Responses of soil fauna community under changing environmental conditions (Postprint)

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Abstract

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Preamble

Responses of Soil Fauna Community Under Changing Environmental Conditions

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Abstract: Soil fauna accounts for 23% of known animal species and plays crucial roles in ecosystem processes such as nutrient mineralization, microbial community regulation, soil aggregate formation, and primary productivity enhancement. However, global climate change is altering soil fauna population density, community composition, and distribution patterns. Understanding these responses to major environmental changes facilitates biodiversity conservation. Therefore, this review analyzes recent research on the effects of key environmental factors—including warming, drought, food quality, and soil physicochemical properties—on soil fauna. For most species, warming may positively affect abundance and population development, yet it can inhibit survival and reproduction of hibernating species. Drought reduces soil porosity and water-holding capacity, decreasing soil fauna populations and altering community composition. Drought also reduces floral coverage and alters soil surface microclimate, indirectly reducing fauna abundance. Climate warming and elevated atmospheric carbon dioxide can reduce litter quality, forcing soil fauna to shift dietary choices from higher-quality to poorer-quality foods and reduce reproduction for survival. However, enhanced plant species richness (or litter mixtures) is predicted to positively affect soil fauna diversity. Habitat loss caused by deteriorating soil physicochemical properties represents the primary factor affecting soil fauna. We discuss the threats of increased salinity—a major factor in arid lands—to soil fauna and their potential responses to anthropogenic disturbance in saline soils. Rising soil salinity can override other factors that favor habitat specialists, leading to negative effects on soil fauna. Moreover, more studies are needed to explore soil fauna responses to human activities in saline soils, and the relationship between important ecological processes and 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 at the foundational core of international agendas such as the Global Soil Biodiversity Initiative (GSBI), the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), and the United Nations Sustainable Development Goals (Briones, 2018). Soil fauna accounts for approximately one-fourth of Earth's biodiversity and three-fourths of all multicellular organisms (Coleman et al., 1996; Hoogen et al., 2019; Josef and Jose, 2021). Yet belowground organisms have received far less attention than aboveground organisms (Decaëns et al., 2006; Fig. 1 [Figure 1: see original paper]). Soil fauna inhabit nearly every terrestrial environment, including deserts, tundra, saline soils, and Antarctica (Fierer et al., 2009). While microbial communities are more influenced by local factors such as land use and soil type than by geomorphology and climate (Ranjard et al., 2010; Lavelle et al., 2022), soil fauna distribution patterns are shaped by climatic conditions, vegetation cover, and soil texture. Researchers typically classify soil fauna into three classes based on body width (Fig. 2 [Figure 2: see original paper]): microfauna (protozoa, nematodes, rotifers, and tardigrades) ranging from 2–100 m in width that inhabit soil water films; mesofauna (100 m–2 mm) including Acari, Collembola, Diplura, and Enchytraeidae that live in air-filled pore spaces; and macrofauna (>2 mm) including earthworms and soil-dwelling vertebrates that create their own microhabitats through bioturbation and other life strategies (Swift et al., 1979; Lavelle and Spain, 2001).

Soil fauna plays vital roles in shaping ecosystem functions, particularly biogeochemical and nutrient cycling (Frouz, 2018; Joly et al., 2018, 2020). They modulate soil nutrients by inducing chemical binding of carbon (C) and phosphorus (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, nitrogen (N) released from earthworm mucus, excreta, and biomass turnover exceeds that from annual litterfall in deciduous forests (Petersen and Luxton, 1982). Earthworms also enhance plant-soil N cycling by mineralizing and translocating organic matter (Blume-Werry et al., 2020). Ecosystem engineers such as earthworms, ants, and termites alter soil physical structure by decreasing bulk density and increasing porosity, which increases water infiltration and nutrient availability (Gong et al., 2019; Hallam and Hodson, 2020).

Microarthropods and millipedes promote litter decomposition and stimulate nutrient mobilization (David, 2014; Kitz et al., 2015; Garcia-Palacios, 2016; Lubbers et al., 2020). In temperate and wet tropical climates, soil fauna increase litter decomposition (Wall et al., 2008), and they accelerate litter mixture decomposition even in dry environments (Denis et al., 2021). A global meta-analysis reported that soil fauna can increase litter decomposition by up to 27% (Garcia-Palacios et al., 2013). Soil fauna activities also affect plant productivity—for instance, protozoa presence stimulates N uptake by spruce seedlings (Jentschke et al., 1995) and wheat growth (Kuikman et al., 2003). Surprisingly, soil fauna also impact microbes and thus contribute to ecosystem functions (Nieminen, 2008; Li et al., 2021; Zahorec et al., 2021). Under nutrient-limited conditions, soil fauna do not use all immobilized nutrients for biomass increase but instead supply microorganisms or plants via excretion (Ingham et al., 1985). The desert soil food web comprises multiple consumers (Whitford, 1999), with nematodes influencing decomposition rates by regulating bacterial prey activity (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 for maintaining multiple ecosystem functions (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). Globally, precipitation and temperature are the most important drivers affecting earthworm biomass and abundance, respectively (Hoogen et al., 2019; Phillips, 2019). At regional and local scales, soil fauna diversity is affected by non-climate drivers such as soil organic matter, pH, and moisture (Curry et al., 2004; Rutgers et al., 2016). For example, N-rich soils contain more bacterial-feeding nematodes (Lagerlof et al., 2002), and nematode community structure and diversity are sensitive to small fluctuations in temperature and moisture (Bakonyi et al., 2007). Pesticides pose hazards to invertebrates (Gunstone et al., 2021), while earthworms fail to thrive in mining regions due to extreme soil pH, high metal content, low moisture, and lack of suitable food (Ronan et al., 2020). Natural events such as flooding or fires affect soil properties and determine soil fauna composition (David and Gillon, 2009; Schelfhout et al., 2017)—for instance, flooding causes sharp decreases in earthworm biomass and abundance by altering soil properties (Kiss, 2019). Emerging concepts such as "biological accessibility" and "trophic cascades" help explain observed faunal responses to environmental changes (Briones, 2018). All these phenomena currently affect soil fauna and are predicted to have increasing impacts in the context of global environmental change (David and Handa, 2010; IPCC, 2014).

This review outlines recent progress in research on soil fauna responses to major environmental change factors, including climate (warming and drought) and non-climate (food quality and soil physicochemical property) factors (Fig. 3 [Figure 3: see original paper]). Given that the simultaneous occurrence of high temperature and dry climate increases soil salinity and has combined effects on soil fauna and ecosystem functioning—such as 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 current knowledge regarding human activities that affect fauna in saline soils.

2.1 Warming

Temperature affects the rate of biochemical processes in organisms. Species in the Southern Hemisphere, living with higher average temperatures, have more specific adaptations to these changes than those in the Northern Hemisphere (Dunn et al., 2009). Warming may have positive effects on soil fauna density and diversity (Table 1). For instance, warming can directly increase nematode density by promoting growth and reproduction or indirectly enhance food supply by 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 significantly and positively affects the polydesmid millipede, causing it to reproduce earlier in spring (David and Handa, 2010). Such positive effects on population growth are common among detritus-consuming arthropods (Sinclair and Stevens, 2006), as plant cover changes associated with warming likely lead to shifts in soil fauna communities (Thakur et al., 2014).

However, warming is not necessarily advantageous for 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, negatively affecting millipede diversity (David and Gillon, 2009). Additionally, warming may increase warm-adapted species while decreasing cold-adapted species (Blankinship et al., 2011). Arctic warming may increase soil fauna diversity, but extreme winter warming decreases Acari populations and shifts Collembola communities from euedaphic (soil-dwelling) species to larger, hemi-edaphic (litter-dwelling) species (Bokhorst et al., 2012).

Evidence suggests that warming's impact 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, Collembola and mite abundance 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 with by soil fauna.

2.2 Drought

Under drought conditions, animals struggle to move due to increased soil compactness and decreased soil water films (Coleman et al., 2004). Changes in precipitation event size and frequency influence invertebrate activity and density in dryland ecosystems (Nielsen and Ball, 2015). Drought effects 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). While drought has less effect on soil fauna diversity, 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 (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 fungus-gardening ants (drought-resistant species) increase in population density during drought periods (Seal and Tschinkel, 2010). Almost all functional groups of nematodes are sensitive to drought, though Qudsianematidae species appear less significantly affected (Williams and Jackson, 2007). Holmstrup et al. (2007, 2017) found that springtails can recover from recurring drought events because they employ survival strategies including moving to moist microsites, assuming an anhydrobiotic state, and reducing integument permeability to resist drought (Greenslade, 1981; Liu et al., 2021).

Drought also indirectly affects soil fauna communities (Franklin et al., 2016), for example by causing species distribution shifts. Drying conditions in southwestern Australia have caused moisture-favoring millipedes (e.g., Sphaerotheriida and Polyzoniida) to be outcompeted by drought-tolerant species (e.g., *Antichiropus* sp.), creating new species boundaries (Moir et al., 2009). Drought also influences soil fauna through food availability, as low water availability reduces microbial activity and leads to decreased faunal populations (Peguero et al., 2021). The abundance of collembolans and oribatid mites decreased by 80.6% and 77.8%, respectively, in drought areas because only 40% of litterfall occurred during drought treatment (Lindberg et al., 2002).

2.3 Food Quality

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

Researchers divide nematodes into five trophic groups based on 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* produces more offspring after consuming its preferred bacterial species but reduces brood size when preferred food is limited (Mukhopadhyay and Tissenbaum, 2007; Yu et al., 2015). *Acrobeloides* sp. feeding on preferred soil-dwelling bacterial species had the largest brood size and moderate survival time, whereas it produced the smallest brood size and shortest survival time when consuming 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. One study found that ash only formed arbuscular mycorrhiza but lacked ectomycorrhizal fungi, which benefited bacterial-feeding nematodes but suppressed fungal feeders, whereas beech beneficially affected fungal feeders by increasing fungi (Cesarz et al., 2013). However, when nematodes are exposed to stressful environments (parasites, predators, and toxins), they can switch dietary choices from higher-quality to poorer-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 significantly correlate with soil fauna (Frouz, 2018; Peng et al., 2020). High litter quality with high N, low phenolics, low lignin, and structural carbohydrates supports 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 high densities of enchytraeid worms and macro-microarthropods (Wardle et al., 2004). Increased aboveground productivity may support greater soil fauna abundance due 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, some secondary compounds in certain litter types can be detrimental to microbial decomposers and detritivorous consumers (Gessner et al., 2010). Experimental plots with rich plant diversity maintain greater soil fauna abundance and diversity than plant monocultures (David and Handa, 2010). Multiple resources in litter mixtures 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 plant community composition and 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, soil fauna diversity is predicted to increase with plant (or litter) mixture species richness. Nutrients are scarce and/or supply is discontinuous in extreme environments (i.e., cold and arid ecosystems), resulting in low soil biodiversity and shortened food chains. Any nutritional surplus creates a “hot moment” under these conditions (Kuzyakov and Blagodatskaya, 2015). Extreme events (e.g., extreme heat, cold, or precipitation) occurring frequently could affect food quality and thereby "cascade" along the soil food web, bringing other pressures (e.g., predation and competition) that 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). Increased soil organic matter content provides more food resources for soil fauna, which in turn increases their abundance and diversity (Yin et al., 2018). Soil fauna group numbers and abundance increase with soil water content, whereas higher soil temperatures result in lower soil fauna diversity (Coulibaly et al., 2022). Soil pH also affects soil fauna communities. For example, pH is negatively correlated with soil fauna density in weakly alkaline soils (pH 7.52–8.96) but positively correlated in acidic soils (pH 5.21–5.72) (Liu et al., 2021). Studies show that pH can affect soil food web composition, indirectly influencing nematode community structure (Matute et al., 2013; Yang et al., 2022). Low pH and high soil inorganic N may cause soil fauna diversity to negatively correlate with aboveground biodiversity (Wu et al., 2011), though the mechanism by which pH directly affects soil organisms remains unclear.

The primary factor affecting soil fauna extinction is habitat loss caused by deteriorating soil physicochemical properties (Veresoglou et al., 2015). Urbanization fragments the soil surface, eliminating autotrophic organisms and subsequently reducing macrofaunal biomass (Pavao-Zuckerman and Coleman, 2007). Soil tillage negatively affects soil fauna by destroying soil aggregates (Rillig and Mummey, 2006). Increased atmospheric carbon dioxide concentrations indirectly decrease soil aggregation and pore size, potentially eliminating some soil fauna species (e.g., Collembola) living in pore spaces (Niklaus et al., 2003). Soil contamination alters predator/prey ratios (Edwards, 2002). For example, enchytraeid and earthworm survival declines in petroleum-contaminated soil, while isopod abundance is higher in contaminated than uncontaminated areas (Faulkner and Lochmiller, 2000). Habitat loss caused by chemical stressors (e.g., soil pollution) can eliminate the most sensitive species and promote tolerance in invasive or opportunistic species (Syrek et al., 2006; Piola and Johnston, 2008; Beaumelle et al., 2021).

Soil salinity significantly affects soil organism distribution (Placella et al., 2012). Saline soils (>800\$×10^{6}\$ hm^{2}) represent 6% of the world's total land area (FAO, 2008) and harbor numerous soil animals (Andronov et al., 2012). Yin et al. (2018) reported that Prostigmata, Oribatida, Gamasina, Collembola, Entomobryidae, and Isotomidae are dominant groups in the salinized soils of Songnen Grasslands, China. By comparison, enchytraeids and most arthropods (except collembolans) are more abundant at salinization sites in Northwest England (Kevin and Butt Maria, 2017). Increasing salinity affects soil animal distribution, so the following section focuses on the relationship between salinity and soil fauna and discusses responses to increasing salinity.

2.4.1 Responses of Soil Fauna to Soil Salinity

Soil salinity is hazardous to soil fauna (Table 3). High salinity poses direct physiological challenges, primarily through osmotic and ionic stress (Price et al., 2004). Ionic stress causes protozoan death via cytoplasmic membrane rupture and cell death (Li et al., 2017). Nematodes cannot survive in high-saline soils at 4100 µS/cm (Nkem et al., 2006). Salinity causes a sharp decline in soil nematode abundance (averaging 1/100 mL soil) compared to non-salinized areas (averaging 25/100 mL 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 toxicity and significantly decreases earthworm activity (Raiesi et al., 2020). Additionally, salinity reduces litter decomposition rates (Roache et al., 2006; Zhai et al., 2020), indirectly affecting detritivore numbers that rely on decomposing plant litter (De et al., 2021; Venâncio et al., 2021). Salinity stress is also associated with drought and warming—for example, high salt concentrations are expected in soils due to sea level rise and warming (Bindoff et al., 2019), leading to declines in hydraulic conductivity, water infiltration, organic matter solubility, and soil porosity (Wong et al., 2010; Amini et al., 2016). Such environmental deterioration can aggravate salinity's detrimental effects on organisms (Wang et al., 2001; Kristin and Johannes, 2015).

The basic behavioral response of soil fauna to detrimental soil salt increases is movement. To avoid high-salinity environments, the collembolan *Cryptopygus antarcticus* migrates to more suitable microhabitats (Elnitsky et al., 2008). Earthworms show 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 soil properties or ionic composition. Physiological adaptations such as a continuous exoskeleton can reduce organism contact with 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 (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 food is absent but is attracted to salt after food exposure (Adachi et al., 2010). The beetle *Merizodus* and spider *Arctosa fulvolineata* increase body fluid osmotic pressure 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 osmoregulatory substances 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 (secondary salinization), combined with climate change, causes greater harm than salinity alone (Yeo, 1998). Many strategies have been applied to cope with increased salinity, including extensive fertilizer use (Zheng et al., 2019) and biological treatment of saline soils (Wang et al., 2020). Soil fauna responses to fertilization vary greatly depending on fertilizer type. Higher carbon-to-nitrogen ratios promote increased fungal activity and biomass, providing more food for fungivorous nematodes (Deng et al., 2016). Long-term organic manure application increases predatory soil fauna and earthworm diversity in grassland soils (López-Hernandez et al., 2004). Soil fauna abundance, community composition, structure, and diversity increase after adding organic fertilizer to saline soil (Banerjee et al., 2009). Nitrogen application significantly reduces soil nematode and protozoa numbers (Qi et al., 2011). N fertilization can be increased with salinization degree to improve aboveground crop biomass in saline soils—this led to 50% more fertilizer use in heavily salinized fields in China (Zheng et al., 2019). Since aboveground productivity positively affects soil fauna, the question is whether such effects can offset the negative influence of N fertilizers.

Halophytes are salt-tolerant plants often employed to reclaim saline soils. Planting halophytes affects soil fauna through several mechanisms: (1) halophytes reduce soil salinity by absorbing salt, and lower salt stress may promote soil fauna growth while increasing soil microbiome populations (Wang et al., 2020), potentially benefiting predators that prey on microorganisms; (2) habitat heterogeneity favors microarthropod diversity (Tews et al., 2004; Samways, 2007), and one study found that millipede abundance in nature reserves depends more on land cover heterogeneity than reserve size (Sadler, 2008), suggesting that cropping halophytes would trigger habitat heterogeneity in saline soils, positively affecting soil fauna; and (3) small differences in litter quality and quantity in forest ecosystems determine arthropod diversity (Sayer et al., 2010), with springtail abundance higher in young European subalpine spruce forests and Oribatida abundance higher in mature forests with high litter input (Salmon et al., 2006). Halophyte litter may increase resources (e.g., organic matter and proteins) beneficial to consumers. Moreover, plants are not merely litter suppliers or habitat providers—they produce secondary metabolites that attract beneficial soil invertebrates such as entomopathogenic nematodes that kill herbivores (Bonkowski et al., 2009). Halophytes might directly affect belowground communication through rhizospheres, warranting further study.

2.4.3 Research Implications for Fauna Communities Under Soil Salinity

Saline areas are experiencing general increases predicted to intensify with 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), so salinity increases will impact ecosystem structure and functioning by affecting soil fauna. A better understanding of soil fauna in saline soils is essential not only for biodiversity conservation but also for ensuring maintenance of key ecosystem services amid climate change, particularly in the context of FAO's proposed "halt soil salinization, boost soil productivity" (FAO, 2021). Future studies can focus on two aspects: (1) establishing 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 defense/protection needs; and (2) developing 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, extreme event frequency, and increased human pressure can have cumulative joint effects on soil fauna communities (David and Handa, 2010). Additionally, ecological consequences of biotic interactions (e.g., microorganisms, disease, parasitism, and predation) can affect soil fauna abundance and distribution. Therefore, building bridges between disciplines and integrating available information—such as molecular biological data (environmental DNA and various 'omics' approaches), activity proxies, acoustic signatures, and response traits—will allow more realistic assessment of their responses to environmental change.

3 Conclusions

This review addressed key environmental factors affecting soil fauna and the potential risks posed to fauna communities by changing climate. Warming may positively impact the abundance and development of most species but will inhibit survival and reproduction of hibernating species. Drought reduces soil fauna populations in many areas and alters community composition. Reduced food quality will force soil fauna to change dietary choices (from higher-quality to poorer-quality foods) and reduce reproduction for survival. However, enhanced floral diversity will still contribute positively to soil fauna diversity. Any habitat loss caused by deteriorating soil physicochemical properties may be directly detrimental to soil fauna. Notably, increased soil salinity could override other factors that favor 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 guide preventive strategies (e.g., biodiversity conservation) and/or corrective measures (e.g., inclusion of specific species in restoration projects) to protect threatened ecosystems.

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