforestation Urbanization Agricultural intensification Loss of SOM/SOC Fire Erosion Desertification	Soil loss and erosion	Loss of pore space Reduced oxygen availability Changes in soil temperature Change in water holding capacity Changes in soil horizon structure Loss of topsoil Reduction in SOM Reduction in soil nutrients
Deforestation Compaction and soil sealing Desertification	Soil compaction	Loss of pore space Reduced oxygen availability Change in water holding capacity
Urbanization Compaction and soil sealing	Soil sealing	Loss of pore space Reduced rainwater infiltration Loss of soil nutrients Disrupt soil aggregates Changes in soil temperature Reduced oxygen and other gas exchange
Deforestation Compaction and soil sealing Climate Change	Changes in soil temperature	Changes in soil moisture Influence metabolic activity (enzymes, growth)
Deforestation Agricultural intensification Compaction and soil sealing Climate Change	Changes in soil moisture	Influence metabolic activity (enzymes, growth) Reduce oxygen availability Influence redox potential
Agricultural intensification	Chemical fertilizers	Alter nutrient availability Increase soil acidification Increase soil salinization Toxicity
Urbanization Agricultural intensification Pollution	Pollutants and contaminants	Toxicity Changes in soil porosity Changes in water infiltration Influence metal transport
Acidification and nutrient imbalances	Acidification	Solubility of soil nutrients and nutrient availability
Agricultural intensification Compaction and soil sealing Acidification and nutrient imbalances Salinization and sodification	Salinization and sodification	Affects soil structure (disperse clay particles) and breakdown soil aggregates Form soil crusts Influence availability of soil nutrients Creates osmotic stress and affects water availability Leach nutrients Toxicity
Climate Change	Changes in redox potential	Influence oxygen availability Influence availability of soil nutrients
Urbanization Climate Change Invasive species	Invasive species	Affects SOM quality and quantity Influence soil acidity Influence soil nutrients Modify soil structure Affects soil water infiltration

Table 1 continued

Threat as outlined by UN-FAO	Stressor	Mechanism
Agricultural intensification Fire Invasive species	Changes in plant-soil interactions	Affects SOM quality and quantity Modify soil structure Influence soil moisture availability Toxicity
Invasive species Loss of SOM/SOC	Changes in soil food webs	Altered predator-prey interactions Reduced systems stability
Deforestation Urbanization Agricultural intensification Loss of SOM/SOC Fire Climate Change Desertification	Loss in SOM	Affects cation exchange capacity Affects pH buffer and soil acidity Loss of nutrient availability Reduce oxygen and other gas exchange Reduce water holding capacity Diminished soil pore space Increase erosion potential Affects soil temperatures Loss of soil aggregates Loss of soil food web basal resource



**Figure 1.** Main threats to soil biodiversity as outlined by the UN-FAO report on the Status of Soil Biodiversity (2020). Threats operate as interconnected and interacting factors that drive soil biodiversity loss through diverse mechanisms, and often culminate in the loss of soil organic matter (SOM), either directly or indirectly. The complex interactions within this network of threats is referred to as the „soil biodiversity threat-work“. Understanding these interactions is essential for developing sustainable soil management practices aimed at preserving soil biodiversity, and mitigating soil biodiversity loss.

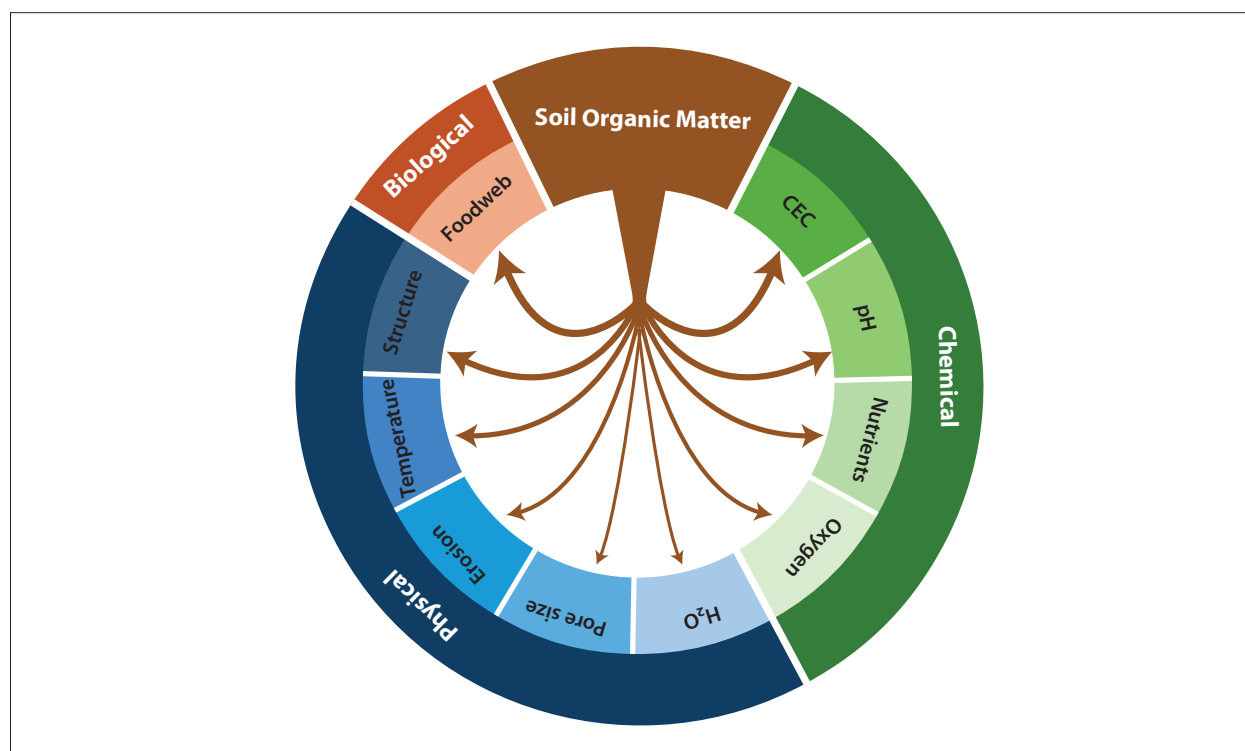
In this review, we address how an interconnected network of threats to soil biodiversity cumulate in losses to SOM and soil organic carbon (SOC) across local, regional and global scales that drive changes in physical, chemical and biological attributes of the soil environment that lead to soil biodiversity loss. We refer to this network of interconnected threats to soil biodiversity as the threat-work.

## 2. Soil Organic Matter Loss as a Mechanism of Soil Biodiversity Loss

The importance of SOM cannot be understated. Soil organic matter interacts dynamically with physical, chemical, and biological attributes of soil, influencing soil structure, fertility, nutrient cycling, and ecosystem functioning (Powlson et al. 2011, Cotrufo et al. 2013). Yet, nearly all the FAO listed threats (of which loss of SOM is one) culminate in losses of SOM (Figure 1). Agricultural intensification, deforestation, and climate change

typically lead to a net loss of SOM and SOC through a variety of mechanisms, largely related to disturbing soil structure, removing or altering organic inputs, and promoting decomposition (Lal 2004, Haddaway et al. 2015). The loss of SOM can be considered habitat loss at the scale of most soil organisms, and a main mechanism of soil biodiversity loss (Newbold et al. 2015). The loss of SOM is also a significant concern for biologically mediated soil functions, particularly those associated with the cycling of carbon and nutrients, moisture-holding capacity and soil structure (Figure 2). Hence, the preservation of SOM content and composition plays a key role in supporting, conserving, and promoting soil biodiversity.

**SOM contributes to the Physical soil environment** influencing its porosity, water-holding capacity, and aeration. Soil organic matter acts as a natural cementing agent in soil, promoting the formation of stable aggregates through the binding action of organic compounds such as polysaccharides and microbial by-products (Haynes & Swift 1990). These aggregates play a crucial role in soil structure, stability, and fertility,



**Figure 2.** Losses of soil organic matter (SOM) and soil organic carbon (SOC) at local, regional, and global scales drive changes in the physical, chemical, and biological attributes of the soil environment, ultimately leading to soil biodiversity loss. Declines in SOM are particularly detrimental to biologically mediated soil functions, including carbon and nutrient cycling, moisture retention, and maintaining soil structure. Key chemical attributes of SOM include maintaining cation exchange capacity (CEC), pH, nutrient availability, and oxygen levels; physical attributes include moisture retention, the creation of diverse pore sizes, erosion resistance, temperature regulation, and soil structure. SOM also forms the biological foundation of the soil food web. Hence, the preservation of SOM content and composition plays a key role in supporting, conserving, and promoting soil biodiversity.

influencing water retention, nutrient cycling, and plant growth. The promotion of soil aggregation plays a critical role in creating and maintaining macropores (larger channels for air and water movement) and micropores (smaller spaces between soil particles) that enhance soil aeration and facilitate water infiltration, root growth, and nutrient movement. These pore spaces also provide habitat and facilitate the movement of non-burrowing soil organisms (Porre et al. 2016). Soil organic matter provides physical support for plant roots and forms a protective layer on the soil surface, reducing the impact of raindrops and erosive forces, which helps prevent soil erosion. Soil organic matter also acts as an insulating layer, regulating soil temperature and reducing moisture loss (Rinke et al. 2008).

**SOM affects the Chemical soil environment** by influencing nutrient cycling, pH buffering, cation exchange capacity, chemical stability, and metal chelation. Soil organic matter improves the cation exchange capacity (CEC) of soil (Stevenson 1982) by providing binding sites for positively charged ions (cations; e.g., Ca, Mg, K,  $\text{NH}_4^{+}$ ) because SOM contains many negatively charged functional groups such as carboxyl, phenolic, and hydroxyl groups that attract and retain cations in the soil matrix. This increased CEC conferred by SOM enhances nutrient retention, soil fertility, and cation availability in soil ecosystems (Solly et al. 2020). The organic acids and bases in SOM can neutralize excess acidity or alkalinity in soil and buffer the soil pH, keeping it within a relatively stable range. Soil organic matter can also chelate metals in soil, influencing their solubility, mobility, and bioavailability, reducing their toxicity and potential for leaching or runoff, which can reduce ecological impacts on soil organisms and plants. SOM serves as a reservoir and source of essential nutrients (N, P, K) and micronutrients, and the chemically stable forms of organic matter contribute to soil carbon sequestration, soil organic carbon storage, and climate change mitigation efforts.

**SOM influences the Biological environment** of soil, serving as the basal resource for the soil food web, providing habitat for the myriad of species living in the soil, and facilitating the cycling of nutrients and energy (Hunt et al. 1987). Soil organic matter consists of a diverse array of organic compounds that serve as substrates for microbial metabolism and contributes to the chemical diversity of the soil environment, thus supporting diverse trophic interactions. Soil organic matter is also the source of food for bioturbating invertebrates like earthworms that are crucial in producing the stable macroaggregates that constitute a major proportion of the friable soil

structure in many ecosystems (Six et al. 2004). The soil food web feeds back into the detrital pool of SOM through decomposition and necromass production (Delgado-Baquerizo et al. 2020), which is estimated at 30-50% of total SOM for temperate soils (Liang et al. 2019) and forms persistent SOM (Wang et al. 2021). Biodiversity and SOM are so closely related that, in some cases, SOM is used as a proxy for soil biodiversity (Jones et al. 2021). The loss of SOM is a critical issue driven by interconnected physical, chemical, and biological threats, which act through reinforcing processes that accelerate SOM decline and reduce soil biodiversity. Physically, soil erosion and compaction disrupt the structural stability essential for SOM protection, exposing organic matter to decomposition. Chemically, acidification, salinization, and nutrient imbalances alter soil chemistry, reducing SOM stability and impairing its sequestration. Biologically, biodiversity loss diminishes microbial activity and ecosystem functions critical for SOM formation and decomposition regulation. These threats and associated stressors operate synergistically, creating feedback loops that exacerbate SOM depletion and soil degradation. The following sections explore these physical, chemical, and biological dimensions, emphasizing their mechanisms, interactions, and cascading impacts.

### 3. Physical Threats to Soil Biodiversity Loss

Threats to soil biodiversity that alter the physical soil environment include direct effects of soil erosion, compaction and soil sealing, as well as indirect effects of intensive agriculture, deforestation and climate change on soil structure, temperature and moisture. Physical disturbances to soil structure, both compaction and erosion can lead to loss of pore space, reduced oxygen availability, changes in soil temperature, changes in water infiltration, soil moisture and water holding capacity, that affect soil biodiversity, including disruption of fungal networks, and changes in whole biotic community composition or structure.

**Soil loss and erosion** through the removal of the soil cover by urbanization, landslides, water or wind erosion, and fire affect soil biodiversity directly and indirectly. Erosion can physically remove topsoil leading to a direct loss of soil biodiversity and a reduction in SOM and soil nutrients (Qiu et al. 2023). This loss of the uppermost soil layer, where most soil microbial and faunal species inhabit, has a direct impact on soil biodiversity through



habitat loss at these small spatial scales. The removal of this nutrient-rich layer can also deprive soil organisms of essential resources since the organic matter in this layer serves as the basal resource for the soil food web. The loss of this resource shifts community composition and reduces soil biodiversity (Guerra et al. 2020b). Erosion can also change soil properties, such as surface soil texture and structure, as the finer particles and organic matter are lost from the surface soil.

Altering these soil characteristics can impact habitat suitability for various soil organisms because changes in soil texture and structure can affect water retention, aeration, and nutrient availability, influencing the survival and distribution of soil biodiversity (Brussaard et al. 2007). Erosion can also lead to soil compaction, especially in areas where soil is exposed and vulnerable to compaction by external forces such as rainfall and traffic. The disturbance caused by erosion creates opportunities for pioneer species that may have different ecological requirements than the original soil community. This can shift the composition of the soil community, potentially favouring invasive species that can outcompete native species and further contribute to soil biodiversity loss.

**Soil compaction and loss of soil pore space** not only impact soil structure but also diminish habitat heterogeneity within soil ecosystems. Pore spaces serve multiple functions that support soil biodiversity and ecosystem functioning. Compaction reduces soil porosity and air space, limiting the movement of air, water, and nutrients within the soil profile and removing habitat for mesofauna and microfauna who cannot create habitable pore space for themselves (Porre et al. 2016). Soil pore spaces are also exploited by plant roots as anchor points and for access to soil water and oxygen, nutrient uptake and interactions with soil biota. The presence of pore spaces creates microhabitats within the soil environment, contributing to habitat heterogeneity and offers regions of the soil profile that differ based on factors such as moisture, aeration, protection from predators, and nutrient availability. The availability of varied microenvironments created by soil pore spaces supports the coexistence of multiple species and promotes biodiversity within soil ecosystems (Anderson 1975, Giller 1996).

Oxygen is vital for the aerobic respiration of most soil organisms and the exchange of gases through pore spaces helps maintain aerobic conditions in the soil, facilitating the metabolic activities of soil organisms and preventing the accumulation of other gases. Moreover, pore spaces function as conduits for water movement within the soil profile via capillary action and gravity, distributing moisture throughout the soil matrix (Bodner et al.

2023) and, in doing so, transporting nutrients. Adequate water movement within the soil profile helps maintain optimal moisture levels for soil organisms, preventing waterlogging or drought conditions that can negatively impact soil biodiversity (e.g., Larsen et al. 2004, Turnbull & Lindo 2015).

**Soil sealing** is the process by which the soil surface becomes compacted and impermeable due to human activities. Soil sealing, typically associated with urbanization and infrastructure development, involves the covering of soil surfaces with impermeable materials such as concrete or asphalt for roads and pavement. This process disrupts natural soil processes and reduces the permeability of the soil, leading to altered water infiltration and runoff patterns. Soil sealing can also limit the exchange of gases between the soil and the atmosphere, affecting soil aeration and microbial activity (Pereira et al. 2021). As a result, soil biodiversity is impacted, with many soil organisms unable to survive or thrive in sealed environments (Wei et al. 2013). Soil sealing is often concomitant with compaction, reducing the overall porosity of the soil, while sealed surfaces create a barrier that prevents rainwater from infiltrating into the soil and seedling emergence, increasing run-off that can cause flooding and enhancing erosion and losses of soil nutrients, as well as impeding the exchange of gases, especially oxygen (Scalenghe & Marsan 2009). Sealed surfaces tend to absorb and reflect heat, leading to enhanced temperature fluctuations in the underlying soil.

**Soil temperature** influences the metabolic rates of microorganisms. As temperatures rise, microbial activity generally increases, promoting higher rates of decomposition, nutrient cycling, and organic matter turnover (Hopple et al. 2020). Conversely, high temperatures can inhibit microbial activity or exceed the thermal death points of organisms (Gonzalez & Aranda 2023). Different species have distinct temperature preferences, and changes in soil temperature can influence their activity levels, reproduction rates, carbon and nutrient use efficiencies, and overall abundances, as well as predator-prey interactions (Meehan et al. 2022). Soil temperature influences plant growth and root development, which in turn affects soil biodiversity through the availability of root exudates (Zhang et al. 2016). Thus, changes in plant growth patterns due to temperature variations can impact the availability of these resources, thereby influencing the composition and activity of soil microbial communities, and can affect the establishment and activity of mycorrhizal networks.

Increases in soil temperature in the context of climate change can significantly affect soil biodiversity in boreal

and polar regions, particularly through changes in permafrost (Markkula et al. 2019, Barreto et al. 2023). Permafrost thawing changes soil moisture levels and nutrient availability and can stimulate plant growth or lead to shifts in plant community composition (Standen & Baltzer 2021), which in turn affects soil biodiversity by altering the availability of resources and habitat structure. Increases in soil temperature across many regions can lead to increased evapotranspiration and affect soil moisture levels (warming-induced drying), particularly in regions where precipitation does not compensate for the increased water loss. Persistent soil moisture deficits can also lead to changes in soil properties, such as decreased soil organic matter content, increased soil compaction, and alterations in soil structure.

**Soil moisture** (both drying (including drought and desertification) and wetting (including flooding and waterlogging)) affects the distribution, abundance, and activity of various soil organisms. Soil moisture influences soil structure and porosity, which in turn affects the diffusion of gases, water, and nutrients in the soil (Du et al. 2023). Thus, changes in soil moisture can impact the metabolic processes of soil organisms. Excessively wet or waterlogged conditions reduce oxygen availability in the soil, leading to anaerobic conditions, which favour processes such as denitrification (Soana et al. 2022). Waterlogged soils can also increase soil erosion and loss, and increase surface soil compaction, further affecting soil pore space and gas exchange. The presence of earthworms, specifically anecic earthworms can help lessen the negative impacts of flooding by reducing soil moisture after intense rainfall events (Andriuzzi et al. 2015). Conversely, dry conditions can lead to nutrient immobilization, where nutrients become less available for plant uptake and microbial activity, or impede root growth, burrowing and the movement of soil organisms (Zheng et al. 2017). Drought (prolonged absence of precipitation) and desertification (land degradation in already dry, arid and semi-arid regions) are increasing under climate change, as well as from human activities such as deforestation and the overexploitation of aquifers. Drought and desertification often result in a loss of aboveground vegetation that corresponds with reductions of SOM (Junting et al. 2021).

#### 4. Chemical Threats to Soil Biodiversity Loss

Direct chemical disturbances include pollution, salinization, and acidification through activities such

as contamination, the application of lime, chemicals and fertilizers, and the indirect results of other activities that change soil pH, ions, metals, and salt contents, or ubiquitous global microplastic pollutants. Soil organisms exhibit varying degrees of sensitivity to changes in soil chemical properties (Beaumelle et al. 2021). Shifts in soil chemistry can directly affect the physiological processes, behaviour, and survival of soil organisms, leading to changes in population dynamics and community structure. Consequently, chemical disturbances can have cascading effects throughout the soil food web (Carrascosa et al. 2015), ultimately influencing ecosystem functioning and services provided by soil biodiversity.

**Pollution and contaminants** can significantly impact soils and soil biodiversity. The extent of their impact depends on factors such as the type, quantity, concentration, and location of pollutants, as well as the duration of exposure. Industrial, agricultural, and urban activities often release pollutants such as heavy metals (e.g., lead, cadmium, and mercury), organic compounds, and other chemicals into the environment. Chemical fertilizers and pesticides, largely in association with intensive agricultural practices, can lead to high levels of nutrients, such as nitrogen and phosphorus, that result in nutrient imbalances and eutrophication (Pahalvi et al. 2021). They also have direct toxic effects on beneficial soil-dwelling organisms and other non-target organisms. Certain chemical fertilizers, especially those containing ammonium-based nitrogen, contribute to soil acidification (Zhang et al. 2024), while others containing soluble salts contribute to soil salinization (Omuto et al. 2024). Some hydrocarbon compounds, such as those in herbicides, can have immediate, direct, and toxic effects on soil organisms. For instance, long-term applications of glyphosate were shown to decrease microbial diversity and alter community composition (Lancaster et al. 2010, Newman et al. 2016, Gonzalez et al. 2021).

Microplastics enter soil ecosystems through various pathways, including the application of plastic mulches in agriculture, the breakdown of larger plastic debris, atmospheric deposition, and the use of sewage sludge as fertilizer. Once in the soil, microplastics can have detrimental effects on soil biodiversity in several ways (Han et al. 2024), including physical interference with movement and through the release of chemicals into the soil environment, including plasticizers, flame retardants, and heavy metals that can pose toxicological risks to soil organisms. Indirectly, microplastics can alter soil structure by filling pore spaces, potentially leading to changes in soil porosity and water infiltration, although these effects may not be immediately apparent (Barreto et al. 2020).



**Acidification, or alternatively liming**, of soils leads to changes in soil pH, which can influence the solubility and availability of nutrients and pollutants in the soil; some nutrients, like aluminum and manganese, become more available under acidic conditions, while others, such as calcium and magnesium, may be leached away. Acidic conditions can mobilize certain toxic elements (e.g., aluminum) in the soil, posing a threat to soil organisms (Tibbett et al. 2019). Different species have optimal pH ranges for their growth and activity, but changes in pH can also influence soil structure and aggregation, as well as various biogeochemical processes, including carbon and nitrogen cycling through altering rates of processes, affecting the availability and movement of nutrients and pollutants. Acidification can indirectly contribute to salinization or sodification through the soils ability to hold cations such as  $\text{Ca}^{2+}$  or  $\text{Mg}^{2+}$  which can be replaced by sodium cations, yet liming, often used to counteract soil acidity can potentially worsening salinization in already saline soils by increasing the solubility of salts.

**Salinization and sodification** (the process by which salts accumulate in the soil and soils with high levels of sodium, respectively) increase the dispersal of clay particles in soil, resulting in the breakdown of soil aggregates and the collapse of soil structure that can be mitigated by higher levels of soil organic carbon (Rezapour et al. 2023). Sodium ions that replace calcium and magnesium ions on clay and organic matter surfaces have weaker binding capacities than calcium and magnesium leading to the dispersion of clay particles and the breakdown of soil aggregates. The displacement of calcium by sodium can substantially increase soil pH, shifting the availability of essential nutrients (Cramer et al. 1985).

Certain ions associated with salinity, such as sodium and chloride, can accumulate in plant tissues and soil, and high concentrations of these ions can be toxic (Kronzucker et al. 2013). Sodium also tends to replace calcium in the soil, leading to the formation of a crust on the soil surface, while excess salts, such as sodium, can interfere with the availability of other soil cation nutrients like potassium and magnesium, as well as calcium, leading to nutrient imbalances. High salt concentrations in the soil create osmotic stress, reducing water availability, and sodification can result in the leaching of essential nutrients from the root zone, contributing to decreased soil fertility (Palacino et al. 2024).

**Redox potential**, which refers to the tendency of a soil to undergo oxidation-reduction reactions, plays a crucial role in shaping soil biodiversity by influencing nutrient cycling, microbial activity, and the availability of essential elements. Redox potential is closely linked to

oxygen availability and affects the solubility and mobility of elements like iron and manganese. Well-drained soils with ample oxygen have a positive redox potential, favouring aerobic (oxygen-dependent) processes (Husson 2013). In oxidized conditions (higher redox potential), elements like iron and manganese are more likely to form solid phases, while under reduced conditions (lower redox potential), they tend to become more soluble and mobile. Redox potential will influence nutrient transformations in soils, affecting the availability of different sulphur and nitrogen species (e.g., nitrate and ammonium) depending on the prevailing conditions.

## 5. Biological Threats to Soil Biodiversity Loss

Reductions in bioregulation and biocontrol within soil systems also lead to soil biodiversity loss. These stem from species additions, such as invasive species (Brosseau et al. 2021), or changes in the dominance of certain species, such as pests and pathogens. Losses of select species that maintain soil food web stability and/or play key roles in mutualisms can lead to the cascading loss of other species.

**Invasive species**, spanning plants, animals, and microorganisms, can have a significant influence on soil systems and affect soil biodiversity. Invasive plant species can alter the composition of plant communities, affecting SOM quantity and quality, and thereby nutrient availability as well as altering soil chemistry via chemical releases or exudates (see next section). Certain plant species like Black Walnut (*Julans nigra*) additionally emit allelopathic chemicals (Nicolescu et al. 2020), impacting other vegetation and lowering soil pH. Invasive plants that associate with nitrogen-fixing bacteria may change nitrogen availability in the soil, which has the potential to enhance soil biodiversity through increased aboveground productivity, but these changes can also impact soil biodiversity by altering competitive outcomes and favouring non-mycorrhizal or less mutualistic mycorrhizal fungi over more mutualistic species, leading to shifts in mycorrhizal community composition and diversity (Ma et al. 2023). These changes can also alter resource availability for other soil organisms that feed on the microbial and fungal biomass, further impacting soil biodiversity.

Invasive microorganisms, including fungi and bacteria, can be themselves novel pathogens to a naïve soil system that can alter or disrupt microbial communities and plant-soil interactions (van der Putten et al. 2007). Animal

invasives, such as burrowing mammals or invertebrates, reshape soil structure through their digging and burrowing activities, disrupting soil stability, aeration, and nutrient distribution. Notably, invasive earthworm species, particularly in non-native locales, can profoundly reshape soil structure through their burrowing activities (Langmaid 1964, Addison 2009, Klaminder et al. 2023), affecting soil aeration, water infiltration, and nutrient distribution, and drastically altering SOC dynamics.

**Plant-soil interactions** (aboveground-belowground linkages) are fundamental processes that shape the structure and functioning of terrestrial ecosystems. These interactions encompass a wide range of complex relationships between plants and the soil environment, including the exchange of nutrients, water, carbon, and energy. Shifts in plant communities can alter the types and amounts of root exudates (chemical, nutrients) and litter properties (quantity and quality of SOM inputs), affecting basal resources for soil organisms and influencing decomposition rates (Barreto & Lindo 2018). Different plant species also form specific relationships with mycorrhizal fungi and nitrogen-fixing bacteria and feedback between these relationships can have cascading effects on the establishment of native vs non-native species (Reinhart & Callaway 2006).

**Soil food webs** refer to the networks of interactions among soil organisms that participate in complex consumer-resource interactions that govern rates of nutrient cycling and mineralization, decomposition, and biomass production (Hunt et al. 1987). Changes in the abundance or composition of soil organisms can disrupt trophic interactions within soil food webs, affecting the flow of energy and nutrients through the system (Buchkowski et al. 2023, Barreto et al. 2024, Potapov et al. 2024). Intensive agricultural practices, including the use of chemical pesticides or biological control agents, can inadvertently eradicate or suppress non-target soil organisms that play beneficial roles in soil food webs such as beneficial predators or decomposers, disrupting predator-prey relationships and altering soil biodiversity. Loss of natural enemies or decomposers can lead to pest outbreaks, reduced pest regulation, and impaired ecosystem services that are provided by soil organisms. Conversion of natural habitats to agricultural land or urban development may favour certain species over others, leading to changes in species diversity, density, distribution, or trophic interactions (Potapov et al. 2019). These shifts in community structure can affect ecosystem stability, resilience, and the provision of ecosystem services by soil organisms (de Castro et al. 2021).

## 6. SOM as the Integrator in the Soil 'Threat-work' and Promoting Soil Biodiversity

The complex and diverse network of threats and stressors and their influence on soil biodiversity through various physical, chemical, and biological mechanisms cannot and should not be counteracted separately. Across all scenarios, some effects on soil systems may be acute, while others may be more chronic, and either can carry legacy effects that lead to time lags and feedbacks that make a full understanding for preventing or ameliorating these threats and stressors difficult. Restoration, remediation, and reclamation procedures may be required to address any or all the aforementioned physical, chemical, and biological mechanisms while considering changes in land use (both past and present).

Maintaining or increasing SOM content is increasingly recognized as a potential mitigation for climate change on a global scale. For instance, the "4 per 1000" initiative, stemming from the agreement established at the 21st Conference of the Parties in Paris in 2015 underscores the imperative to annually increase carbon storage in soil by 4‰ (Minasny et al. 2017). The primary goal of the "4 per 1000" initiative is to increase soil carbon sequestration rates by promoting the adoption of agricultural practices that enhance soil organic matter accumulation and retention (<http://4p1000.org>). This ambitious undertaking aims to offset a significant portion of the carbon emissions released into the atmosphere by human activities each year. The "4 per 1000" initiative promotes the conservation of soil biodiversity by fostering sustainable land management practices that enhance soil habitat quality and support soil food webs, alongside carbon sequestration and ecosystem resilience in agricultural landscapes.

The inclusion of soil management, particularly within agricultural contexts, as a key strategy for carbon sequestration and climate change mitigation was further underscored in the 2022 report of the Intergovernmental Panel on Climate Change (IPCC 2022). Management of soil, in particular agricultural soils, is among the most promising pathways to capture and store atmospheric carbon and mitigate climate change (IPCC 2022). While climate change, driven by atmospheric greenhouse gases and resulting in warming trends, poses direct and imminent threats to soil biodiversity, its broader impacts may also manifest as cascading effects, including alterations to fire regimes and the proliferation of invasive species. Climate change can alter the abundances of soil trophic groups (Blankinship et al. 2011) and this restructuring of soil food webs, particularly in sensitive ecosystems like boreal peatlands, can impact carbon

storage potential (Barreto et al. 2024), causing serious feedback effects on climate change. Recognizing the multifaceted importance of SOM management extends beyond soil biodiversity considerations, encompassing its pivotal role in climate change mitigation efforts and its potential to alleviate the far-reaching consequences of environmental destabilization on soil ecosystems.

Understanding the complex interactions among multiple threats (i.e., the threat-work) to soils and their biodiversity is essential for sustainable soil management practices aimed at preserving soil health, productivity, and resilience in the face of environmental change. However, by enhancing SOM interactions with soil physical, chemical and biological properties, we can promote soil conservation, biodiversity conservation, and ecosystem services in terrestrial ecosystems. We propose that managing SOM offers a holistic approach with the potential to bolster, safeguard, and enrich soil biodiversity and overall soil health in a practical and sustainable manner. Practices geared towards enhancing SOM levels, such as the integration of trees into the production system (e.g., agroforestry, alley cropping, agrosilviculture, silvopastoral), cover cropping, incorporating crop residues, and adopting reduced tillage methods, augment SOM content effectively. These strategies not only contribute to the accumulation of organic materials in soil but also preserve and promote soil biodiversity. While there may be initial costs associated with adopting practices to enhance SOM levels, the long-term economic benefits, market opportunities, government support, and environmental co-benefits can make these practices economically viable and attractive for farmers and land managers. Importantly, these management techniques have demonstrated cost-effectiveness and feasibility, rendering them readily incorporable into agricultural practices (Sperow 2020). Recognizing the fundamental significance of SOM is paramount in crafting and implementing comprehensive best practices for managing soils that will nurture resilient and biodiverse soil ecosystems across a spectrum of landscapes. Soil organic matter is a central node in the network of interconnected threats and stressors affecting soil biodiversity, and is key to designing effective strategies to conserve and protect soil biodiversity.

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## References

- Addison, J. A. (2009). Distribution and impacts of invasive earthworms in Canadian forest ecosystems. *Biological Invasions*, 11, 59–79.
- Adhikari, K., & Hartemink, A. E. (2016). Linking soils to ecosystem services—A global review. *Geoderma*, 262, 101–111.
- Anderson, J. M. (1975). The enigma of soil animal species diversity. In J. Vaněk (Ed.), *Progress in Soil Zoology* (pp. 51–58). Springer. [https://doi.org/10.1007/978-94-010-1933-0\\_5](https://doi.org/10.1007/978-94-010-1933-0_5)
- Andriuzzi, W. S., Pulleman, M. M., Schmidt, O., Brussaard, L., & Faber, J. H. (2015). Anecic earthworms (*Lumbricus terrestris*) alleviate negative effects of extreme rainfall events on soil and plants in field mesocosms. *Plant and Soil*, 397, 103–113. <https://doi.org/10.1007/s11104-015-2604-4>
- Anthony, M. A., Bender, S. F., & van der Heijden, M. G. (2023). Enumerating soil biodiversity. *Proceedings of the National Academy of Sciences*, 120, e2304663120.
- Barreto, C., & Lindo, Z. (2018). Drivers of decomposition and the detrital invertebrate community differs across a hummock-hollow microtopology in boreal peatlands. *Écoscience*, 25, 39–48. <https://doi.org/10.1080/11956860.2017.1412282>
- Barreto, C., & Lindo, Z. (2022). Response of soil biodiversity to global change. *Pedobiologia*, 90, 150792. <https://doi.org/10.1016/j.pedobi.2022.150792>
- Barreto, C. R. A., Rillig, M., & Lindo, Z. (2020). Addition of polypropylene and polyester in soil affects decomposition rates but not microarthropod communities. *Soil Organisms*, 92(2), 109–119. <https://doi.org/10.25674/so92iss2pp109>
- Barreto, C., Conceição, P. H. S., de Lima, E. C. A., Stievano, L. C., Zeppelini, D., Kolka, R. K., Hanson, P. J., & Lindo, Z. (2023). Large-scale experimental warming reduces soil faunal biodiversity through peatland drying. *Frontiers in Environmental Science*, 11, 1153683.
- Barreto, C., Buchkowski, R. W., & Lindo, Z. (2024). Restructuring of soil food webs reduces carbon storage potential in boreal peatlands. *Soil Biology and Biochemistry*, 193, 109413. <https://doi.org/10.1016/j.soilbio.2024.109413>
- Beaumelle, L., Thouvenot, L., Hines, J., Jochum, M., Eisenhauer, N., & Phillips, H. R. P. (2021). Soil fauna diversity and chemical stressors: A review of knowledge gaps and roadmap for future research. *Ecography*, 44, 845–859.
- Biswas, B., Qi, F., Biswas, J. K., Wijayawardena, A., Khan, M. A. I., & Naidu, R. (2018). The fate of chemical pollutants with soil properties in the climate change paradigm – A review. *Soil Systems*, 2(3), 51.

- Blankinship, J. C., Niklaus, P. A., & Hungate, B. A. (2011). A meta-analysis of responses of soil biota to global change. *Oecologia*, 165(3), 553–565. <https://doi.org/10.1007/s00442-011-1909-0>
- Bodner, G., Zeiser, A., Keiblinger, K., Rosinger, C., Winkler, S. K., Stumpp, C., & Weninger, T. (2023). Managing the pore system: Regenerating the functional pore spaces of natural soils by soil-health oriented farming systems. *Soil & Tillage Research*, 234, 105862. <https://doi.org/10.1016/j.still.2023.105862>
- Brousseau, P.-M., Chauvat, M., De Almeida, T., & Forey, E. (2021). Invasive knotweed modifies predator–prey interactions in the soil food web. *Biological Invasions*, 23, 1987–2002. <https://doi.org/10.1007/s10530-020-02431-0>
- Brussaard, L., de Ruiter, P. C., & Brown, G. G. (2007). Soil biodiversity for agricultural sustainability. *Agriculture, Ecosystems & Environment*, 121(3), 233–244. <https://doi.org/10.1016/j.agee.2006.12.013>
- Buchkowski, R. W., Barreto, C., & Lindo, Z. (2023). soilfoodwebs: An R package for analyzing and simulating nutrient fluxes through food webs. *European Journal of Soil Biology*, 119, 103556. <https://doi.org/10.1016/j.ejsobi.2023.103556>
- Cadel, M., Cousin, I., & Therond, O. (2023). Relationships between soil ecosystem services in temperate annual field crops: A systematic review. *Science of the Total Environment*, 902, 165930. <https://doi.org/10.1016/j.scitotenv.2023.165930>
- Camenzind, T., Mason-Jones, K., Mansour, I., Rillig, M. C., & Lehmann, J. (2023). Formation of necromass-derived soil organic carbon determined by microbial death pathways. *Nature Geoscience*, 16, 115–122. <https://doi.org/10.1038/s41561-022-01109-w>
- Carrascosa, M., Sánchez-Moreno, S., & Alonso-Prados, J. L. (2015). Effects of organic and conventional pesticides on plant biomass, nematode diversity and the structure of the soil food web. *Nematology*, 17(1), 11–26. <https://doi.org/10.1163/15685411-00002837>
- Coleman, D. C. (2008). From peds to paradoxes: Linkages between soil biota and their influences on ecological processes. *Soil Biology and Biochemistry*, 40(2), 271–279. <https://doi.org/10.1016/j.soilbio.2007.08.005>
- Cotrufo, F. M., Wallenstein, M. D., Boot, C. M., Deneff, K., & Paul, E. (2013). The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization. *Global Change Biology*, 19(4), 988–995. <https://doi.org/10.1111/gcb.12113>
- Cramer, G. R., Läuchli, A., & Polito, V. S. (1985). Displacement of  $\text{Ca}^{2+}$  by  $\text{Na}^{+}$  from the plasmalemma of root cells. *Plant Physiology*, 79(1), 207–211. <https://doi.org/10.1104/pp.79.1.207>
- de Castro, Berdugo, M., Eldridge, D.J., Eisenhauer, N., Singh, B.K., Cui, H., Abades, S., Alfaro, F.D., Bamigboye, A.R., Bastida, F., et al. (2021). Local stability properties of complex, species-rich soil food webs with functional block structure. *Ecology and Evolution*, 11(23), 16070–16081. <https://doi.org/10.1002/ece3.8303>
- de Vries, F. T., & Caruso, T. (2016). Eating from the same plate? Revisiting the role of labile carbon inputs in the soil food web. *Soil Biology and Biochemistry*, 102, 4–9. <https://doi.org/10.1016/j.soilbio.2016.06.023>
- Delgado-Baquerizo, M., Reich, P. B., Trivedi, C., Eldridge, D. J., Abades, S., Alfaro, F. D., ... & Singh, B. K. (2020). Multiple elements of soil biodiversity drive ecosystem functions across biomes. *Nature Ecology & Evolution*, 4, 210–220. <https://doi.org/10.1038/s41559-019-1084-y>
- Du, Y., Guo, S., Wang, R., Song, X., & Ju, X. (2023). Soil pore structure mediates the effects of soil oxygen on the dynamics of greenhouse gases during wetting-drying phases. *Science of the Total Environment*, 895, 165192. <https://doi.org/10.1016/j.scitotenv.2023.165192>
- FAO, ITPS, GSBI, SCBD, & EC. (2020). *State of knowledge of soil biodiversity – Status, challenges and potentialities: Report 2020*. FAO. <https://doi.org/10.4060/cb1928en>
- Gardi, C., Jeffery, S., & Saltelli, A. (2013). An estimate of potential threats levels to soil biodiversity in EU. *Global Change Biology*, 19(5), 1538–1548. <https://doi.org/10.1111/gcb.12159>
- Geisen, S., Wall, D. H., & van der Putten, W. H. (2019). Challenges and opportunities for soil biodiversity in the Anthropocene. *Current Biology*, 29(19), R1036–R1044. <https://doi.org/10.1016/j.cub.2019.08.007>
- Giller, P. S. (1996). The diversity of soil communities: The ‘poor man’s tropical rainforest’. *Biodiversity and Conservation*, 5(2), 135–168. <https://doi.org/10.1007/BF00055827>
- Gonzalez, J. M., & Aranda, B. (2023). Microbial growth under limiting conditions—Future perspectives. *Microorganisms*, 11(7), 1641. <https://doi.org/10.3390/microorganisms11071641>
- Gonzalez, R., Kavouras, J., Barragan, V., Bernhard, E., Dawalibi, S., Diaz, M., ... & Pawlica, N. (2021). Use the metabolic fingerprint in microbial communities to evaluate the anthropogenic impact on soils. In FAO (Ed.), *Keep soil alive, protect soil biodiversity – Global Symposium on Soil Biodiversity 19–22 April 2021: Proceedings*. FAO. <https://www.fao.org/documents/card/en/c/cb1928en>
- Gregory, A. S., Ritz, K., McGrath, S. P., Quinton, J. N., Goulding, K. W. T., Jones, R. J. A., ... & Whitmore, A. P. (2015). A review of the impacts of degradation threats on soil properties in the UK. *Soil Use and Management*, 31(1), 1–15. <https://doi.org/10.1111/sum.12118>
- Guerra, C. A., Heintz-Buschart, A., Sikorski, J., Chatzinotas, A., Guerrero-Ramírez, N., Cesarz, S., Beaumelle, L., Rillig, M.C., Maestre, F.T., Delgado-Baquerizo, M., et al. (2020a). Blind spots in global soil biodiversity and ecosystem function research. *Nature Communications*, 11, 3870. <https://doi.org/10.1038/s41467-020-17688-2>
- Guerra, C. A., Rosa, I. M. D., Valentini, E., Wolf, F., Filipponi, F., Karger, D. N., ... & Eisenhauer, N. (2020b). Global



- vulnerability of soil ecosystems to erosion. *Landscape Ecology*, 35, 823–842. <https://doi.org/10.1007/s10980-020-00992-9>
- Guerra, C. A., Berdugo, M., Eldridge, D. J., Eisenhauer, N., Singh, B. K., Cui, H., ... & Delgado-Baquerizo, M. (2022). Global hotspots for soil nature conservation. *Nature*, 610(7930), 693–698. <https://doi.org/10.1038/s41586-022-05399-z>
- Haddaway, N. R., Hedlund, K., Jackson, L. E., Kätterer, T., Lugato, E., Thomsen, I. K., ... & Söderström, B. (2015). What are the effects of agricultural management on soil organic carbon in boreo-temperate systems? *Environmental Evidence*, 4, 23. <https://doi.org/10.1186/s13750-015-0049-0>
- Han, L., Chen, L., Feng, Y., Kuzyakov, Y., Chen, Q., Zhang, S., ... & Rillig, M. C. (2024). Microplastics alter soil structure and microbial community composition. *Environment International*, 185, 108508. <https://doi.org/10.1016/j.envint.2024.108508>
- Hayne, R. J., & Swift, R. S. (1990). Stability of soil aggregates in relation to organic constituents and soil water content. *Journal of Soil Science*, 41(1), 73–83. <https://doi.org/10.1111/j.1365-2389.1990.tb00045.x>
- Hopple, A. M., Wilson, R. M., Kolton, M., Zalman, C. A., Chanton, J. P., Kostka, J., ... & Bridgman, S. D. (2020). Massive peatland carbon banks vulnerable to rising temperatures. *Nature Communications*, 11, 2373. <https://doi.org/10.1038/s41467-020-16311-8>
- Hunt, H. W., Coleman, D. C., Ingham, E. R., Ingham, R. E., Elliott, E. T., Moore, J. C., ... & Morley, C. R. (1987). The detrital food web in a shortgrass prairie. *Biology and Fertility of Soils*, 3(1–2), 57–68. <https://doi.org/10.1007/BF00260580>
- Husson, O. (2013). Redox potential (Eh) and pH as drivers of soil/plant/microorganism systems: A transdisciplinary overview pointing to integrative opportunities for agronomy. *Plant and Soil*, 362, 389–417. <https://doi.org/10.1007/s11104-012-1429-7>
- Intergovernmental Panel on Climate Change (IPCC). (2022). *Climate Change 2022: Impacts, Adaptation and Vulnerability*. Cambridge University Press. <https://doi.org/10.1017/9781009325844>
- Jeffery, S., & Gardi, C. (2010). Soil biodiversity under threat: A review. *Acta Societatis Zoologicae Bohemicae*, 74, 7–12.
- Jeffery, S., Gardi, C., & Jones, A. (2010). *European atlas of soil biodiversity*. Publications Office of the European Union. <https://data.europa.eu/doi/10.2788/94222>
- Johnston, A. E., Poulton, P. R., & Coleman, K. (2009). Soil organic matter: Its importance in sustainable agriculture and carbon dioxide fluxes. In D. L. Sparks (Ed.), *Advances in Agronomy* (Vol. 101, pp. 1–57). Academic Press. [https://doi.org/10.1016/S0065-2113\(08\)00801-8](https://doi.org/10.1016/S0065-2113(08)00801-8)
- Jones, S. K., Estrada-Carmona, N., Juventia, S. D., Dooloo, M. E., Laporte, M. A., Villani, C., & Remans, R. (2021). Agrobiodiversity Index scores show agrobiodiversity is underutilized in national food systems. *Nature Food*, 2(10), 712–723. <https://doi.org/10.1038/s43016-021-00342-7>
- Junting, Y., Xiaosong, L., Bo, W., Junjun, W., Bin, S., Changzhen, Y., & Zhihai, G. (2021). High spatial resolution topsoil organic matter content mapping across desertified land in Northern China. *Frontiers in Environmental Science*, 9, 668912. <https://doi.org/10.3389/fenvs.2021.668912>
- Klaminder, J., Krab, E. J., Larsbo, M., Jonsson, H., Fransson, J., & Koestel, J. (2023). Holes in the tundra: Invasive earthworms alter soil structure and moisture in tundra soils. *Science of the Total Environment*, 859, 160125. <https://doi.org/10.1016/j.scitotenv.2022.160125>
- Kronzucker, H. J., Coskun, D., Schulze, L. M., Wong, J. R., & Britto, D. T. (2013). Sodium as nutrient and toxicant. *Plant and Soil*, 369, 1–23. <https://doi.org/10.1007/s11104-013-1801-2>
- Lal, R. (2004). Soil carbon sequestration to mitigate climate change. *Geoderma*, 123, 1–22. <https://doi.org/10.1016/j.geoderma.2004.01.032>
- Lancaster, S. H., Hollister, E. B., Senseman, S. A., & Gentry, T. J. (2010). Effects of repeated glyphosate applications on soil microbial community composition and the mineralization of glyphosate. *Pest Management Science*, 66(1), 59–64. <https://doi.org/10.1002/ps.1831>
- Langmaid, K. K. (1964). Some effects of earthworm invasion in virgin podzols. *Canadian Journal of Soil Science*, 44, 34–37.
- Larsen, T., Schjønning, P., & Axelsen, J. (2004). The impact of soil compaction on euedaphic Collembola. *Applied Soil Ecology*, 26, 273–281.
- Li, J., Ramirez, G. H., Kiani, M., Quideau, S., Smith, E., Janzen, H., Larney, F., & Puurveen, D. (2018). Soil organic matter dynamics in long-term temperate agroecosystems: Rotation and nutrient addition effects. *Canadian Journal of Soil Science*, 98, 232–245.
- Liang, C., Amelung, W., Lehmann, J., & Kästner, M. (2019). Quantitative assessment of microbial necromass contribution to soil organic matter. *Global Change Biology*, 25, 3578–3590.
- Lindo, Z. (2015). Warming favours small-bodied organisms through enhanced reproduction and compositional shifts in belowground systems. *Soil Biology and Biochemistry*, 91, 271–278.
- Ma, X., Ni, X., Guo, Z., Zou, X., Chen, J., Shen, W., & Kuzyakov, Y. (2023). Nitrogen addition influences fine root growth and mycorrhizal symbiosis formation in trees with contrasting root morphology. *Applied Soil Ecology*, 189, 104987.
- Markkula, I., Cornelissen, J. H. C. R., & Aerts, R. (2019). Sixteen years of simulated summer and winter warming have contrasting effects on soil mite communities in a sub-Arctic peat bog. *Polar Biology*, 42, 581–591.



- McGill, W. B., & Spence, J. R. (1985). Soil fauna and soil structure: Feedbacks between size and architecture. *Quaestiones Entomologicae*, 21, 645–654.
- Meehan, M. L., Turnbull, K. F., Sinclair, B. J., & Lindo, Z. (2022). Predators minimize energy costs, not maximize energy gains when feeding under warming: Evidence from a microcosm experiment. *Functional Ecology*, 36, 2279–2288.
- Minasny, B., Malone, B. P., McBratney, A. B., Angers, D. A., Arrouays, D., Chambers, A., Chaplot, V., Chen, Z. S., Cheng, K., Das, B. S. et al. (2017). Soil carbon 4 per mille. *Geoderma*, 292, 59–86.
- Newbold, T., Hudson, L. N., Hill, S. L. L., & Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, 520, 45–50. <https://doi.org/10.1038/nature14324>
- Newman, M. M., Hoilett, N., Lorenz, N., Dick, R. P., Liles, M. R., Ramsier, C., & Kloepper, J. W. (2016). Glyphosate effects on soil rhizosphere-associated bacterial communities. *Science of the Total Environment*, 543, 155–160. <https://doi.org/10.1016/j.scitotenv.2015.11.008>
- Nicolescu, V.-N., Rédei, K., Vor, T., Bastien, J.-C., Brus, R., Benčat, T., Đodan, M., Cvjetković, B., Andrašev, S., La Porta, N., Lavnyy, V., Petkova, K., Perić, S., Bartlett, D., Hernea, C., Pástor, M., Mataruga, M., Podrázský, V., Sfeclă, V., & Štefančík, I. (2020). A review of black walnut (*Juglans nigra* L.) ecology and management in Europe. *Trees*, 34, 1087–1112.
- Oades, J. M. (1984). Soil organic matter and structural stability: Mechanisms and implications for management. *Plant and Soil*, 76, 319–337.
- Omuto, C. T., Kome, G. K., Ramakhanna, S. J., Muzira, N. M., Ruley, J. A., Jayeoba, O. J., ... & Nyamai, M. (2024). Trend of soil salinization in Africa and implications for agro-chemical use in semi-arid croplands. *Science of the Total Environment*, 951, 175503.
- Orgiazzi, A., Bardgett, R. D., & Barrios, E. (2016a). *Global Soil Biodiversity Atlas*. European Commission.
- Orgiazzi, A., Panagos, P., Yugini, Y., Dunbar, M. B., Gardi, C., Montanarella, L., & Ballabio, C. (2016b). A knowledge-based approach to estimating the magnitude and spatial patterns of potential threats to soil biodiversity. *Science of the Total Environment*, 545–546, 11–20.
- Pahalvi, H. N., Rafiya, L., Rashid, S., Nisar, B., & Kamili, A. N. (2021). Chemical fertilizers and their impact on soil health. In Dar et al. (Eds.), *Microbiota and Biofertilizers* (Vol. 2, pp. 1–20). Springer. [https://doi.org/10.1007/978-3-030-61010-4\\_1](https://doi.org/10.1007/978-3-030-61010-4_1)
- Palacino, B., Ascaso, S., Valero, A., & Valero, A. (2024). Regeneration costs of topsoil fertility: An exergy indicator of agricultural impacts. *Journal of Environmental Management*, 369, 122297.
- Pereira, M. C., O’Riordan, R., & Stevens, C. (2021). Urban soil microbial community and microbial-related carbon storage are severely limited by sealing. *Journal of Soils and Sediments*, 21, 1455–1465.
- Philippot, L., Chenu, C., Kappler, A., Rillig, M. C., & Fierer, N. (2024). The interplay between microbial communities and soil properties. *Nature Reviews Microbiology*, 22, 226–239.
- Porre, R. J., van Groenigen, J. W., De Deyn, G. B., de Goede, R. G. M., & Lubbers, I. M. (2016). Exploring the relationship between soil mesofauna, soil structure and N<sub>2</sub>O emissions. *Soil Biology and Biochemistry*, 96, 55–64.
- Potapov, A. M., Drescher, J., Darras, K., Wenzel, A., Janotta, N., Nazaretta, R., Kasmiatun, Laurent, V., Mawan, A., Utari, E. H., et al. (2024). Rainforest transformation reallocates energy from green to brown food webs. *Nature*, 627, 116–127.
- Potapov, A. M., Klarner, B., Sandmann, D., Widayastuti, R., & Scheu, S. (2019). Linking size spectrum, energy flux and trophic multifunctionality in soil food webs of tropical land-use systems. *Journal of Animal Ecology*, 88, 1845–1859.
- Powlson, D. S., Gregory, P. J., Whalley, W. R., Quinton, J. N., Hopkins, D. W., Whitmore, A. P., Hirsch, P. R., & Goulding, K. W. T. (2011). Soil management in relation to sustainable agriculture and ecosystem services. *Food Policy*, 36, S72–S87.
- Qiu, L., Zhang, Q., Zhu, H., Reich, P. B., Banerjee, S., van der Heidjen, M. G. A., Sadowsky, M. J., Ishii, S., Jia, X., Shao, M., Liu, B., Jiao, H., Li, H., & Wei, X. (2021). Erosion reduces soil microbial diversity, network complexity and multifunctionality. *ISME*, 15, 2474–2489.
- Reinhart, K. O., & Callaway, R. M. (2006). Soil biota and invasive plants. *New Phytologist*, 170, 445–457. <https://doi.org/10.1111/j.1469-8137.2006.01715.x>
- Rezapour, S., Nouri, A., Asadzadeh, F., Barin, M., Erpul, G., Jagadamma, S., & Qin, R. (2023). Combining chemical and organic treatments enhances remediation performance and soil health in saline-sodic soils. *Communications Earth & Environment*, 4, 285. <https://doi.org/10.1038/s43247-023-00948-6>
- Rillig, M. C., Masahiro, R., Lehmann, A., Aguilar-Trigueros, C. A., Buchert, S., Wulf, A., Iwasaki, A., Roy, J., & Yang, G. (2019). The role of multiple global change factors in driving soil functions and microbial biodiversity. *Science*, 366, 886–890. <https://doi.org/10.1126/science.aay2832>
- Rinke, A., Kuhry, P., & Dethloff, K. (2008). Importance of a soil organic layer for Arctic climate: A sensitivity study with an Arctic RCM. *Geophysical Research Letters*, 35, L13709.
- Rousk, J., Smith, A. R., & Jones, D. L. (2013). Investigating the long-term legacy of drought and warming on the soil microbial community across five European shrubland ecosystems. *Global Change Biology*, 19, 3872–3884.
- Scalenghe, R., & Marsan, F. A. (2009). The anthropogenic sealing of soils in urban areas. *Landscape and Urban Planning*, 90, 1–10.
- Semple, K. T., Morriss, A. W. J., & Paton, G. I. (2003). Bioavailability of hydrophobic organic contaminants in soils: Fundamental concepts and techniques for analysis. *European Journal of Soil Science*, 54, 809–818. <https://doi.org/10.1046/j.1351-0754.2003.0564.x>

- Six, J., Bossuyt, H., Degryze, S., & Denef, K. (2004). A history of research on the link between (micro)aggregates, soil biota, and soil organic matter dynamics. *Soil and Tillage Research*, 79, 7–31.
- Soana, E., Vincenzi, F., Colombani, N., Mastrocicco, M., Fano, E. A., & Castaldelli, G. (2022). Soil denitrification, the missing piece in the puzzle of nitrogen budget in lowland agricultural basins. *Ecosystems*, 25, 633–647.
- Solly, E. F., Weber, V., Zimmermann, S., Walther, L., Hagedorn, F., & Schmidt, M. W. I. (2020). A critical evaluation of the relationship between the effective cation exchange capacity and soil organic carbon content in Swiss Forest soils. *Frontiers in Forests and Global Change*, 3, 98. <https://doi.org/10.3389/ffgc.2020.00098>
- Sperow, M. (2020). What might it cost to increase soil organic carbon using no-till on U.S. cropland? *Carbon Balance and Management*, 15, 26. <https://doi.org/10.1186/s13021-020-00162-3>
- Standen, K. M., & Baltzer, J. L. (2021). Permafrost condition determines plant community composition and community-level foliar functional traits in a boreal peatland. *Ecology and Evolution*, 11, 10133–10146. <https://doi.org/10.1002/ece3.7818>
- Stevenson, F. J. (1982). *Humus chemistry*. Wiley.
- Tibbett, M., Gil-Martínez, M., Fraser, T., Green, I. D., Duddigan, S., de Oliveira, V. H., Raulund-Rasmussen, K., Sizmur, T. A., & Díaz, A. (2019). Long-term acidification of pH neutral grasslands affects soil biodiversity, fertility and function in a heathland restoration. *Catena*, 180, 401–415.
- Tibbett, M., Fraser, T. D., & Duddigan, S. (2020). Identifying potential threats to soil biodiversity. *PeerJ*, 8, e9271. <https://doi.org/10.7717/peerj.9271>
- Turnbull, M. S., & Lindo, Z. (2015). Combined effects of abiotic factors on Collembola communities reveal precipitation may act as a disturbance. *Soil Biology and Biochemistry*, 82, 36–43.
- van der Putten, W., Klironomos, J., & Wardle, D. (2007). Microbial ecology of biological invasions. *ISME Journal*, 1, 28–37. <https://doi.org/10.1038/ismej.2007.9>
- Wagg, C., Bender, S. F., Widmer, F., & Van Der Heijden, M. G. (2014). Soil biodiversity and soil community composition determine ecosystem multifunctionality. *Proceedings of the National Academy of Sciences*, 111(14), 5266–5270.
- Wall, D. H., Bardgett, R. D., Behan-Pelletier, V., Herrick, J. E., Jones, T. H., Six, J., ... & Ritz, K. (Eds.). (2012). *Soil ecology and ecosystem services*. OUP Oxford.
- Wan, B., Liu, T., Gong, X., Zhang, Y., Li, C., Chen, X., Hu, F., Griffiths, B. S., & Liu, M. (2022). Energy fluxes across multitrophic levels drive ecosystem multifunctionality: Evidence from nematode food webs. *Soil Biology and Biochemistry*, 169, 108656.
- Wang, B., An, S., Liang, C., Liu, Y., & Kuzyakov, Y. (2021). Microbial necromass as the source of soil organic carbon in global ecosystems. *Soil Biology and Biochemistry*, 162, 108422.
- Wei, Z., Wu, S., Zhou, S., & Lin, C. (2013). Installation of impervious surface in urban areas affects microbial biomass, activity (potential C mineralisation), and functional diversity of the fine earth. *Soil Research*, 51(1), 59–67.
- Wu, H., Cui, H., Fu, C., Li, R., Qi, F., Liu, Z., Yang, G., Xiao, K., & Qiao, M. (2024). Unveiling the crucial role of soil microorganisms in carbon cycling: A review. *Science of the Total Environment*, 909, 168627.
- Zhang, L., Zhao, Z., Jiang, B., Baoyin, B., Cui, Z., Wang, H., Li, Q., & Cui, J. (2024). Effects of long-term application of nitrogen fertilizer on soil acidification and biological properties in China: A meta-analysis. *Microorganisms*, 12(7), 1683.
- Zhang, H., Wang, L., Fu, W., Xu, C., Zhang, H., Xu, X., Ma, H., Wang, J., & Zhang, Y. (2024). Soil acidification can be improved under different long-term fertilization regimes in a sweetpotato–wheat rotation system. *Plants*, 13(13), 1740.
- Zhang, Z., Qiao, M., Li, D., Yin, H., & Liu, Q. (2016). Do warming-induced changes in quantity and stoichiometry of root exudation promote soil N transformations via stimulation of soil nitrifiers, denitrifiers and ammonifiers? *European Journal of Soil Biology*, 74, 60–68.
- Zheng, J., Guo, R., Li, D., Zhang, J., & Han, S. (2017). Nitrogen addition, drought and mixture effects on litter decomposition and nitrogen immobilization in a temperate forest. *Plant and Soil*, 416, 165–179.

