



Responses of soil fauna community under changing environmental conditions

KUDURETI Ayijiamali^{1,2}, ZHAO Shuai^{1*}, Dina ZHAKYP³, TIAN Changyan^{1*}

¹ State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, China;

² University of Chinese Academy of Sciences, Beijing 100049, China;

³ Saken Seifullin Kazakh Agrotechnical University, Astana 010000, Kazakhstan

Abstract: Soil faunas account for 23% of known animal species and play a crucial role in ecosystem processes such as mineralizing nutrients, regulating microbial community composition, forming soil aggregates, and enhancing primary productivity. However, due to global climate change, population density, community composition, and distribution patterns of soil fauna vary. Understanding the responses of soil fauna to major environmental change facilitate the conservation of biodiversity. Therefore, a review work of recent researches for analysing the effects of key environmental factors on soil fauna, such as warming, drought, food quality, and soil physical-chemical properties was studied. For most species, warming may exert a positive effect on their abundance and population development, however, it can inhibit the survival and reproduction of hibernating species. Drought leads to low soil porosity and water holding capacity, which reduces soil fauna population and changes their community composition. Drought also can reduce the coverage of flora and alter microclimate of the soil surface, which in turn indirectly reduces fauna abundance. Climate warming and elevated atmospheric carbon dioxide can reduce litter quality, which will force soil fauna to change their dietary choices (from higher-quality foods to poor quality foods) and reduce reproduction for survival. However, it is still predicted that enhanced species richness of plant (or litter) mixtures will positively affect soil fauna diversity. Habitat loss caused by the deterioration of soil physical-chemical property is primary factor affecting soil fauna. We mainly discuss the threats of increased salinity (a major factor in arid land) to soil fauna and their potential responses to anthropogenic disturbance in saline soils. The increase in soil salinity can override other factors that favour habitat specialists, leading to negative effects on soil fauna. Moreover, we find that more studies are needed to explore the responses of soil fauna in saline soils to human activities. And the relationship of important ecological processes with soil fauna density, community structure, and diversity needs to be redefined.

Keywords: biodiversity; habitat; soil fauna; species distribution; stress factors

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1 Introduction

Soil biodiversity lies in the foundational core of the international agendas, for example, Global Soil Biodiversity Initiative (GSBI) and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), and in the United Nations Sustainable Development Goals (Briones, 2018). Soil faunas account for approximately one-fourth of the biodiversity on Earth and approximately three-fourths of all multicellular organisms (Coleman et

*Corresponding authors: TIAN Changyan (E-mail: tianchy@ms.xjb.ac.cn); ZHAO Shuai (E-mail: zhaoshuai@ms.xjb.ac.cn)

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al., 1996; Hoogen et al., 2019; Josef and Jose, 2021). Yet, belowground organisms have received little attention compared with aboveground organisms (Decaëns et al., 2006; Fig. 1). Soil fauna can be found in almost every terrestrial environment on Earth, including deserts, tundra, saline soils, and Antarctica (Fierer et al., 2009). Distribution patterns of soil fauna are influenced by climatic conditions, vegetation cover, and soil texture, but microbial communities are more influenced by local factors such as land use and soil type rather than by geomorphology and climate (Ranjard et al., 2010; Lavelle et al., 2022). Generally, researchers separate soil fauna into three classes based on body width (Fig. 2). Microfaunas (protozoa, nematodes, rotifers, and tardigrades) range from 2 to 100 μm in body width and inhabit soil water films. Mesofaunas range

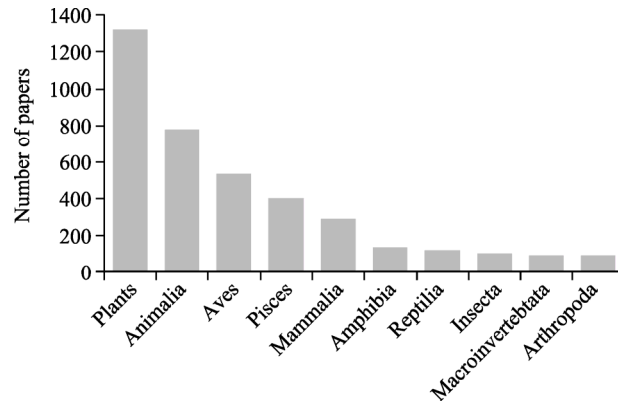


Fig. 1 Number of papers published in Web of Science on biodiversity conservation in 2021

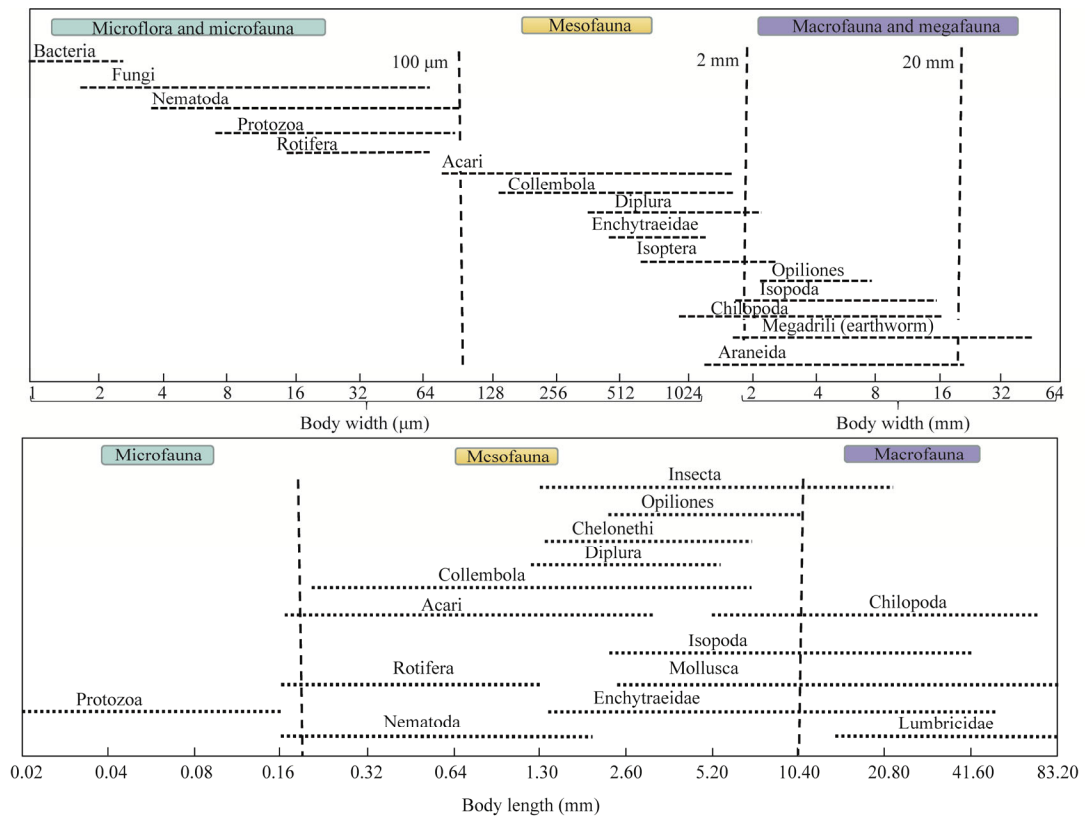


Fig. 2 Classification of soil fauna by body width and body length. On the basis of body width: microfauna (2–100 μm), mesofauna (100 μm –2 mm), and macrofauna (2–20 mm). On the basis of body length: microfauna (0.02–0.20 mm), mesofauna (0.20–10.00 mm), and macrofauna (10.00–80.00 mm).

from 100 μm to 2 mm in width and include Acari, Collembola, Diplura, and Enchytraeidae. They live in air-filled pore spaces in the soil. Macrofaunas are >2 mm wide and include earthworms and soil-dwelling vertebrates. They are able to create their own microhabitats due to their life strategy (e.g., earthworm bioturbation) (Swift et al., 1979; Lavelle and Spain, 2001).

Soil faunas play a vital role in shaping ecosystem functions, especially biogeochemical and nutrient cycling (Frouz, 2018; Joly et al., 2018, 2020). They can modulate soil nutrients by inducing the chemical binding of carbon (C) and phosphorous (P), thereby promoting the movement of organic and mineral particles (Bohlen et al., 2004; Aubert et al., 2010; Briones, 2018; Fanin et al., 2019). For example, the nitrogen (N) released from earthworm mucous, excreta, and biomass turnover is higher than that of annual litter falls in deciduous forests (Petersen and Luxton, 1982). Earthworms can also increase plant-soil N cycling by mineralizing and translocating organic matter (Blume-Werry et al., 2020). Earthworms, ants, and termites—that are referred to as ecosystem engineers—alter soil physical structure by decreasing its bulk density and increasing porosity. Such processes result in increased water infiltration, with a concomitant increase in the availability of N and other nutrients (Gong et al., 2019; Hallam and Hodson, 2020). Microarthropods and millipedes promote litter decomposition and stimulate the mobilization of various nutrients (David, 2014; Kitz et al., 2015; Garcia-Palacios, 2016; Lubbers et al., 2020). In temperate and wet tropical climates, soil faunas increased litter decomposition (Wall et al., 2008). Also, soil faunas accelerated litter mixture decomposition in dry environments (Denis et al., 2021). A global meta-analysis reported that the contribution of soil fauna to increased litter decomposition can be up to 27% (Garcia-Palacios et al., 2013). The activities of the soil fauna also affect plant productivity (Bardgett et al., 2014), e.g., the presence of protozoa stimulates N uptake by spruce seedlings (Jentschke et al., 1995) and wheat growth (Kuikman et al., 2003). Surprisingly, some studies have shown that soil fauna impact microbes and thus contribute to ecosystem functions (Nieminen, 2008; Li et al., 2021; Zahorec et al., 2021). Under nutrient-limited conditions, soil faunas do not use all immobilized nutrients to increase their biomass but supply microorganisms or plants via excretion (Ingham et al., 1985). The soil food web in deserts is composed of multiple consumers (Whitford, 1999); nematodes as consumers can influence decomposition rates by regulating activity of bacterial prey in deserts (Santos et al., 1978). Nematodes, protozoa, and their microbial food resources constitute the soil microbial food web, which influences nutrient cycling and trophic dynamics (Lavelle et al., 1997; Wardle, 2002; Yang et al., 2021). Therefore, soil fauna is crucial to maintain multiple functions of the ecosystem (Jing et al., 2015).

Soil fauna density, community structure, and diversity are susceptible to various environmental conditions (Kardol et al., 2011; Zhou et al., 2020; Yang et al., 2021). On a global scale, precipitation and temperature are the most important driving factors that affect earthworm biomass and abundance, respectively (Hoogen et al., 2019; Phillips, 2019). On regional and local scales, soil fauna diversity is affected by non-climate-related drivers, such as soil organic matter, pH, and moisture (Curry et al., 2004; Rutgers et al., 2016). For example, N-rich soils contain a greater number of bacterial-feeding nematodes (Lagerlof et al., 2002). Nematode community structure and diversity are sensitive to small fluctuations in temperature and moisture (Bakonyi et al., 2007). Pesticides are one hazard to invertebrates (Gunstone et al., 2021), and earthworms do not thrive in mining regions because of extreme soil pH, high metal content, low soil moisture, and lack of suitable food (Ronan et al., 2020). Natural events (e.g., flooding or fires) can also affect soil properties and determine the composition of soil fauna (David and Gillon, 2009; Schelfhout et al., 2017), e.g., flooding causes sharp decreases in earthworm biomass and abundance by altering soil properties (Kiss, 2019). Some newly emerging concepts, such as "biological accessibility" and "trophic cascades", are used to explain the observed faunal responses to environmental changes (Briones, 2018). All these phenomena currently affect soil fauna and are predicted to have an increasing impact in the context of global environmental changes (David and Handa, 2010; IPCC, 2014).

This review outlines recent progress in research on the responses of soil fauna to major

environmental change factors, including climate (warming and drought) and non-climate (food quality and soil physical-chemical property) factors (Fig. 3). Considering that the simultaneous occurrence of high temperature and dry climate increases soil salinity and has combined effects on soil fauna and ecosystem functioning, e.g., by modifying the quality of natural resources available to consumers (FAO, 2021), we emphasize the impact of concurrent factors on soil salinity in the soil fauna community. We then provide a holistic overview of the current knowledge regarding human activities that affect fauna in saline soils.

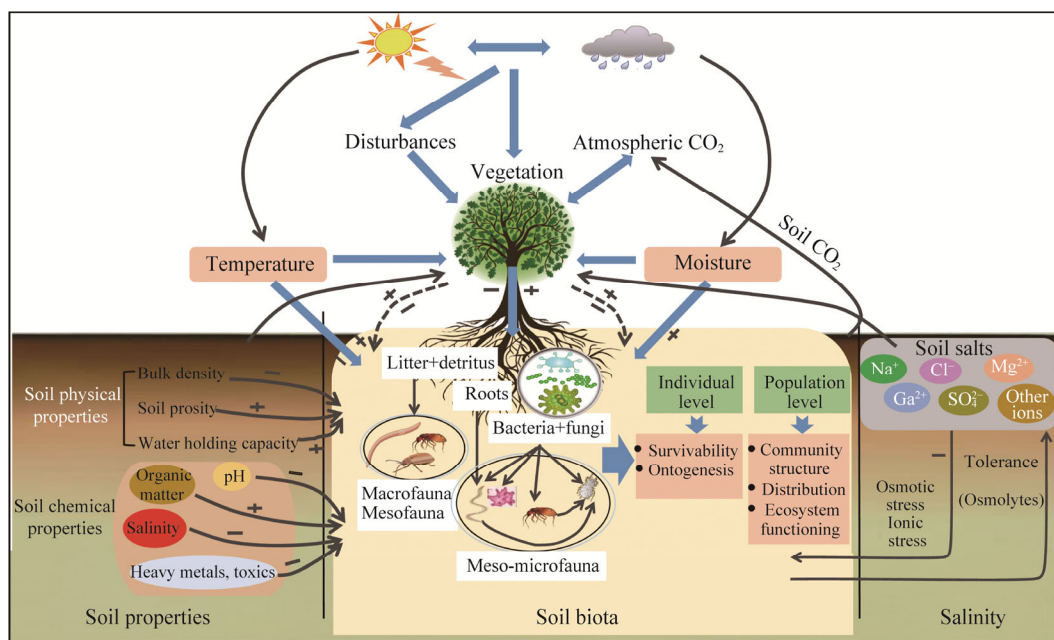


Fig. 3 Impact of key ecological factors on soil fauna and interactions of soil fauna with plants, organisms, and soil properties. Each arrow represents interaction. The solid arrows depict direct interactions, whereas the dashed arrows depict indirect effects. Plus (+) represents positive effects, and minus (–) was negative.

2 Effects of changing environmental factors on soil fauna community

2.1 Warming

Temperature affects the rate of biochemical processes in organisms. Living with higher average temperatures, species in the Southern Hemisphere have more specific adaptations to these temperature changes than those in the Northern Hemisphere (Dunn et al., 2009). Warming may have positive effects on the density and diversity of soil fauna (Table 1). For instance, warming can directly increase nematode density by promoting growth and reproduction or enhancing food supply by indirectly increasing litter input and microbial activities (Kardol et al., 2010; Mueller et al., 2016; Guo et al., 2021). A temperature increase of 3.3°C has a significant and positive effect on the polydesmid millipede, causing it to reproduce earlier in spring (David and Handa, 2010). Such positive effects of warming on population growth are common among detritus-consuming arthropods (Sinclair and Stevens, 2006), as plant cover changes associated with warming are likely to lead to changes in soil fauna communities (Thakur et al., 2014).

Yet, warming is not necessarily advantageous to population growth, particularly for macro-arthropods (Table 1; Castaneda and Aballay, 2016). For example, warming and increased carbon dioxide levels can reduce the availability of high-quality food, which negatively affects the diversity of millipedes (David and Gillon, 2009). Additionally, warming may increase the number of warm-adapted species and decrease cold-adapted species (Blankinship et al., 2011).

Table 1 Effect of warming on soil fauna community

Soil fauna community	Warming treatment		Influence	Reference
	Timing	Amount of warming		
Nematode	7 a	1.5 °C during the day; 3.0 °C during the night	Changed the community structure of nematodes. Increased the abundance of bacteria feeders and fungivores. Decreased the abundance of herbivores, predators, and omnivores.	Mueller et al. (2016)
<i>Polydesmus angustus</i>	300 d	3.3 °C	Positive effects on abundance and higher population growth rates.	David and Handa (2010)
Microarthropods	2 a	4.0 °C	The richness and diversity of microarthropods increased.	Meehan et al. (2020)
Millipedes	Four seasons	3.3 °C	The diversity and growth of millipedes decreased.	David and Gillon (2009)
Microarthropods	Extreme winter warming	(0.6–3.2) °C (soil); 3.5 °C (soil surface)	Acari populations decreased by 39%; Collembola shifted from smaller soil-dwelling (euedaphic) species to larger litter-dwelling (hemiedaphic) species.	Bokhorst et al. (2012)
Spirostreptid millipede (<i>Orthoporus ornatus</i>)	Desert warming for a season	Slight warming	High temperatures depleted the fat reserves of hibernating species, negatively affecting their growth in the following season.	Crawford et al. (1987)
Microarthropods	2 a	1.3 °C	Warming had insignificant effects on the abundance of mites and Collembola.	Wu et al. (2011)
Soil fauna community	Experimental stage	(1.0–2.0) °C	Warming did not affect the density and diversity of soil fauna community.	Peng et al. (2022)

Arctic warming may lead to an increase in soil fauna diversity, but extreme winter warming decreases Acari population sizes and shifts Collembola communities from euedaphic, soil-dwelling species to larger, hemi-edaphic, and litter-dwelling species (Bokhorst et al., 2012). Evidence suggests that the impact of warming on soil fauna depends on precipitation (Lindberg et al., 2002; Blankinship et al., 2011; Landesman et al., 2011; Kardol et al., 2011; Meehan et al., 2020). A recent study showed that soil faunal diversity is resistant to global warming, whereas soil faunal density is mainly affected by rainfall (Peng et al., 2022). In arid soils, the abundance of Collembola and mites is affected by drought but not by climate warming (Wu et al., 2011). Because global warming stimulates temperature-associated drought in many areas (Yue et al., 2019), drought has become a strong force to be reckoned by soil fauna.

2.2 Drought

Under drought conditions, it is difficult for animals to move because of the increased compactness of the soil and decreased soil water film (Coleman et al., 2004). Changes in event size and frequency of precipitation influences invertebrate activity and density in dryland ecosystems (Nielsen and Ball, 2015). The effects of drought on soil fauna tend to be negative (Table 2). Many groups, including Collembola, nematodes, enchytraeids, and earthworms, are highly sensitive to soil moisture (Holmstrup et al., 2001; Wang et al., 2020). Drought has less effect on soil fauna diversity, but it can decrease soil fauna density by 27.4% (Peng et al., 2022). The reproduction and survival rates of the potworm (*Enchytraeus crypticus*), and white worm (*Enchytraeus albidus*), decline by >23% under drought conditions, particularly after prolonged exposure to drought (Maraldo et al., 2009). However, some species, such as the oribatid mite *Licnodamaeus pulcherrimus* and *Pseudosinella alba*, adapt well to drought (Guidi et al., 2002). The range and abundance of Argentine ants (*Iridomyrmex humilis*) decrease in dry soil, whereas the population density of fungus-gardening ants (drought-resistant species) increases during periods of drought (Seal and Tschinkel, 2010). Almost all functional groups of nematodes are sensitive to drought, but Qudsianematidae species do not appear to be significantly affected (Williams and Jackson,

2007). Holmstrup et al. (2007, 2017) found that springtails could recover from recurring drought events. This is because springtails have survival strategies that include moving to moist microsites, assuming an anhydrobiotic state, and resisting drought by reducing the permeability of their integument (Greenslade, 1981; Liu et al., 2021).

Drought also indirectly affects soil fauna community (Franklin et al., 2016), e.g., causing a shift in species distribution. Drying conditions in southwestern Australia have caused moisture-favouring millipedes (e.g., Sphaerotheriida and Polyzoniida) to be outcompeted by drought-tolerant species (e.g., *Antichiropus* sp.), thus creating new species boundaries (Moir et al., 2009). Drought is also correlated with food availability and thus influences soil fauna. Low water availability reduces the activity of microorganisms and leads to a decrease in faunal populations (Peguero et al., 2021). The abundance of collembolans and oribatid mites decreased by 80.6% and 77.8%, respectively, at a drought area because only 40% of the litterfall occurred during the drought treatment (Lindberg et al., 2002).

Table 2 Effect of drought on soil fauna community

Soil fauna	Drought treatment	Influence	Reference
<i>Enchytraeus crypticus</i> and <i>Enchytraeus albidus</i>	4 d exposed to a decreasing relative humidity from 99.8% to 98.4% 99.8% relative humidity (−2.7 Pa) 98.4% relative humidity (−22.1 Pa)	Reproduction and survival of <i>Enchytraeus crypticus</i> and <i>Enchytraeus albidus</i> declined >23% under drought conditions.	Maraldo et al. (2009)
Soil dwelling springtail	28 d exposed to a water potential from 0 to −85 kPa (with an accuracy of ±20 kPa)	Reproduction stopped at soil water potentials (−15 kPa), which did not influence body water content or growth. Body growth and activities continued until −100 kPa.	Wang et al. (2020)
Earthworm (<i>Aporrectodea Caliginosa</i>)	Drought exposure 14 d between −2 and −300 kPa	Cocoon production was arrested when water potential was lower than −12 kPa and below −40 kPa. Under severe drought levels (−330 kPa), cocoon production was significantly impaired 2 months after drought exposure.	Holmstrup et al. (2001)
Soil fauna community	Extracted drought data from the WorldClim database	Soil fauna density was reduced by 27.4% under the drought condition.	Peng et al. (2022)
Soil fauna community	Preventing 70% of the throughfall on the plots from reaching the ground from April to September	The Oribatida abundance decreased by 77.8% in the drought treatment. Collembola abundance was reduced by 80.6%. Enchytraeids, mesostigmatid mites, and macroarthropod predator density decreased.	Lindberg et al. (2002)
Soil fauna community	Dry control: 15% (±1%) water content from May to July	Acari and Collembola community composition shifted, with a higher presence of drought-sensitive species in irrigated soils.	Guidi et al. (2002)
Fungus-gardening ant	Dry treatment for 3 a, April to June every year	Fungus-gardening ants (drought-resistant species) increased in abundance during multiyear droughts.	Seal and Tschinkel (2010)

2.3 Food quality

Feeding habit is critical to the health of individuals and populations, as well as basic driver of food web structure (Ho et al., 2019). Macro-arthropods have a diverse diet (Steinwandter and Seeber, 2020) and prefer litter mixtures to single litters (De Oliveira et al., 2010). Microarthropods are omnivorous and feed on decaying plants, nematodes, bacteria, fungi, algae, and other collembolans (Eisenbeis and Wichard, 1987). As an important food resource for collembolans, the fungal growth rate and morphology have been found to change in response to predation (*Folsomia candida*) (Wood et al., 2006). The composition and function of soil microorganisms may also affect the growth and propagation of Collembola, resulting in abundance changes that affect grazing intensity (Tordoff et al., 2008). However, the feeding preference of Collembola is more affected by litter type than by fungi, whereas their reproduction is affected by both fungal species and litter type (Heděc et al., 2013).

Researchers divided nematodes into five trophic groups according to their feeding habits: bacteria feeders, fungivores, predators (feeding on other nematodes), omnivores (feeding on

protozoa, bacteria, algae, fungi, and plant roots), and herbivores (feeding on plant roots) (Yang et al., 2020). Nematodes choose food and adjust their diet to maintain a balance between reproduction and survival (Laskowski et al., 2020). For example, *Caenorhabditis elegans* produced more offspring after consuming its preferred bacterial species, but reduced brood size when the preferred food was limited (Mukhopadhyay and Tissenbaum, 2007; Yu et al., 2015). *Acrobeloides* sp. feeding on their preferred soil-dwelling bacterial species had the largest brood size and a moderate survival time. By comparison, *Acrobeloides* sp. produced the smallest brood size and had the shortest survival time when they consumed their least-preferred bacterial species (Liu et al., 2017). Plants, soil properties, and climate influence soil microbiomes (Fierer et al., 2009; Joly et al., 2018, 2020; Fanin et al., 2019), and thus can indirectly affect bacterivores and fungivores. A study found ash only formed arbuscular mycorrhiza but lacked ectomycorrhizal fungi, which benefited bacterial-feeding nematodes, but suppressed fungal feeders. By contrast, beech beneficially affected fungal feeders by increasing fungi (Cesarz et al., 2013). However, if nematodes are exposed to a stressful environment (parasites, predators, and toxins), they can switch their dietary choices from higher-quality foods to poor-quality foods (Zhang et al., 2005). Amoebae and phagocytic protists can feed on fungi, bacteria, and nematodes, whereas some probiotic protists primarily feed on decomposing plant material (Geisen et al., 2016).

Plant diversity and composition may have a significant correlation with soil fauna (Frouz, 2018; Peng et al., 2020). High litter quality with high N, low phenolics, low lignin, and structural carbohydrates support bacterial-based energy channels (fast nutrient turnover), which may affect bacterial-feeding animals (e.g., dipteran larvae); in contrast, low-quality litter may affect fungal feeding animals (e.g., Collembola and mites), while maintaining a high density of enchytraeid worms and macro-microarthropods (Wardle et al., 2004). Increased aboveground productivity may support a greater abundance of soil fauna owing to higher root biomass (Ma and Chen, 2016), litter content (Saetre and Baath, 2000; Zheng et al., 2019), and microbial community diversity (Bardgett et al., 1999; Chen et al., 2019). However, few secondary compounds in some litter types can be detrimental to microbial decomposers and detritivorous consumers (Gessner et al., 2010).

Experimental plots with rich plant diversity were also found to maintain greater soil fauna abundance and diversity than that with plant monocultures (David and Handa, 2010). Multiple resources in litter mixtures can increase microhabitat complexity and food diversity (Gessner et al., 2010), which significantly supports higher soil faunal diversity (Wardle, 2006). Climate warming and elevated atmospheric carbon dioxide can alter the composition of plant communities and thus reduce litter quality; however, negative impacts on macroarthropod diversity are unlikely to counteract the positive effects of warming on population growth rates (David and Handa, 2010). Therefore, it is predicted that the diversity of soil fauna increases with the species richness of plant (or litter) mixtures. Nutrients are scarce and/or supply is discontinuous in extreme environments (i.e., cold and arid ecosystems), thus resulting in low soil biodiversity and shortage of food chains. Any nutritional surplus leads to a "hot moment" under these conditions (Kuzakov and Blagodatskaya, 2015). Extreme events (e.g., extreme hot, cold, or precipitation) occurring frequently could affect food quality, and thereby will "cascade" along the soil food web bringing other pressures (e.g., predation and competition), which will influence soil fauna.

2.4 Habitat

Soil nutrient availability is often positively correlated with soil fauna community abundance and diversity (Zhang et al., 2014; Zhang et al., 2017). An increase in soil organic matter content provides more food resources for soil fauna which, in turn, increases their abundance and diversity (Yin et al., 2018). Group numbers and abundance of soil fauna increase with increasing soil water content, whereas higher soil temperatures result in lower soil fauna diversity (Coulibaly et al., 2022). Soil pH also affects soil fauna community. For example, pH is negatively correlated with soil fauna density in weakly alkaline soils (pH ranging from 7.52 to 8.96), whereas it is positively correlated with soil fauna density in acidic soils (pH ranging from 5.21 to 5.72) (Liu et al., 2021). A study showed that pH can affect soil food web composition, indirectly affecting nematode

community structure (Matute et al., 2013; Yang et al., 2022). Low pH and high soil inorganic N may lead to soil fauna diversity having a negative correlation with aboveground biodiversity (Wu et al., 2011). However, the mechanism by which pH directly affects soil organism remains unclear.

The primary factor affecting the extinction of soil fauna is habitat loss caused by the deterioration of soil physical-chemical property (Veresoglou et al., 2015). For example, urbanization fragments the soil surface, leading to the elimination of autotrophic organisms and a subsequent reduction in macrofaunal biomass (Pavao-Zuckerman and Coleman, 2007). Soil tillage can negatively affect soil fauna by destroying soil aggregates (Rillig and Mummey, 2006). Increases in atmospheric carbon dioxide concentrations indirectly lead to decreases in soil aggregation and pore size, which may cause the elimination of some soil fauna species (e.g., Collembola) living in pore spaces (Niklaus et al., 2003). Soil contamination alters the predator/prey ratio in the soil (Edwards, 2002). For example, the survival of enchytraeids and earthworms declines in the soil containing petroleum, and the abundance of isopods in contaminated areas is higher than that in uncontaminated areas (Faulkner and Lochmiller, 2000). Habitat loss caused by chemical stressors (e.g., soil pollution) can lead to the loss of the most sensitive species and promote the tolerance of invasive or opportunistic species (Syrek et al., 2006; Piola and Johnston, 2008; Beaumelle et al., 2021).

Soil salinity significantly affects the distribution of soil organisms (Placella et al., 2012). Saline soils ($>800 \times 10^6$ hm²) represent 6% of the world's total land area (FAO, 2008) and harbor a large number of soil animals (Andronov et al., 2012). Yin et al. (2018) reported that Prostigmata, Oribatida, Gamasina, Collembola, Entomobryidae, and Isotomidae are the dominant groups in the salinized soils of Songnen Grasslands, China. By comparison, enchytraeids and the majority of arthropods, except for collembolans, are more abundant in the salinization sites in Northwest England (Kevin and Butt Maria, 2017). Increases in salinity affect the distribution of soil animals. Therefore, the following section of this paper focuses on the relationship between salinity and soil fauna, and discusses the responses of soil fauna to increasing salinity.

2.4.1 Responses of soil fauna to soil salinity

Soil salinity is a hazardous factor for soil fauna (Table 3). High salinity poses a direct physiological challenge to soil fauna, primarily via osmotic and ionic stress (Price et al., 2004). Ionic stress causes the death in protozoa by cytoplasmic membrane rupture and cell death (Li et al., 2017). Nematodes cannot survive in high-saline soils at 4100 μ S/cm (Nkem et al., 2006). Salinity causes a sharp decline in soil nematode abundance (on average 1/100 mL of soil) compared with non-salinized areas (on average 25/100 mL of soil) (De et al., 2020). Earthworms can grow only at salinity levels ≤ 5436 mg/kg NaCl and breed only when salinity is below 4985 mg/kg NaCl (Owojori et al., 2008). Soil salinity increases Pb (lead) toxicity and significantly decreases earthworm activity (Raiesi et al., 2020). In addition, salinity decreases the litter decomposition rate (Roache et al., 2006; Zhai et al., 2020), which indirectly affects the number of soil fauna detritivores that rely on decomposing plant litter as a food resource (De et al., 2021; Venâncio et al., 2021). Salinity stress is also associated with drought and warming, for example, high salt concentration is expected in soils as a result of sea level rise and warming (Bindoff et al., 2019), which leads to the decline in hydraulic conductivity, water infiltration, organic matter solubility, and soil porosity (Wong et al., 2010; Amini et al., 2016). Such environment deterioration can aggravate the detrimental effects of salinity on organisms (Wang et al., 2001; Kristin and Johannes, 2015).

The basic behavioural response of soil fauna to detrimental increases in soil salt is to move. To avoid high-salinity environments, the collembolan *Cryptopygus antarcticus* migrates to more suitable microhabitats (Elnitsky et al., 2008). Earthworms have clear avoidance responses to higher soil salinity (Owojori et al., 2009; Owojori et al., 2014). In avoidance tests, *Aporrectodea caliginosa* was a sensitive species, regardless of the soil properties or ionic composition. Physiological adaptations, such as a continuous exoskeleton, can reduce contact between an organism and soil salt (O'Connor, 2003; Pereira et al., 2015). Due to their impermeable membranes, *Heterochaeta costata* and *Enchytraeus albidus* (annelids) can survive in saline soils

Table 3 Effects of salinity on the soil fauna community

Soil fauna	Salinity treatment	Influence	Response	Reference
Protozoa	NaHCO ₃ , NaCl, KHCO ₃ , and KCl at 160 mM	Ionic stress led to cell death of protozoa. NaHCO ₃ was shown to be the most effective inhibitor.	Although protozoa do not contain a rigid cell wall, they can develop osmoregulatory mechanisms to minimize the damage caused by hyper-osmotic conditions.	Li et al. (2017)
Nematode <i>Scottinema lindsayae</i> and <i>Plectus antarcticus</i>	NaCl, MgSO ₄ , KNO ₃ and NaCl+MgSO ₄ , concentrations ranging from 0.1–3.0 M	Salinity reduced the survival of both nematode species.	Species have different salt tolerance. <i>S. lindsayae</i> survived in <0.2 M NaCl and <0.5 M MgSO ₄ . They did not survive in any concentration of NaCl+MgSO ₄ . <i>P. antarcticus</i> survived in <0.5 M NaCl, <0.5 M MgSO ₄ , and <0.2 M (NaCl+MgSO ₄).	Nkem et al. (2006)
Earthworm	NaCl concentrations: 0, 1000, 2000, 4000, 6000, and 8000 mg/kg	The survival, growth, and cocoon production were limited above the concentrations of 5436, 4985, and 2020 mg/kg NaCl.	Behavioural strategy: earthworms escaped a high salinity environment. The avoidance of <i>A. caliginosa</i> of 667 mg/kg NaCl. The avoidance of <i>E. feida</i> of 1164 mg/kg NaCl.	Owojori et al. (2009); Owojori et al. (2008)
Spider (<i>Arctosa fulvolineata</i>)	Three concentrations of substrate salinity (0‰, 35‰, and 70‰)	Survival and egg-laying were significantly impaired when exposed to hypersaline conditions for 12 d.	Morphological adaptations: having a continuous exoskeleton reduced body contact with salt. Physiological adaptation: accumulation of osmo-induced amino acids increased the osmolality of body fluids, enhancing the survival ability of spiders.	O'Connor (2003); Foucreau et al. (2012)
Nematode	Salinized Caatinga EC: 65.6, 106.2 dS/m; Natural Caatinga EC: 0.98, 1.30 dS/m	Salinity caused a sharp decline in nematode abundance.	Nematodes employed anhydrobiosis (reduced metabolic activity) to survive in dry and salty conditions.	Zhi et al. (2008)
Soil fauna community	Salinization habitat: 0.19%, 0.26%, 0.47%, 0.68%, and 1.12%.	High salinity decreased the number of taxa. Community composition changed significantly.	Different soil fauna taxa exhibited various tolerance to salinity.	Yin et al. (2018)
Decomposer fauna	Water salinity treatment: 10.0%, 5.0%, 3.0%, 1.0%, and 0.4%	High salinity (>5%) decreased the litter decomposition rate. Modest salinity increased the litter decomposition rate	Plots with 3% salinity showed higher decomposition rates than plots with 1.0% salinity and 0.4% salinity.	Zhai et al. (2020)

Note: EC, electrical conductivity.

(Generlich and Giere, 1996). Osmoregulatory organs, such as coxal glands and sclerotized rings in the cuticle, have been reported in mites (Bayartogtokh and Chatterjee, 2010).

Some species adjust their metabolic states to cope with environmental stressors. For example, nematodes employ anhydrobiosis (reduced metabolic activity) to survive in the dry and saline Negev Desert (Zhi et al., 2008). Fungivorous nematodes (*Aphelenchoides*, *Ditylenchus*, and *Filenchus*) and bacterivorous nematodes (*Chronogaster* and *Rhabdolaimus*) dominate in salt-affected alluvial soils (Nguyen et al., 2021). *Caenorhabditis elegans* avoids salt when faced with an absence of food, but is attracted to salt after exposure to food (Adachi et al., 2010). The beetle *Merizodus* and spider *Arctosa fulvolineata* increase the osmotic pressure of their body fluids by accumulating amino acids (Foucreau et al., 2012). Some terrestrial arthropods can survive in soils with up to 70% salinity (Pétillon et al., 2011) because they accumulate substances that contribute to osmoregulation, including disaccharides, monosaccharides, and quaternary amino acids (Misra and Misra, 2012).

2.4.2 Human activities to remediate soil salinity are changing the fauna community

Human activity-induced salinity (generally referred to as secondary salinization), in combination with climate change, leads to greater harm than salinity alone (Yeo, 1998). We have applied many strategies to cope with increased salinity, including the extensive use of fertilizers (Zheng et al., 2019) and biologically treating saline soils (Wang et al., 2020). The responses of soil fauna

organisms to fertilization vary greatly, depending on the type of fertilizer used. Higher carbon and N ratios promote the increases in fungal activity and biomass, providing more food for fungivorous nematodes (Deng et al., 2016). Long-term application of organic manure increases the diversity of predatory soil fauna and earthworms in grassland soils (López-Hernandez et al., 2004). The abundance, community composition, structure, and diversity of soil fauna increase after the addition of organic fertilizer to saline soil (Banerjee et al., 2009). N application significantly reduces the number of soil nematodes and protozoa (Qi et al., 2011). N fertilization can be increased with the degree of salinization to improve aboveground crop biomass in saline soils—this led to a 50% increase in fertilizer use in heavily salinized fields in China (Zheng et al., 2019). As aboveground productivity has positive effects on soil fauna, the question is whether such effects can be offset by the negative influence of N fertilizers.

Halophytes are salt-tolerant plants and their culture is often employed to reclaim saline soils. Planting halophytes would affect soil fauna due to the following reasons: (1) halophytes reduce soil salinity by absorbing salt from soils, and lower salt stress may promote the growth of soil fauna. Also, lower salt stress led to an increase in soil microbiome populations (Wang et al., 2020), which may be beneficial to predators that prey on microorganisms; (2) habitat heterogeneity is favourable for microarthropod diversity (Tews et al., 2004; Samways, 2007). A study found that the abundance of millipedes in nature reserves depends more on land cover heterogeneity than the size of the reserve (Sadler, 2008). Therefore, cropping halophytes would trigger habitat heterogeneity in saline soils, which may positively affect soil fauna; and (3) small differences in litter quality and quantity in forest ecosystems are determinants of arthropod diversity (Sayer et al., 2010). In European subalpine spruce forests, the abundance of springtails is higher in young forests, whereas that of Oribatida is higher in mature forests with high litter input (Salmon et al., 2006). Halophyte litter may increase resources (e.g., organic matter and proteins) that are beneficial to consumer organisms. Moreover, plants are not merely suppliers of litter or habitat for soil fauna—they produce secondary metabolites that attract beneficial soil invertebrates, such as entomopathogenic nematodes to kill herbivores (Bonkowski et al., 2009). Halophytes might directly affect belowground communication through rhizospheres and this warrants further study.

2.4.3 Research implications for fauna communities under soil salinity

Saline areas are experiencing a general increase. This is predicted to intensify in the future due to climate change. Soil biodiversity plays an essential role in regulating ecosystem services (Wagg et al., 2014; Delgado-Baquerizo et al., 2020; Fan et al., 2021). Therefore, increases in salinity will have an impact on the structure and functioning of ecosystem by affecting soil fauna. A better understanding of soil fauna in saline soils is essential not only to conserve biodiversity, but also to ensure the maintenance of key ecosystem services in the face of climate change, particularly in the context of the FAO's proposed "halt soil salinization, boost soil productivity" (FAO, 2021). Studies can focus on two aspects: (1) establish a monitoring system for soil ecosystems using soil fauna communities (e.g., biodiversity or components) as indicators of specific ecosystem functions, as they are linked to fauna adaptation strategies in response to climate, soil resources, disturbances (e.g., land-use change), and defence/protection needs; and (2) develop methods to predict future changes in soil fauna communities and soil faunal-driven ecosystem processes. Interactions between environmental factors, such as N deposition, carbon dioxide enrichment, the frequency of extreme events, and increased human pressure, can have cumulative joint effects on soil fauna communities (David and Handa, 2010). Additionally, the ecological consequences of biotic interactions (e.g., microorganism, disease, parasitism, and predation) can affect the abundance and distribution of soil fauna. Therefore, building bridges between disciplines and bringing together available information, e.g., molecular biological information (environmental DNA (deoxyribonucleic acid) and various 'omics' approaches), activity proxies, acoustic signatures, and response traits, will allow a more realistic assessment of their response to environmental change.

3 Conclusions

This review addressed the key environmental factors affecting soil fauna and the potential risk posed to fauna communities by changing climate. Warming may have a positive impact on the abundance and development of most species, but will inhibit the survival and reproduction of hibernating species. Drought reduces soil fauna populations in many areas and alters their community composition. The reduced food quality will make soil fauna change their dietary choices (from higher-quality foods to poor quality foods) to reduce the reproduction for survival. However, enhanced floral diversity will still contribute positively to the diversity of soil fauna. Any loss in habitat caused by deterioration of soil physical-chemical property may be directly detrimental to soil fauna. It should be noted that an increase in soil salinity could override other factors that favour habitat specialists, leading to negative effects on soil fauna. The response of soil fauna to environmental factors in saline soils requires further study. This information may help to guide preventive strategies (e.g., biodiversity conservation) and/or corrective measures (e.g., inclusion of specific species in restoration projects) to protect the threatened ecosystem.

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References

- Adachi T, Kunitomo H, Tomioka M, et al. 2010. Reversal of salt preference is directed by the Insulin/PI3K and Gq/PKC signaling in *Caenorhabditis elegans*. *Genetics*, 186(4): 1309–1319.
- Amini S, Ghadiri H, Chen C, et al. 2016. Salt-affected soils, reclamation, carbon dynamics, and biochar: A review. *Journal of Soils Sediments*, 16(3): 939–953.
- Andronov E E, Petrova S N, Pinaev A G, et al. 2012. Analysis of the structure of microbial community in soils with different degrees of salinization using T-RFLP and real-time PCR techniques. *Eurasian Soil Science*, 45(2): 147–156.
- Aubert M, Margerie P, Trap J, et al. 2010. Aboveground-belowground relationships in temperate forests: Plant litter composes and microbiota orchestrates. *Forest Ecology and Management*, 259(3): 563–572.
- Bakonyi G, Nagy P, Kovacs-Lang E, et al. 2007. Soil nematode community structure as affected by temperature and moisture in a temperate semiarid shrubland. *Applied Soil Ecology*, 37(1–2): 31–40.
- Banerjee S, Sanyal A K, Moitra M N. 2009. Abundance and group diversity of soil mite population in relation to four edaphic factors at Chintamani Abhayaranya, Narendrapur, South 24-Parganas, West Bengal. *Proceedings of the Zoological Society*, 62(1): 57–65.
- Bardgett R D, Mawdsley J L, Edwards S, et al. 1999. Plant species and nitrogen effects on soil biological properties of temperate upland grasslands. *Functional Ecology*, 13(5): 650–660.
- Bardgett R D, van der Putten W H. 2014. Belowground biodiversity and ecosystem functioning. *Nature*, 515(7528): 505–511.
- Bayartogtokh B, Chatterjee T. 2010. Oribatid mites from marine littoral and freshwater habitats in India with remarks on world species of *Thalassozetes* (Acari: Oribatida). *Zoological Studies*, 49(6): 839–854.
- Beaumelle L, Thouvenot L, Hines J, et al. 2021. Soil fauna diversity and chemical stressors: A review of knowledge gaps and roadmap for future research. *Ecography*, 44(6): 845–859.
- Bindoff N L, Cheung W W L, Kairo J G, et al. 2019. IPCC special report: The ocean and cryosphere in a changing climate.

- [2022-07-15]. <https://www.ipcc.ch/srocc/home/>.
- 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.
- Blume-Werry G, Krab E J, Olofsson J, et al. 2020. Invasive earthworms unlock arctic plant nitrogen limitation. *Nature Communications*, 11(1): 1766, doi: 10.1038/s41467-020-15568-3.
- Bohlen P J, Scheu S, Hale C M, et al. 2004. Non-native invasive earthworms as agents of change in northern temperate forests. *Frontiers in Ecology and the Environment*, 2(8): 427–435.
- Bokhorst S, Phoenix G K, Bjerke J W, et al. 2012. Extreme winter warming events more negatively impact small rather than large soil fauna: Shift in community composition explained by traits not taxa. *Global Change Biology*, 18(3): 1152–1162.
- Bonkowski M, Villenave C, Griffiths B. 2009. Rhizosphere fauna: The functional and structural diversity of intimate interactions of soil fauna with plant roots. *Plant and Soil*, 321(1): 213–233.
- Briones M J I. 2018. The serendipitous value of soil fauna in ecosystem functioning: The unexplained explained. *Frontiers in Environmental Science*, 20(6): 149.
- Castaneda A C, Aballay E. 2016. Rhizobacteria with nematicide aptitude: Enzymes and compounds associated. *World Journal of Microbiology and Biotechnology*, 32(12): 203.
- Cesarz S, Ruess L, Jacob M, et al. 2013. Tree species diversity versus tree species identity: Driving forces in structuring forest food webs as indicated by soil nematodes. *Soil Biology and Biochemistry*, 62(2): 36–45.
- Chen C, Chen H Y H, Chen X, et al. 2019. Meta-analysis shows positive effects of plant diversity on microbial biomass and respiration. *Nature Communications*, 10(1): 1332.
- Coleman D C, Crossley J D A. 1996. *Fundamentals of Soil Ecology*. New York: Academic Press, 10–25.
- Coleman D C, Crossley D A, Hendrix P F. 2004. *Fundamentals of Soil Ecology*. Burlington: Elsevier Academic Press, 17.
- Coulbaly S F M, Aubert M, Brunet N, et al. 2022. Short-term dynamic responses of soil properties and soil fauna under contrasting tillage systems. *Soil & Tillage Research*, 215: 105191, doi: 10.1016/j.still.2021.105191.
- Crawford C S, Bercovitz K, Warburg M R. 1987. Regional environments, life-history patterns, and habitat use of spirostreptid millipedes in arid regions. *Zoological Journal of the Linnean Society*, 89(1): 63–88.
- David J F, Gillon D. 2009. Combined effects of elevated temperatures and reduced leaf litter quality on the life-history parameters of a saprophagous macroarthropod. *Global Change Biology*, 15(1): 156–165.
- David J F, Handa I T. 2010. The ecology of saprophagous macroarthropods (millipedes, woodlice) in the context of global change. *Biological Reviews*, 85(4): 881–895.
- David J F. 2014. The role of litter-feeding macroarthropods in decomposition processes: A reappraisal of common views. *Soil Biology & Biochemistry*, 76(1): 109–118.
- De Oliveira T, Hattenschwiler S, Handa I T. 2010. Snail and millipede complementarity in decomposing Mediterranean forest leaf litter mixtures. *Functional Ecology*, 24(4): 937–946.
- Decaëns T, Jiménez J J, Gioia C, et al. 2006. The values of soil animals for conservation biology. *European Journal of Soil Biology*, 42(1): 23–38.
- Delgado-Baquerizo M, Reich P B, Trivedi C, et al. 2020. Multiple elements of soil biodiversity drive ecosystem functions across biomes. *Nature Ecology & Evolution*, 4(2): 210–220.
- Denis M N, Chen S C, Juan Z, et al. 2021. Soil fauna accelerate litter mixture decomposition globally, especially in dry environments. *Journal of Ecology*, 110(3): 659–672.
- Deng Q, Cheng X, Hui D, et al. 2016. Soil microbial community and its interaction with soil carbon and nitrogen dynamics following afforestation in central China. *Science of the Total Environment*, 541: 230–237.
- Dunn R R, Agosti D, Andersen A N, et al. 2009. Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. *Ecological Letters*, 12(4): 324–333.
- Edwards C A. 2002. Assessing the effects of environmental pollutants on soil organisms, communities, processes and ecosystems. *European Journal of Soil Biology*, 38(3–4): 225–231.
- Eisenbeis G, Wichard W. 1987. *Atlas on the Biology of Soil Arthropods*. New York: Springer, 25.
- Elnitsky M A, Benoit J B, Denlinger D L, et al. 2008. Desiccation tolerance and drought acclimation in the Antarctic collembolan *Cryptopygus antarcticus*. *Journal of Insect Physiology*, 54(10–11): 1432–1439.
- Fan K, Delgado-Baquerizo M, Guo X, et al. 2021. Biodiversity of key-stone phylotypes determines crop production in a 4-decade fertilization experiment. *The ISME Journal*, 15(2): 550–561.
- Fanin N, Kardol P, Farrell M, et al. 2019. The ratio of Gram-positive to Gram-negative bacterial PLFA markers as an indicator of carbon availability in organic soils. *Soil Biology and Biochemistry*, 128(1): 111–114.
- FAO. 2008. Management of irrigation-induced salt-affected soils. In: *Practices of Irrigation & On-farm Water Management*. New York: Springer, 21–34.

- FAO. 2021. Soils: Where food begins. Food and Agriculture Organization of the United Nations. [2022-08-12]. <https://www.un.org/en/observances/world-soil-day>.
- Faulkner B C, Lochmiller R L. 2000. Increased abundance of terrestrial isopod populations in terrestrial ecosystems contaminated with petrochemical wastes. *Archives of Environmental Contamination and Toxicology*, 39(1): 86–90.
- Fierer N, Strickland M S, Liptzin D, et al. 2009. Global patterns in belowground communities. *Ecology Letters*, 12(11): 1238–1249.
- Foucreau N, Renault D, Hidalgo K, et al. 2012. Effects of diet and salinity on the survival, egg laying and metabolic fingerprints of the ground-dwelling spider *Arctosa fulvolineata* (Araneae, Lycosidae). *Comparative Biochemistry and Physiology*, 162(3–4): 388–395.
- Franklin J, Serra-Diaz J M, Syphard A D, et al. 2016. Global change and terrestrial plant community dynamics. *Proceedings of the National Academy of Sciences of the United States of America*, 113(14): 3725–3734.
- Frouz J. 2018. Effects of soil macro- and mesofauna on litter decomposition and soil organic matter stabilization. *Geoderma*, 332: 161–172.
- Garcia-Palacios P, Maestre F T, Kattge J, et al. 2013. Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. *Ecology Letters*, 16(8): 1045–1053.
- Garcia-Palacios P, Mckie B G, Handa I T, et al. 2016. The importance of litter traits and decomposers for litter decomposition: A comparison of aquatic and terrestrial ecosystems within and across biomes. *Functional Ecology*, 30(5): 819–829.
- Geisen S, Koller R, Hünninghaus M, et al. 2016. The soil food web revisited: Diverse and widespread mycophagous soil protists. *Soil Biology and Biochemistry*, 94: 10–18.
- Generlich O, Giere O. 1996. Osmoregulation in two aquatic oligochaetes from habitats with different salinity and comparison to other annelids. *Hydrobiologia*, 334(1): 251–261.
- Gessner M O, Swan C M, Dang C K, et al. 2010. Diversity meets decomposition. *Trends in Ecology & Evolution*, 25(6): 363–380.
- Gong X, Wang S, Wang Z, et al. 2019. Earthworms modify soil bacterial and fungal communities through enhancing aggregation and buffering pH. *Geoderma*, 347: 59–69.
- Greenslade P. 1981. Survival of Collembola in arid environments: Observations in South Australia and the Sudan. *Journal of Arid Environments*, 4(3): 219–228.
- Guidi N, Frey B, Brunner I. 2002. Effects of experimental irrigation and drought on the composition and diversity of soil fauna in a coniferous stand. *Global Change Biology*, 40(1): 191–192.
- Gunstone T, Cornelisse T, Klein K, et al. 2021. Pesticides and soil invertebrates: A hazard assessment. *Frontiers in Environmental Science*, 9(64): 643847, doi: 10.3389/fenvs.2021.643847.
- Guo X, Endler A, Poll C, et al. 2021. Independent effects of warming and altered precipitation pattern on nematode community structure in an arable field. *Agriculture, Ecosystems & Environment*, 316(15): 107467, doi: 10.1016/j.agee.2021.107467.
- Hallam J, Hodson M E. 2020. Impact of different earthworm ecotypes on water stable aggregates and soil water holding capacity. *Biology and Fertility of Soils*, 56(5): 607–617.
- Heděnc P, Radochová P, Nováková A, et al. 2013. Grazing preference and utilization of soil fungi by *Folsomia candida* (Isotomidae: Collembola). *European Journal of Soil Biology*, 55: 66–70.
- Ho H C, Tylanakis J M, Zheng J X, et al. 2019. Predation risk influences food-web structure by constraining species diet choice. *Ecology Letters*, 22(11): 1734–1745.
- Holmstrup M, Sjursen H, Ravn H, et al. 2001. Dehydration tolerance and water vapour absorption in two species of soil-dwelling Collembola by accumulation of sugars and polyols. *Functional Ecology*, 15(5): 647–653.
- Holmstrup M, Maraldo K, Krogh P H. 2007. Combined effect of copper and prolonged summer drought on soil microarthropods in the field. *Environmental Pollution*, 146(2): 525–533.
- Holmstrup M, Damgaard C, Schmidt I K, et al. 2017. Long-term and realistic global change manipulations had low impact on diversity of soil biota in temperate heathland. *Scientific Reports*, 25: 41388, doi: 10.1038/srep41388.
- Hoogen J, Geisen S, Routh D, et al. 2019. Soil nematode abundance and functional group composition at a global scale. *Nature*, 572(7768): 194–198.
- Ingham E R, Klein D A, Trlica M J. 1985. Responses of microbial components of the rhizosphere to plant management strategies in a semiarid rangeland. *Plant and Soil*, 85(1): 65–76.
- IPCC. 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Switzerland: IPCC, 85–88.
- Jentschke G, Bonkowski M, Douglas L, et al. 1995. Soil protozoa and forest tree growth: Non-nutritional effects and interaction with mycorrhizae. *Biology and Fertility of Soils*, 20(4): 263–269.
- Jing X, Sanders N J, Shi Y, et al. 2015. The links between ecosystem multifunctionality and above- and belowground

- biodiversity are mediated by climate. *Ecological Indicators*, 115(6): 1–11.
- Joly F X, Coq S, Coulis M, et al. 2018. Litter conversion into detritivore faeces reshuffles the quality control over C and N dynamics during decomposition. *Functional Ecology*, 32(11): 2605–2614.
- Joly F X, Coq S, Coulis M, et al. 2020. Detritivore conversion of litter into faeces accelerates organic matter turnover. *Communications Biology*, 3: 660, doi: 10.1038/s42003-020-01392-4.
- Josef H G, Jose A A. 2021. *The soil fauna. Principles and Applications of Soil Microbiology* (3rd ed.). New Jersey: Prentice Hall, 191–212.
- Kardol P, Cregger M A, Campany C E, et al. 2010. Soil ecosystem functioning under climate change: Plant species and community effects. *Ecology*, 91(3): 767–781.
- Kardol P, Reynolds W N, Norby R J, et al. 2011. Climate change effects on soil microarthropod abundance and community structure. *Applied Soil Ecology*, 47(1): 37–44.
- Kevin R, Butt Maria J I B. 2017. Earthworms and mesofauna from an isolated, alkaline chemical waste site in Northwest England. *European Journal of Soil Biology*, 78: 43–49.
- Kiss T B W. 2019. Earthworms, flooding, and sewage sludge. PhD Dissertation. York: University of York.
- Kitz F, Steinwandter M, Traugott M, et al. 2015. Increased decomposer diversity accelerates and potentially stabilizes litter decomposition. *Soil Biology and Biochemistry*, 83: 138–141.
- Kristin M R, Johannes R. 2015. Salt effects on the soil microbial decomposer community and their role in organic carbon cycling: A review. *Soil Biology & Biochemistry*, 81: 108–123.
- Kuikman P J, Lekkerkerk L, Veen J. 2003. Carbon dynamics of a soil planted with wheat under an elevated atmospheric CO₂ concentration. *Journal of Nuclear Agricultural Science*, 28(3): 141–153.
- Kuzyakov Y, Blagodatskaya E. 2015. Microbial hotspots and hot moments in soil: Concept and review. *Soil Biology and Biochemistry*, 83: 184–199.
- Lagerlof J, Goffre B, Vincent C. 2002. The importance of field boundaries for earthworms (Lumbricidae) in the Swedish agricultural landscape. *Agriculture Ecosystem and Environment*, 89(1–2): 91–103.
- Landesman W J, Treonis A M, Dighton J. 2011. Effects of a one-year rainfall manipulation on soil nematode abundances and community composition. *Pedobiologia*, 54(2): 87–91.
- Laskowski K L, Moiron M, Niemela P T. 2020. Integrating behavior in life-history theory: Allocation versus acquisition? *Trends in Ecology & Evolution*, 36(2): 132–138.
- Lavelle P, Bignell D, Lepage M, et al. 1997. Soil function in a changing world: The role of invertebrate ecosystem engineers. *European Journal of Soil Biology*, 33(4): 159–193.
- Lavelle P, Spain A V. 2001. *Soil Ecology*. Dordrecht: Kluwer Academic Publishers, 101–110.
- Lavelle P, Mathieu J, Spain A, et al. 2022. Soil macroinvertebrate communities: A world-wide assessment. *Global Ecology and Biogeography*, 31(7): 1261–1276.
- Li C H, Li J Y, Lan C Q, et al. 2017. Protozoa inhibition by different salts: Osmotic stress or ionic stress? *Biotechnology Progress*, 33(5): 1418–1424.
- Li Z H, Li Y, Shao W, et al. 2021. Evaluating the interaction of soil microorganisms and gut of soil fauna on the fate and spread of antibiotic resistance genes in digested sludge-amended soil ecosystem. *Journal of Hazardous Materials*, 420(1): 126672, doi: 10.1016/j.jhazmat.2021.126672.
- Lindberg N, Engtsson J B, 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(6): 924–936.
- Liu C H, Shao Y, Cao S. 2021. Soil fauna community diversity and response to wetland degradation in Nanniwan wetland, Shaanxi, China. *Sains Malaysiana*, 50(6): 1511–1520.
- Liu T, Yu L, Xu J, et al. 2017. Bacterial traits and quality contribute to the diet choice and survival of bacterial-feeding nematodes. *Soil Biology and Biochemistry*, 115: 467–474.
- Liu W P A, Phillips L M, Terblanche J S, et al. 2021. An unusually diverse genus of Collembola in the cape floristic region characterised by substantial desiccation tolerance. *Oecologia*, 195(4): 873–885.
- López-hernández D, Araujo Y, López A, et al. 2004. Changes in soil properties and earthworm populations induced by long-term organic fertilization of a sandy soil in the Venezuelan Amazonia. *Soil Science*, 169(3): 188–194.
- Lubbers I M, Berg M P, De Deyn G B, et al. 2020. Soil fauna diversity increases CO₂ but suppresses N₂O emissions from soil. *Global Change Biology*, 26(3): 1886–1898.
- Ma Z L, Chen H Y. 2016. Effects of species diversity on fine root productivity in diverse ecosystems: A global meta-analysis. *Global Ecology Biogeography*, 25(11): 1387–1396.
- Maraldo K, Ravn H W, Slotsbo S, et al. 2009. Responses to acute and chronic desiccation stress in *Enchytraeus* (Oligochaeta: Enchytraeidae). *Journal of Comparative Physiology*, 179(2): 113–123.

- Matute M M, Manning Y A, Kaleem M I. 2013. Community structure of soil nematodes associated with *Solanum tuberosum*. *Journal of Agricultural Science (Toronto)*, 5(1): 44–53.
- Meehan M L, Barreto C, Turnbull M S, et al. 2020. Response of soil fauna to simulated global change factors depends on ambient climate conditions. *Pedobiologia*, 83: 150672, doi: 10.1016/j.pedobi.2020.150672.
- Misra N, Misra R. 2012. Salicylic acid changes plant growth parameters and proline metabolism in *Rauwolfia serpentina* leaves grown under salinity stress. *Environmental Science*, 12(12): 1601–1609.
- Moir M L, Brennan K E C, Harvey M S. 2009. Diversity, endemism and species turnover of millipedes within the south-western Australian global biodiversity hotspot. *Journal of Biogeography*, 36(10): 1958–1971.
- Mueller K E, Blumenthal D M, Carrillo Y, et al. 2016. Elevated CO₂ and warming shift the functional composition of soil nematode communities in a semiarid grassland. *Soil Biology and Biochemistry*, 103: 46–51.
- Mukhopadhyay A, Tissenbaum H A. 2007. Reproduction and longevity: Secrets revealed by *C. elegans*. *Trends in Cell Biology*, 17(2): 65–71.
- Nguyen S V, Chau M K, Vo Q M, et al. 2021. Impacts of saltwater intrusion on soil nematodes community in alluvial and acid sulfate soils in paddy rice fields in Vietnamese Mekong Delta. *Ecological Indicators*, 122(1): 107284, doi: 10.1016/j.ecolind.2020.107284.
- Nielsen U N, Ball B A. 2015. Impacts of altered precipitation regimes on soil communities and biogeochemistry in arid and semi-arid ecosystems. *Global Change Biology*, 21(4): 1407–1421.
- Nieminen J K. 2008. Soil animals and ecosystem processes: How much does nutrient cycling explain? *Pedobiologia*, 51(5–6): 367–373.
- Niklaus P A, Alphei J, Ebersberger D, et al. 2003. Six years of *in situ* CO₂ enrichment evoke changes in soil structure and soil biota of nutrient poor grassland. *Global Change Biology*, 9(4): 585–600.
- Nkem J N, Virgina R A, Barrett J E, et al. 2006. Salt tolerance and survival thresholds for two species of Antarctic soil nematodes. *Polar Biology*, 29(8): 643–651.
- O'Connor B M. 2003. Acari in encyclopedia of insects. In: Resh V H, Ring T C. *Encyclopedia of Insects*. New York: Academic Press, 1295.
- Owojori O J, Reinecke A J, Rozanov A B. 2008. Effects of salinity on partitioning, uptake and toxicity of zinc in the earthworm *Eisenia fetida*. *Soil Biology and Biochemistry*, 40(9): 2385–2393.
- Owojori O J, Reinecke A J, Voua-Otomo P, et al. 2009. Comparative study of the effects of salinity on life-cycle parameters of four soil-dwelling species (*Folsomia candida*, *Enchytraeus doerjesi*, *Eisenia fetida* and *Aporrectodea caliginosa*). *Pedobiologia*, 52(6): 351–360.
- Owojori O J, Waszak K, Roembke J. 2014. Avoidance and reproduction tests with the predatory mite *Hypoaspis aculeifer*: Effects of different chemical substances. *Environmental Toxicology and Chemistry*, 33(1): 230–237.
- Pavao-Zuckerman M A, Coleman D C. 2007. Urbanization alters the functional composition, but not taxonomic diversity, of the soil nematode community. *Applied Soil Ecology*, 35(2): 329–339.
- Peguero G, Folch E, Liu L, et al. 2021. Divergent effects of drought and nitrogen deposition on microbial and arthropod soil communities in a Mediterranean forest. *European Journal of Soil Biology*, 103: 103275, doi: 10.1016/j.ejsobi.2020.103275.
- Peng Y, Schmidt I K, Zheng H, et al. 2020. Tree species effects on topsoil carbon stock and concentration are mediated by tree species type, mycorrhizal association, and N-fixing ability at the global scale. *Forest Ecology Management*, 478: 118510, doi: 10.1016/j.foreco.2020.118510.
- Peng Y, Peñuelas J, Vesterdal L, et al. 2022. Responses of soil fauna communities to the individual and combined effects of multiple global change factors. *Ecology Letters*, 25(9): 1961–1973.
- Pereira C S, Lopes I, Sousa J P, et al. 2015. Effects of NaCl and seawater induced salinity on survival and reproduction of three soil invertebrate species. *Chemosphere*, 135: 116–122.
- Petersen H, Luxton M. 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. *Oikos*, 39(3): 287–388.
- Pétillon J, Lambeets K, Ract-Madoux B, et al. 2011. Saline stress tolerance partly matches with habitat preference in ground-living wolf spiders. *Physiological Entomology*, 36(2): 165–172.
- Phillips P. 2019. Global distribution of earthworm diversity. *Science*, 370(6519): 922–923.
- Piola R F, Johnston E L. 2008. Pollution reduces native diversity and increases invader dominance in marine hard-substrate communities. *Diversity Distributions*, 14(2): 329–342.
- Placella S A, Brodie E L, Firestone M K. 2012. Rainfall-induced carbon dioxide pulses result from sequential resuscitation of phylogenetically clustered microbial groups. *Proceedings of the National Academy of Sciences of the United States of America*, 109(27): 10931–10936.
- Price P B, Sowers T. 2004. Temperature dependence of metabolic rates for microbial growth, maintenance, and survival.

- Proceedings of the National Academy of Sciences of the United States of America, 101(13): 4631–4636.
- Qi S, Zhao X R, Zheng H X, et al. 2011. Changes of soil biodiversity in Inner Mongolia steppe after 5 years of N and P fertilizer applications. *Acta Ecologia Sinica*, 30(20): 3745–3757. (in Chinese)
- Raiesi F, Motaghian H R, Nazarizadeh M. 2020. The sublethal lead (Pb) toxicity to the earthworm *Eisenia fetida* (Annelida, Oligochaeta) as affected by NaCl salinity and manure addition in a calcareous clay loam soil during an indoor mesocosm experiment. *Ecotoxicology and Environmental Safety*, 190(1): 110083, doi: 10.1016/j.ecoenv.2019.110083.
- Ranjard L, Dequiedt S, Jolivet C, et al. 2010. Biogeography of soil microbial communities: A review and a description of the ongoing French national initiative. *Agronomy for Sustainable Development*, 30(2): 857–865.
- Rillig M C, Mummey D L. 2006. Mycorrhizas and soil structure. *New Phytology*, 171(1): 41–53.
- Roache M C, Bailey P C, Boon P I. 2006. Effects of salinity on the decay of the freshwater macrophyte, *Triglochin procerum*. *Aquatic Botany*, 84(1): 45–52.
- Ronan C, Elisa D C, Olaf S. 2020. Soil properties and earthworm populations associated with bauxite residue rehabilitation strategies. *Environmental Science and Pollution Research*, 27(27): 33401–33409.
- Rutgers M, Orgiazzi A, Gardi C, et al. 2016. Mapping earthworm communities in Europe. *Applied Soil Ecology*, 97(1): 98–111.
- Sadler A B. 2008. Habitat heterogeneity overrides the species-area relationship. *Journal of Biogeography*, 35(4): 675–681.
- Saetre P, Baath E. 2000. Spatial variation and patterns of soil microbial community structure in a mixed spruce-birch stand. *Soil Biology and Biochemistry*, 32(7): 909–917.
- Salmon S, Mantel J, Frizzera L, et al. 2006. Changes in humus forms and soil animal communities in two developmental phases of Norway spruce on an acidic substrate. *Forest Ecology and Management*, 237(1–3): 47–56.
- Samways M J. 2007. Insect conservation: A synthetic management approach. *Annual Review of Entomology*, 52: 465–487.
- Santos P F, DePree E, Whitford W G. 1978. Spatial distribution of litter and microarthropods in a Chihuahuan Desert ecosystem. *Journal of Arid Environments*, 1(1): 41–48.
- Sayer E J, Sutcliffe L M E, Ross R I C, et al. 2010. Arthropod abundance and diversity in a lowland tropical forest floor in Panama: The role of habitat space vs. nutrient concentrations. *Biotropica*, 42(2): 194–200.
- Schelfhout S, Mertens J, Verheyen K, et al. 2017. Tree species identity shapes earthworm communities. *Forests*, 8(10): 85.
- Seal J N, Tschinkel W R. 2010. Distribution of the fungus-gardening ant (*Trachymyrmex septentrionalis*) during and after a record drought. *Insect Conservation Diversity*, 3(2): 134–142.
- Sinclair B J, Stevens M I. 2006. Terrestrial microarthropods of Victoria Land and Queen Maud Mountains, Antarctica: Implications of climate change. *Soil Biology Biochemistry*, 38(10): 3158–3170.
- Steinwandter M, Seeber J. 2020. The buffet is open: Alpine soil macro-decomposers feed on a wide range of litter types in a microcosm cafeteria experiment. *Soil Biology and Biochemistry*, 144: 107786, doi: 10.1016/j.soilbio.2020.107786.
- Swift M J, Heal O W, Anderson J M. 1979. *Decomposition Interrestrial Ecosystems*. California: University of California Press, 161–175.
- Syrek D, Weiner W M, Wojtylak M, et al. 2006. Species abundance distribution of collembolan communities in forest soils polluted with heavy metals. *Applied Soil Ecology*, 31(3): 239–250.
- Tews J, Brose U, Grimm V, et al. 2004. Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. *Journal of Biogeography*, 31(1): 79–92.
- Thakur M P, Reich P B, Fisichelli N A, et al. 2014. Nematode community shifts in response to experimental warming and canopy conditions are associated with plant community changes in the temperate-boreal forest ecotone. *Oecologia*, 175(2): 713–723.
- Tordoff G M, Boddy L, Jones T H. 2008. Species-specific impacts of Collembola grazing on fungal foraging ecology. *Soil Biology and Biochemistry*, 40(2): 434–442.
- Venâncio C, Rui R, Lopes I. 2021. Seawater intrusion: An appraisal of taxa at most risk and safe salinity levels. *Biological Review*, 97(1): 361–382.
- Veresoglou S D, Halley J M, Rillig M C. 2015. Extinction risk of soil biota. *Nature Communication*, 6: 8862, doi: 10.1038/ncomms9862.
- Wagg C, Bender S F, Widmer F, et al. 2014. Soil biodiversity and soil community composition determine ecosystem multifunctionality. *Proceedings of the National Academy of Sciences of the United States of America*, 111(14): 5266–5270.
- Wall D H, Bradford M A, John M G, et al. 2008. Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Global Change Biology*, 14(11): 2661–2677.
- Wang W X, Vinocur B, Shoseyov O, et al. 2001. Biotechnology of plant osmotic stress tolerance: Physiological and molecular considerations. *Acta Horticulturae*, 560(1): 285–292.
- Wang X, Sun R, Tian Y, et al. 2020. Longterm phytoremediation of coastal saline soil reveals plant species-specific patterns of microbial community recruitment. *mSystems*, 5(2): e007411-19, doi: 10.1128/msystems.00741-19.

- Wardle D A. 2002. *Communities and Ecosystems: Linking the Aboveground and Belowground Components*. Princeton: Princeton University Press, 26–45.
- Wardle D A, Bardgett R D, Klironomos J N, et al. 2004. Ecological linkages between aboveground and belowground biota. *Science*, 304(5677): 1629–1633.
- Wardle D A. 2006. The influence of biotic interactions on soil biodiversity. *Ecology Letters*, 9(7): 870–886.
- Whitford W G, Sobhy H M. 1999. Effects of repeated drought on soil microarthropod communities in the northern Chihuahuan Desert. *Biology and Fertility of Soils*, 28(2): 117–120.
- Williams J W, Jackson S T. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecological Environment*, 5(9): 475–482.
- Wong V N L, Greene R S B, Dalal R C, et al. 2010. Soil carbon dynamics in saline and sodic soils: A review. *Soil Use and Management*, 26(1): 2–11.
- Wood J, Tordoff G M, Jones T H, et al. 2006. Reorganization of mycelial networks of *Phanerochaete velutina* in response to new woody resources and collembola (*Folsomia candida*) grazing. *Mycological Research*, 110(8): 985–993.
- Wu T, Ayres E, Bardgett R D, et al. 2011. Molecular study of worldwide distribution and diversity of soil animals. *Proceedings of the National Academy of Sciences of the United States of America*, 108(43): 17720–17725.
- Yang B, Chen Q, Liu X, et al. 2020. Effects of pest management practices on soil nematode abundance, diversity, metabolic footprint and community composition under paddy rice fields. *Frontiers in Plant Science*, 11: 88, doi: 10.3389/fpls.2020.00088.
- Yang B, Banerjee S, Herzog C, et al. 2021. Impact of land use type and organic farming on the abundance, diversity, community composition and functional properties of soil nematode communities in vegetable farming. *Agriculture, Ecosystem and Environment*, 318: 107488, doi: 10.1016/j.agee.2021.107488.
- Yang B, Li P, Entemake W, et al. 2022. Concentration-dependent impacts of microplastics on soil nematode community in bulk soils of maize: Evidence from a pot experiment. *Frontiers in Environmental Science*, 10: 872898, doi: 10.3389/fenvs.2022.872898.
- Yang X, Shao M, Li T C, et al. 2021. Community characteristics and distribution patterns of soil faunas after vegetation restoration in the northern Loess Plateau. *Ecological Indicators*, 122(1): 107236, doi: 10.1016/j.ecolind.2020.107236.
- Yeo A. 1998. Predicting the interaction between the effects of salinity and climate change on crop plants. *Scientia Horticulturae*, 78(1–4): 159–174.
- Yin X Q, Ma C, He H, et al. 2018. Distribution and diversity patterns of soil fauna in different salinization habitats of Songnen Grasslands, China. *Applied Soil Ecology*, 123: 375–383.
- Yu L, Yan X, Ye C, et al. 2015. Bacterial respiration and growth rates affect the feeding preferences, brood size and lifespan of *Caenorhabditis elegans*. *PLoS ONE*, 10(7): e0134401, doi: 10.1371/journal.pone.0134401.
- Yue K, Peng Y, Fornara D A, et al. 2019. Responses of nitrogen concentrations and pools to multiple environmental change drivers: a meta-analysis across terrestrial ecosystems. *Global Ecology and Biogeography*, 28(5): 690–724.
- Zahorec A, Reid M L, Tiemann L K, et al. 2021. Perennial grass bioenergy cropping systems: Impacts on soil fauna and implications for soil carbon accrual. *Global Change Biology Bioenergy*, 14(1): 4–23.
- Zhai J X, Yan G, Cong L, et al. 2020. Assessing the effects of salinity and inundation on halophytes litter breakdown in Yellow River Delta wetland. *Ecological Indicators*, 115(2): 106405, doi: 10.1016/j.ecolind.2020.106405.
- Zhang N, Wang D, Liu Y, et al. 2014. Effects of different plant root exudates and their organic acid components on chemotaxis, biofilm formation and colonization by beneficial rhizosphere-associated bacterial strains. *Plant and Soil*, 374(1): 689–700.
- Zhang Y, Lu H, Bargmann C I. 2005. Pathogenic bacteria induce aversive olfactory learning in *Caenorhabditis elegans*. *Nature*, 438(7065): 179–184.
- Zhang Y, Bi Y, Li G, et al. 2017. Relationship between earthworm diversity and soil environment in Hebei area. *Journal of China Agricultural University*, 22(1): 60–68. (in Chinese)
- Zheng L T, Chen H Y H, Yan E R. 2019. Tree species diversity promotes litter fall productivity through crown complementarity in subtropical forests. *Journal of Ecology*, 107(4): 1852–1861.
- Zhi D, Li H, Nan W. 2008. Nematode communities in the artificially vegetated belt with or without irrigation in the Tengger Desert, China. *European Journal of Soil Biology*, 44(2): 238–246.
- Zhou Z, Wang C, Luo Y. 2020. Meta-analysis of the impacts of global change factors on soil microbial diversity and functionality. *Nature Communications*, 11(1): 3072, doi: 10.1038/s41467-020-16881-7.