




Review

# Linking Nematode Communities and Soil Health under Climate Change

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**Abstract:** Soil health is intimately intertwined with ecosystem services. Climate change negatively impacts ecosystem functioning, by altering carbon and nitrogen biogeochemical cycles and shifting nutrient bioavailability, thus hampering food production and exacerbating biodiversity loss. Soil ecosystem services are provided by belowground biota, and as the most abundant metazoans on Earth, nematodes are key elements of soil food webs and reliable bioindicators of soil health. Here, we carry out a literature review from 2019, the year that the Intergovernmental Panel on Climate Change published a report relating and expressing serious concerns on the effects of climate change on the land degradation and sustainability of terrestrial ecosystems. We focus on documenting and discussing the composition of nematode communities contributing to improving soil health, and soil management practices to promote their presence and limit the effects of climate change on soils. By recognizing beneficial nematodes as plant-promoting agents, we could harness their potential to our benefit, catalyze decomposition services, improve plant performance, and increase carbon sequestration. This way, we will contribute to soil health and a well-balanced and well-managed system, making it possible to increase productivity, guarantee food security, and reduce the yield gap, with a limited human footprint on the environment.

**Keywords:** abiotic stress; beneficial nematodes; ecosystem services; food webs; functional ecology; soil health; soil microfauna



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## 1. Introduction

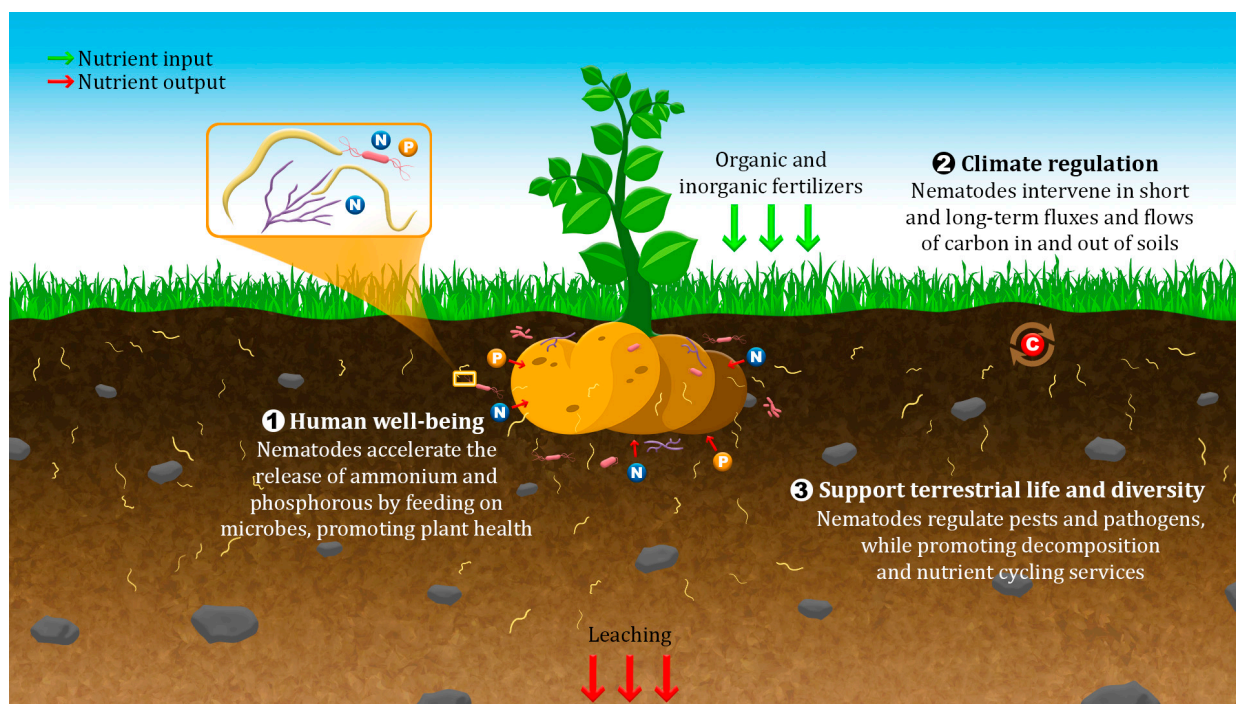
Soil is a complex system and a crucial component of sustainability [1]. Soil health is broadly defined as “the capacity of soil to function as a vital living system, within ecosystem and land-use boundaries, to sustain plant and animal productivity, maintain or enhance water and air quality, and promote plant and animal health” [2]. In other words, the concept highlights the ability of soil to perform important agricultural and ecological functions, including productivity, adaptability to management and inputs, and resilience against biotic and abiotic stressors. It must also exhibit robust resistance to degradation processes and the ability to rebound from disturbances due to its inherent resilience, defined by Holling as “a

measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables" [3,4]. Logically, soil health and ecosystem services are intimately intertwined. Ecosystem services encompass a wide range of benefits obtained from ecosystems, including (i) provisioning services (e.g., food and water), (ii) regulating services (e.g., natural disaster regulation, pest and pathogen control, and soil conservation), (iii) supporting services (e.g., nutrient cycling and pedogenesis), and (iv) cultural services (e.g., spiritual and recreational benefits) [5]. Soil is responsible for net primary production, it sustains plant and animal life, promotes water quality regulation, remediates pollution, intervenes in nutrient cycling, while providing physical stability and support [6,7]. Furthermore, it enhances the environment overall, by moderating climate at local, regional, and global scales [8]. In order to support sustainability, managing soil health must take into account that (i) improving multiple soil ecosystem services requires a multifunctional approach; (ii) enhancing one soil service can have favorable effects on some services but unfavorable outcomes on others; (iii) soil health management must ensure the long-term sustainability of soil services [9].

Climate change has a direct impact on the biological, chemical, and physical properties of soil, as it leads to shifts in temperature regimes and precipitation patterns [10,11]. Consequently, carbon (C), nitrogen (N), and hydrology cycles are likely to suffer the backlash [10], and the presence of multiple environmental stressors caused by human footprint were found to hamper soil ecosystem services across biomes [12]. Semiarid tropical regions of the world are particularly vulnerable, and with soils acting as important C reservoirs, a severe depletion of organic C will inevitably affect soil health [10]. Moreover, the decomposition of soil organic matter is thermosensitive [13,14], and climate change could lead to organic C-exhausted soils in response to altered C and N biogeochemical cycles and shifts in nutrient bioavailability, further exacerbating biodiversity loss [10].

Nematodes are part of the soil microfauna and represent approximately 80% of all multicellular animals of the terrestrial biosphere [6,15]. They are highly adaptable and successful animals, having colonized nearly all ecosystems on the planet [16–18]. According to their feeding habits, soil-dwelling nematodes can be assigned to one of five trophic groups: bacterivores, fungivores, herbivores, omnivores, and predators [19]. Nematode families and genera have been classified into a colonizer–persister scale (*c-p*), and given a rating from 1 to 5, indicative of their life strategy [20]. The *c-p* 1 group is made up of colonizers (*r*-strategists) like opportunistic bacterial feeders that rapidly increase in numbers under favorable conditions, exhibiting a short life cycle, high colonization ability, and tolerance to disturbance [20]. On the other hand, the *c-p* 5 group consists of persisters (*K*-strategists), such as some herbivores, omnivores, and predators, with a low reproduction rate, long life cycle, low colonization ability, and high sensitivity to disturbance [20]. Due to their rapid and taxon-specific response to environmental changes, nematodes are valuable bioindicators [21,22]. Nematofauna diversity is largely influenced by factors such as soil texture, soil moisture, and food availability [21]. However, the response of nematodes to environmental stress varies among trophic groups, with those having shorter generation times and/or high fecundity showing a positive response, while those with longer generation times and/or lower fecundity being more sensitive [23,24]. Free-living nematodes (bacterivores, fungivores, omnivores, and predators), widely referred to as beneficial nematodes, outnumber herbivores in terms of abundance and diversity, and they play critical roles in ecosystem functioning, occupying key ecological niches in belowground food webs, and are involved in C sequestration, energy transfer, and nutrient mineralization, increasing their availability to plants and, thus, improving soil fertility [25–28]. Soil nematodes directly or indirectly contribute to (i) human well-being, by driving key processes to food production; (ii) climate regulation, by intervening in the short and long-term fluxes and flows of C in and out of soils; and (iii) support terrestrial life and diversity, through processes like decomposition, nutrient cycling, and regulation of pests and pathogens (Figure 1) [29]. Healthy soils typically have a high abundance and diversity of free-living nematodes in complex food webs with long chains and feedback loops, and

a low proportion of herbivores [23,30,31]. Indeed, a nematode community analysis can provide invaluable information on the status of soils: (i) a high ratio of bacterial- to fungal-feeding nematodes indicates that organic matter is predominantly decomposed by bacteria and that rapid nutrient cycling is occurring; (ii) a predominance of fungivores indicates that nutrient cycling is relatively slow, as the decomposition channel is dominated by fungi; (iii) low population densities of omnivores and predators suggest disturbance, such as excessive fertilizer inputs, tillage, or the presence of pollutants; (iv) high numbers of omnivores and predators indicate that the system is biologically complex and resilient, and has some natural ability to suppress plant-parasitic nematodes and other soil-borne pathogens [32]. In agricultural systems, plant-parasitic nematodes are problematic, but in a broader ecological context, they are fundamental in shaping aboveground vegetation communities and contributors to plant performance in natural ecosystems by plant–soil feedbacks [33,34]. Upon feeding on their hosts, herbivorous nematodes alter root exudation patterns, and indirectly modify the rhizobiome (the microbial diversity attached to and influenced by roots), thus curbing nutrient availability to plants, especially of N and phosphorous (P), and contributing to plant community dynamics [30,35,36]. On the other hand, while the contributions of beneficial nematodes to plant performance remain largely unknown, they can have positive effects on plants by stimulating microbe-induced C sequestration, and keeping pests and pathogens at bay [37]. Nematodes are aquatic animals that require water to move, feed, and reproduce, and climate extremes are anticipated to shift the structure of nematode communities and their roles in ecosystems [38–40]. However, the impacts of climate change on nematode abundance and functional groups have not been consensual, displaying significant variation across different studies [41–45].



**Figure 1.** Illustrative representation of the main ecosystem services provided by soil-dwelling nematodes.

In this review, we analyze the recent literature from 2019, the year that the Intergovernmental Panel on Climate Change (IPCC) published their special report on climate change and land, relating and expressing serious concerns on the effects of climate change on the land degradation and sustainability of terrestrial ecosystems [46]. Here, we focus on documenting and discussing the composition and functions of nematode communities that contribute to enhance soil health, and soil management practices to promote their presence and improve the resilience of soils under climate change.

## 2. Nematode Community Dynamics under Climate Change

A demographic explosion is driving unprecedented food demand and pushing natural ecosystems to fragmentation. The effects of anthropogenic activities in natural systems are known to reduce aboveground biodiversity, hindering ecosystem services and, consequently, their contributions to human well-being [47], but data of such impacts on belowground taxa are scarce, perhaps because they are difficult to assess. Nevertheless, nematode community structure is a fast and reliable predictor of ecological disturbance, giving us insights into the status of the whole system.

### 2.1. Temperature

To comprehend the impact of elevated CO<sub>2</sub> concentrations and canopy warming interactions on soil nematodes, Wang et al. [48] set up an experiment in a rice paddy field. Nematode abundance benefited from an interaction between high CO<sub>2</sub> concentrations and canopy warming, whereas nematode diversity and soil health were negatively affected. Indeed, elevated CO<sub>2</sub> increased the relative abundance of herbivores and that of fungivores and omnivores–predators remained unaffected. However, warming altered the community composition of soil nematodes by reducing diversity and genera richness, which could hamper functional processes, with direct impacts on crop production and ecosystem health in future agriculture. A long-term experiment with five different gradients of artificial warming was conducted by Liu et al. [49] to study plant–soil mediated effects of rising temperatures on soil nematodes. The abundance of plant-parasitic nematodes was high at moderate warming, eventually subsiding as the temperature increased. Warming also caused a reduction in the abundance of bacterivores, but they ended up recovering over time and their dominant position in the nematode community remained unaffected, most likely due to an increase in organic matter in the soil and, consequently, bacteria. Fungivores, albeit less abundant, followed a similar trend under rising temperatures: their numbers initially dwindled, but increased gradually with warming over time, suggesting a relative tolerance to thermic stress in this alpine meadow system. Contrastingly, the omnivores–predators abundance was only slightly affected by warming. Ultimately, the variation in soil nematode density under increasing temperatures was mainly driven by the soil layer.

The soil nematode community structure seems to be particularly susceptible to warming, favoring some groups in detriment of others, but these negative effects can be limited by aboveground vegetation that counters them to some extent. Both parameters also affect vegetation, with an anticipated indirect effect on nematode communities [50], although these confounding effects are not assessed in this review. The main effects of increasing temperature on nematode communities are summarized in Table 1.

**Table 1.** Effect of increasing temperature on soil nematode communities.

Factor	Effects on Soil Nematodes	Reference
High temperature	Reduction in nematode diversity and genera richness	[48]
	Reduction in herbivores, with a short-term decrease in bacterivores and fungivores who recover over time, and relative tolerance of omnivores–predators	[49]

### 2.2. Water Stress

Precipitation changes can alter nematode community composition both spatially and temporally. Franco et al. [51] reported that higher precipitation during the growing season can promote top–down control of lower trophic nematode groups by predators, leading to overall reduced total nematode abundance. Temporal changes in precipitation patterns can affect nematode community composition, depending on mean annual precipitation, and hence are also modulated by spatial precipitation patterns. These effects can be particularly strong in mesic habitats, where nematodes were most abundant. In fact, nematode abundance has been suggested to follow the trend of increasing long-term mean annual precipitation from arid to mesic grasslands. Therefore, in climate change scenarios



of reduced water availability in mesic habitats, the expected reduced predation could result in the release of plant-parasitic nematodes, aggravating the negative effects of water scarcity on carbon sequestration and plant productivity. In a subsequent study, they addressed the question of how nematode herbivory affects the high allocation of nutrients to root biomass of a dominant shortgrass prairie grass expected under water stress [52]. Water availability was indeed correlated to the proportion of plant-parasitic nematodes and belowground biomass allocation, and this biotic interaction ultimately hampered water uptake, adding more pressure to already stressed plants. Later, they assessed the effects of precipitation on nematode genus diversity, community structure and metabolic footprint, across temporal and spatial scales, in arid, semiarid, and mesic grasslands, and found that free-living nematode diversity and evenness decreased over time with increasing annual precipitation in all systems [53]. The influence of precipitation changes on the nematode metabolic footprint (respiration, production, and biomass C) varied by location and was determined by significant spatial  $\times$  temporal precipitation interactions, and the diversity responses were only observed in mesic grasslands and not in arid and semiarid systems. To investigate the response of range-expanding plant species to extreme drought under two conditions (with live soil from their original range and with live soil from a new range), and how soil organisms are affected by these interactions, Yang et al. [54] performed an outdoor mesocosm experiment. When soils had been conditioned by congeneric native plants, summer drought was responsible for a reduction in total soil nematode abundance, with long-lasting effects that persisted even during higher water input. Likewise, soils conditioned by native plant species were found to dwindle the relative abundance of bacterivores and fungivores under water stress, and the relative abundance of predatory nematodes followed the same trend. Neither soil conditioning nor soil origin affected the relative abundance of plant-parasitic nematodes under water stress, but after a water input, soils recording previous periods of drought were found to harbor the highest relative abundance of herbivores. Therefore, soil conditioning under water stress was hypothesized to exert contrasting effects on soil nematode community composition over time. Using nematodes as bioindicators, Homet et al. [55] analyzed the impact of rainfall reduction on soil food webs of Mediterranean forests over time. Lower water input had large negative effects on nematode abundance, especially at lower trophic groups of the decomposition food web (bacterivores and fungivores), with consistent short and long-term impacts on community composition (residual increase in omnivores and decrease in fungivores) and soil health indicators (higher maturity and structure index, and lower prey:predator ratio), suggesting a high vulnerability of the soil food web to water scarcity.

Drought is a key limitation of soil nematode abundance, even in the short term, and has persistent effects. Nevertheless, the soil nematode community structure recovers gradually as precipitation increases, even though these positive effects are not straightforward, and water uptake by plants can further stress an already fragile system. The main effects of water stress on nematode communities are summarized in Table 2.

**Table 2.** Effects of water stress on soil nematode communities.

Factor(s)	Effects on Soil Nematodes	Reference
Long-term increase in mean annual precipitation	Decline in total nematode abundance due to predation pressure, and increase in nematode abundance	[51]
	High proportion of plant-parasitic nematodes	[52]
	Decrease in free-living nematode diversity and evenness	[53]
Water scarcity	Reduction in total nematode abundance, and decrease in relative abundance of bacterivores, fungivores, and predators; relative abundance of herbivores unaffected	[54]
	Lower bacterivore and fungivore abundance, marginal increase in omnivores and decrease in fungivores, higher maturity and structure index, and lower prey:predator ratio	[55]

### 2.3. Land Use

The land use intensity effects on soil nematode functional groups and indices were studied by Siebert et al. [56] during two consecutive years. Land use was responsible for complex shifts in the nematode community, whereas high temperatures induced weaker effects. Furthermore, high nematode densities were observed in association with altered climatic conditions and intensive land use, translating into higher numbers of opportunists and plant-parasitic nematodes. This underlines the importance of biological diversity and a structured soil nematode community to withstand environmental stress, by preserving soil food webs and crucial ecosystem functions. To determine the effects of three soil types (Stagnosol, Cambisol, and Chernozem) and three ecosystems (natural, semi-natural, and managed) on the structure of soil nematode communities and microbial diversity, Renčo et al. [57] assessed the biodiversity and soil trophic web structure in disturbed and undisturbed systems. Corroborating initial expectations, the results revealed that the biodiversity and C/N ratios were lower in cultivated soils, resulting in a reduction in both nematode and microbial abundance and diversity. Furthermore, most nematode (abundance of trophic groups, total abundance, and diversity) and microbial characteristics were enhanced in soils with a higher pH and C and N contents. The study further highlighted that soil was a stronger predictor of nematode and microbial community stability than ecosystem type. The impacts of land use conversion on soil biodiversity were gauged by Li et al. [58], at the taxonomic, functional, and phylogenetic levels. Overall,  $\alpha$ - and  $\beta$ -diversity were not found to differ between natural and agricultural systems, but both were susceptible to climate variables in natural habitats, contrastingly to agricultural systems. Indeed, land use conversion could affect soil taxa across a large spatial scale, but agronomic practices seem to limit the climatic constraints on belowground biodiversity. Moreover, the greater dissimilarity in the functional composition of nematode communities and higher similarity in phylogenetic composition in agroecosystems suggest asynchrony among different biodiversity facets. Nematode community dynamics in rainforests and monocultures was studied by Krashevska et al. [59]. Land use was not found to negatively affect the total abundance of soil-dwelling nematodes, but the rainforest nematode community differed from that of plantations: fungivores and other nematodes with short generation time increased in monocultures, whereas bacterivores, omnivores–predators, and plant-parasitic nematodes decreased. This suggests a higher pressure on nematodes in monocultures than in an undisturbed system. Likewise, the number of omnivores–predators dropped in banana monocultures with contrasting levels of disturbance, while tillage and manure increased the presence of enrichment opportunists (bacterivores and fungivores) [60]. Seeking to explore whether soil nematode composition could be used as a soil health predictor, Gao et al. [61] determined the soil nematode fauna associated with five contrasting ecosystems. Nematode abundance and diversity, as well as complexity of community structure and diversity-weighted abundance, were positively influenced by vegetation succession from bare land to secondary and old forests. Lower total nematode abundances of bacterivores, fungivores, and herbivores were recorded during the wet season in cultivated soils (eucalyptus plantation and litchi orchards) compared to natural ecosystems, albeit the lowest total abundances were reported in the bare land. Contrastingly, litchi orchards had the highest abundance of total nematodes and of each trophic group during the dry season. Taken together, these findings suggest that soil nematode communities across contrasting land use types are useful to compare soil health conditions in natural and managed ecosystems. The effects of livestock grazing on the soil food web and on ecosystem functioning (mineralization of C and N) were evaluated by Wang et al. [62], and they found that it decreased total microbial biomass and bacterial biomass, without negatively affecting fungal biomass. Similarly, declines in the abundance of bacterivores, herbivores and omnivores–predators resulted in a lower total nematode abundance, but no effects were observed on the abundance of fungivores. These results reveal that microbes were more susceptible to the soil environment (e.g., soil pH and bulk density) than nematodes, which were adversely affected by vegetation and soil substrate

(e.g., C and N contents). The impacts of land degradation on soil nematode communities were explored by Han et al. [63] through experiments on a temperate steppe with varying levels of degradation. Grassland degradation significantly decreased soil quality, with lower nematode trophic diversity and fungal to bacterial ratio in the degraded habitat. Microbial and nematode community composition dissimilarities were further exacerbated by changes in the soil quality index. In order to understand what determines nematode niche width, Vazquez et al. [64] investigated the impacts of intensive land use on the soil's biodiversity. Contrary to initial expectations, habitat generalists were equally abundant in all ecosystems, whereas highly specialized nematodes clearly dominated agricultural landscapes (grasslands, dairy, and arable farms) and were less abundant in soils with the lowest disturbance (shrubland–woodland ecosystems). Indeed, the highest richness and diversity were recorded in grasslands and dairy farms, whereas shrubland–woodland habitats had the lowest densities; this ultimately impacts the ecosystem services these nematodes contribute to. Possible links between soil nematode trophic groups and plant resource-use strategies were explored by Zhang et al. [65], who adopted a trait-based approach in an ex-arable field. Plants with acquisitive strategies (i.e., those that produce fine roots and acquire resources more rapidly) promoted nematode abundance, contrary to species with conservative strategies (i.e., those that invest more in their root systems, slowing down resource uptake). The results further suggested that plant resource-use strategies exerted bottom-up effects on nematode life strategies, and fewer opportunistic nematodes were found in the rhizosphere of acquisitive plants compared to conservative plants, most likely due to indirect effects acting through the food web: by modifying available resources via microbe-induced nutrient limitations, conservative plants promoted stronger top–down regulation. To quantify the global impact of agricultural practices on soil nematodes, Puissant et al. [66] performed a meta-analysis. Conventional practices drove a reduction in abundance, trophic structure, and taxonomic richness of nematode communities. On the other hand, agroecological practices promoted and enhanced the functional and taxonomic diversity of soil nematodes. Indeed, sustainable land use (organic agriculture and conservation agriculture) boosted the total abundance of nematodes and the absolute abundance of fungivores, herbivores, and omnivores–predators. At the trophic group level, agricultural practices had varying impacts on the nematode community: crop rotation caused a reduction in herbivore abundance, cover crops benefited omnivores–predators, while organic fertilization predominantly favored the presence of bacterial and fungal feeders. Overall, this meta-analysis showed that biocides, managing plant diversity and fertilization were more detrimental to nematode communities than tillage and herbicide application. Furthermore, nematode abundance and food web structure were reduced by monoculture and pesticide application, while copiotrophic nematodes (those with greater nutritional requirements) were favored. These findings suggest that the effects of agricultural practices are dependent on both the length of time since the last intervention, including fertilizer or pesticide application, as well as the duration of implementation for a specific practice. To determine the biogeographic patterns and ecological drivers of soil nematode  $\beta$ -diversity, Xiong et al. [67] conducted a field survey in arid and semi-arid regions of northern China. In grasslands, plant type and functional guilds were found to alter the  $\beta$ -diversity of nematodes, and that variation may stem from a combination of spatial distance and environmental filtering, with the latter having a greater impact in the typical steppe and desert regions, whereas geographical distance played a larger role in the desert steppe. Moreover, spatial turnover was identified as the primary process driving the total  $\beta$ -diversity of the nematode community along the transect. In a study aimed at examining the effects of vegetation restoration on primary production, soil food web structure, and C and N mineralization, Wang et al. [68] conducted a four-year revegetation trial on a natural system with varying degrees of degradation (low and high). Replanting vegetation resulted in a significant increase in the biomass of both plants and soil microbiota, as well as bacterial diversity and soil C and N mineralization rates. However, more discrete effects were reported for soil nematode functional groups and fungal diversity. In fact, stronger

effects of vegetation restoration on soil nematodes were observed under low degradation, suggesting that the degree of degradation should be taken into account in restoration efforts. To understand to what extent crop-tree thinning alters the soil nematode community, Yin et al. [69] investigated the drivers of change in the community composition and structure of soil nematodes across three coniferous plantations (pine, Chinese fir and cypress). The abundance of soil nematodes increased significantly due to crop-tree thinning, along with the relative abundance of herbivores in all systems. Furthermore, crop-tree thinning led to an increased proportion of enrichment (*c-p* 1) and general opportunists (*c-p* 2) in cypress plantations, but these effects were not as evident for pine trees. Notably, the effects of crop-tree thinning on soil nematofauna were related to modifications in microbial biomass N and understory vegetation diversity across plantations. The structure of soil nematode communities to contrasting levels of grass harvest frequencies (two, four, and six times annually) and shrubby legume densities (nought, low, and high), were investigated by Zhao et al. [70], over a 2-year period. Legume addition and legume density were considerable drivers of total nematode abundance, especially bacterivores, while improving metabolic activities of total nematodes, bacterivores, and omnivores–predators. However, the positive effects of legume addition on soil nematode communities subsided after increased frequency of grass harvesting, suggesting that frequent aboveground biomass export may alleviate the bottom-up control exerted by legumes on belowground taxa. Seeking to understand how agricultural practices modulate the beneficial activity of bacterivores, Trap et al. [71] carried out experiments in ecosystems under contrasting land use: agroforestry, monoculture, and rotation. The activity of beneficial nematodes on plant nutrition and growth was enhanced by plant diversity. Likewise, positive effects of nematodes on plant growth and function were associated with higher values in soil pH and cation contents.

Land use, with a particular emphasis on the conversion of conventional agriculture to agroecological practices, can have profound effects on soil nematode communities, highlighting the importance of above- and belowground biodiversity to withstand environmental stress, by preserving soil food web complexity and crucial ecosystem functions. Taken together, the above results suggest local anthropogenic effects can outweigh overall effects of climate change according to land-use type and intensity and may introduce severe confounding effects to predictive models of soil nematode community response to climate drivers. The main effects of land use on nematode communities are summarized in Table 3.

**Table 3.** Effects of different land uses on soil nematode communities.

Factor(s)	Effects on Soil Nematodes	Reference
Intensive land use	Increase in bacterivores, fungivores, and herbivores	[56]
Soil type	Lower biodiversity and C/N ratios in cultivated soils, resulting in a reduction in nematode abundance and diversity; increase in abundance of trophic groups, total abundance, and diversity of nematodes in soils with higher pH and C and N contents	[57]
Land use conversion	Negative impacts on soil taxa across a large spatial scale, but agronomic practices limit the climatic constraints on belowground biodiversity	[58]
Monoculture	Increase in fungivores, and decrease in bacterivores, herbivores, and omnivores–predators	[59]
Monoculture, tillage, and manure	Increase in bacterivores and fungivores, and decrease in omnivores–predators	[60]
Vegetation succession	Positive effect on nematode abundance, diversity, complexity of community structure, and diversity-weighted abundance	[61]
Livestock grazing	Decline in bacterivores, herbivores, and omnivores–predators abundance, lower total nematode abundance, and no detrimental effect on fungivore abundance	[62]
Land degradation	Lower nematode trophic diversity	[63]



Table 3. Cont.

Factor(s)	Effects on Soil Nematodes	Reference
Intensive land use	Generalists equally abundant in all ecosystems, with specialists dominating agricultural landscapes and less abundant in low disturbed soils; highest richness and diversity in grasslands and dairy farms, with low abundances in shrubland–woodland habitats	[64]
Plant resource-use strategies	Plants with acquisitive strategies promoted nematode abundance, but fewer opportunistic nematodes in the rhizosphere of acquisitive plants compared to conservative plants	[65]
Agricultural practices	(i) Conventional practices decrease abundance, trophic structure, and taxonomic richness of nematode communities; (ii) agroecological practices enhance the functional and taxonomic diversity of nematodes: total nematode abundance and absolute abundance of fungivores, herbivores, and omnivores–predators; reduction in herbivore abundance in crop rotation; increase in omnivores–predators in cover crops; increase in bacterivores and fungivores in organic fertilization; reduction in nematode abundance and food web structure in monoculture and pesticide application, while copiotrophic nematodes are favored	[66]
Spatial distance and environmental filtering	Plant type altered $\beta$ -diversity of nematodes; spatial turnover was the primary process driving total $\beta$ -diversity of the nematode community	[67]
Vegetation restoration with varying degrees of degradation	Strong effects on soil nematodes observed under low degradation	[68]
Crop-tree thinning	Increase in abundance of soil nematodes, along with the relative abundance of herbivores in all systems; increase in proportion of stress-tolerant enrichment and general opportunists	[69]
Harvest frequency and legume density	Legume addition and density were drivers of total nematode abundance, especially bacterivores, while improving metabolic activities of total nematodes, bacterivores, and omnivores–predators; positive effects of legume addition subsided after increased harvesting frequency	[70]
Agricultural practices	Plant diversity enhanced the activity of beneficial nematodes; positive effects of nematodes on plant growth and function associated with higher values in soil pH and cation contents	[71]

#### 2.4. Nutrient Enrichment

To investigate the impacts of N enrichment on soil biota and functions (C and N mineralization), Chen et al. [72] conducted a long-term N enrichment trial, in a semi-arid steppe on the Mongolian Plateau. N-enriched soils strongly reduced bacterial biomass, as well as abundance of soil biota and C mineralization rates, without negatively affecting fungal richness, suggesting that environmental tolerances for fungi are generally wider than for bacteria. Furthermore, plant removal, which decreased C and N mineralization rates, dwindled nematode taxon richness and abundance of bacterial- and plant-feeding nematodes, most likely resulting from declines in soil bacteria that rely on plant inputs for C and energy. Contrastingly, the abundance of fungal-feeders and omnivores–predators increased under the same conditions. On the other hand, Shaw et al. [73] hypothesized that long-term N fertilization would affect nematode community structure and maturity in a subalpine forest ecosystem, and they found that nematode abundance was greater in fertilized plots, while richness, diversity, and ecological maturity were lower. This enriched food web trend was mostly driven by opportunistic bacterivores and plant-parasitic nematodes. Worryingly, this shift in the nematode community persisted even after 19 years of treatments, and this can lead to significant ecological consequences. To explore how soil nematode communities fare in response to high N deposition, Liu et al. [74] set up a field trial by adding N through the canopy. Forest canopy retained 52% and 44% of N added at two concentration levels, with contrasting responses from the soil nematode community. Indeed, most nematode trophic groups and community diversity

decreased under understory addition of N compared to the canopy addition of N approach. This may be attributed to alterations in the composition of the nematode community and/or fine root biomass due to direct soil entry of high concentrations of N without the interception of the forest canopy. To investigate the influence of soil acidification on the effects exerted by nutrient enrichment on soil food webs and plant communities, a short-term N and P enrichment experiment was conducted by Xiao et al. [75]. N or P enrichment alone did not affect net primary productivity in either non-acidified or acidified soil, but their combination increased it in both cases. Most microbial groups in non-acidified soil showed decreased biomass in response to nutrient enrichment, which was exacerbated by their combined effect. However, this was not observed in acidified soil, and nematode variables were not affected by nutrient enrichment in either soil. Nutrient enrichment did alter plant and microbial community structure in non-acidified soil, but not in acidified soil, and there was no negative effect on the nematode community structure observed in either soil. These results show that nematodes are more tolerant than microorganisms and plants to short-term nutrient enrichment under soil acidification. Field trials were conducted by Wan et al. [76] to examine the longstanding effects of recurrent application of organic amendments and mineral fertilizers on the energetic structure of the nematode community. Most functional guilds were positively affected by organic amendments in terms of abundance, compared to mineral fertilizer treatments. Organic amendments enhanced the energy transfer among nematode communities, while also increasing the relative allocation of energy flux to bacterivores and fungivores and decreasing the relative allocation to herbivores. This study supports the idea that increased organic matter content promotes a diverse nematode community, while sustaining a high energy transfer and flow uniformity within the soil food web. This could be the baseline to explaining how diverse communities transfer more energy to perform ecosystem services. To determine how liming, P and zinc shape nematode community structure, Varga et al. [77] conducted pot experiments with hot pepper. An input of P significantly promoted the highest nematode diversity among treatments. Furthermore, a comparison of ecological indices revealed that the soil nematode community's diversity and maturity were reduced in the absence of liming, indicating negative impacts on soil health and ecosystem functions. Bacterivores and herbivores were the most abundant trophic groups across all treatments, and predators were the least common. Overall, liming did not significantly affect nematode biodiversity, but a P application significantly increased nematode genera in the soil.

The structure of nematode communities can be adversely affected by mineral fertilization, resulting in simplified soil food webs with fewer omnivores–predators and more herbivores and bacterivores, impairing ecosystem functions. On the other hand, organic amendments can increase nematode diversity and promote a higher energy transfer in the system. Although the above studies mainly report on crop nutrition management, they are informative of the nematode community response to nutrient quantities and balance in soils. Global change has been promoting the deposition of N and other nutrients to both agricultural and natural ecosystems, mostly accompanying urbanization. This, combined with the anticipated depletion of P in worldwide terrestrial ecosystems, may tip the balance of soil food webs and aggravate adverse conditions brought about by progressive soil degradation (including acidification) due to climate effects. The main effects of nutrient enrichment on nematode communities are summarized in Table 4.

**Table 4.** Effects of nutrient enrichment on soil nematode communities.

Factor(s)	Effects on Soil Nematodes	Reference
Long-term N enrichment	Plant removal dwindled nematode taxon richness and abundance of bacterivores and herbivores; the abundance of fungivores and omnivores–predators increased under the same conditions	[72]
Long-term N fertilization	Greater nematode abundance in fertilized plots, while richness, diversity, and ecological maturity were lower; enriched food web mostly driven by bacterivores and herbivores, with persisting effects overtime	[73]
High N deposition	Decrease in most nematode trophic groups and community diversity under understory addition of N compared to canopy addition of N	[74]
Short-term N and P enrichment under soil acidification	Nematode variables, including community structure, were largely unaffected by short-term nutrient enrichment under soil acidification	[75]
Long-term organic amendments and mineral fertilization	Positive effect on the abundance of most functional guilds by organic amendments, which enhanced the energy transfer among nematode communities, while increasing the relative allocation of energy flux to bacterivores and fungivores and decreasing the relative allocation to herbivores	[76]
Liming, P, and zinc inputs	P input significantly increased nematode diversity and genera; bacterivores and herbivores were the most abundant trophic groups, and predators the least common; nematode biodiversity was unaffected by liming, and nematode diversity and maturity were reduced in the absence of liming	[77]

### 2.5. Combined Stressors

Individual and interactive multifactorial effects of soil moisture, P addition, and aboveground vegetation on the soil nematode community structure were investigated by Olatunji et al. [78]. Plant type and water availability had a greater impact on soil nematode abundance and community composition than the combined effect of P and water input. Drought was detrimental to the total density of soil nematodes and functional guilds. Bacterivores, herbivores, and omnivores were significantly more abundant in soil with legumes than in their absence. This study found that the impact of drought on soil food web structure depends on the plant type, and that legumes can maintain the soil food web structure despite environmental changes. Seeking to study the co-occurrence and distribution of three common and dominant nematode species (bacterivores *Plectus murrayi* and *Scottinema lindsayae*, and omnivore *Eudorylaimus antarcticus*) in the McMurdo Dry Valleys (Antarctica), Caruso et al. [79] hypothesized that all three species co-occur randomly, regardless of abiotic factors in this extreme environment. The presence of *P. murrayi* significantly curbed the co-occurrence of *S. lindsayae*, most likely resulting from a negative biotic interaction between two bacterivores competing for the same resources in this hostile ecosystem, whereas no negative effects of *E. antarcticus* on *S. lindsayae* were observed. The study found a positive correlation between *S. lindsayae* and the gradient of microbial biomass and richness, and a negative correlation with the soil moisture gradient. Additionally, the microbial biomass gradient had a significant positive effect on *P. murrayi*, while *S. lindsayae* had a significant negative effect on it. The presence of the other two nematode species did not affect *E. antarcticus*, but its occurrence was positively correlated with microbial richness and negatively correlated with salinity and elevation gradients. These results clearly suggest a spatial segregation between *P. murrayi* and *S. lindsayae*, but the measured biotic and abiotic variables do not fully explain it. Furthermore, these models show that both species respond differently to abiotic factors: *S. lindsayae* is best adapted to survive in high salinity and low moisture environments, growing optimally at low temperatures, while *P. murrayi* thrives at higher temperatures and when there is significantly more soil moisture and lower salinity. To assess the weight of historical effects on soil fauna, Li et al. [80] tested the relative importance of climatic, soil, and historical

factors. Soil and historical predictors generally explained less variation in both diversity and composition compared to climate. In addition, a correlation between historical factors and nematode diversity and composition was found, but these factors were typically represented by their interaction with current climatic and soil factors within the studied sites, and their independent effect was deemed negligible. These findings suggest that current factors, particularly climate, are more influential than historical factors in shaping soil nematode diversity patterns on a broader scale. To characterize the soil nematode and microbial communities under four contrasting liming treatments, Neilson et al. [81] carried out a field trial. Both communities interacted with each other, but their structure was minimally impacted by liming. However, while environmental drivers are shared by both nematode and microbial communities in terms of composition, they explained less than a quarter of the variation in both communities. Notwithstanding, this study clearly demonstrated that this interaction was stronger in the presence of an abundant microbial community, in which omnivores and predators concurrently increased, thus curbing the pressure exerted by bacterivores, and implying that microbial community size can be used as a potential predictor of a nematode functional group. Several nematode community indicators were investigated by Xiong et al. [82] to determine their response to increasing aridity across a large spatial scale. As the environment became drier, there was a decline in both total and relative nematode abundance in each functional guild. Likewise, the taxonomic richness of both total nematode community and functional guilds was found to decrease due to moisture scarcity, with variations among feeding groups. At the dry end of the aridity gradient, the richness of bacterivores was higher than that of other feeding groups, while plant-parasitic nematodes declined steadily with increasing aridity. Contrastingly, the richness of fungal grazers and omnivores–predators remained relatively stable up to a certain point, before dropping steeply. Ultimately, the nonlinear responses of soil-dwelling nematodes to aridity may result in ecosystem functioning impairment, as nematodes act across different levels of the soil ecosystem. To test the interactive effects of extreme drought and fertilization on soil biota across seasons, Siebert et al. [83] hypothesized that fertilization would exacerbate drought effects through enhanced plant growth. Drought favored opportunistic nematode guilds (bacterivores and fungivores) and likely had detrimental effects on higher trophic levels, leading to simplified trophic structures of the nematode community altogether. Likewise, the nematode community was highly responsive to fertilization, resulting in a generalized decline in feeding activity (which may be explained by a drop in soil pH), but with a prominent increase in bacterivores and an equally significant drop in fungal feeders, indicating that nutrient enrichment had detrimental effects on soil fungi. Overall, global change drivers and their interaction negatively impacted soil invertebrate activity, whereas enhanced nutrient availability benefited microbial biomass. Microbial activity, however, was largely unaffected by these disturbances. This study could provide an insight into the bigger picture of the soil community buffering prospective global change effects to a certain extent. To better comprehend how soil taxa respond and potentially adapt to environmental factors (elevated CO<sub>2</sub>, elevated N, warming, and summer drought), Thakur et al. [84] performed a long-term and multi-factor experiment. At elevated N and ambient CO<sub>2</sub>, and ambient N and elevated CO<sub>2</sub>, nematode density increased. The combined effect of high CO<sub>2</sub> and temperature was the main cause of shifts in microbial biomass. To explore the impact of warming and precipitation on soil nematode communities, Zhang et al. [85] undertook a 10-year experiment in an Inner Mongolian desert steppe. Soil nematode abundance decreased significantly under artificial warming, with a significant decrease in the abundance of bacterivores and herbivores and having minor effects on the abundance of fungivores, but the nematode community diversity remained stable and their functions relatively unaffected over the course of the experiment. On the other hand, reduced precipitation significantly decreased soil nematode abundance, especially of bacterial feeders and omnivores–predators, albeit fungivores and plant-parasitic nematodes were relatively insensitive to water stress. Conversely, both soil nematode abundance and community diversity increased significantly with water



availability, leading to an increased food web connectivity and food chain length. To evaluate how ecological and edaphic factors influence soil nematode diversity and structure across five ecosystems, Nisa et al. [86] collected soil samples across the Kashmir valley. Altitudinal gradients revealed a reduced nematode abundance and diversity as the altitude increased. Likewise, nematode diversity was highest in forest soil and decreased with increasing elevation. In all soil patches, bacterivores were consistently the dominant group. Nematode diversity was mostly influenced by temperature and moisture, with the highest diversity observed at temperatures above 21 °C and 30% humidity. Additionally, nematode abundance decreased with increasing soil acidity, while soil nutrient levels (N and P) had a negative effect on nematode richness across ecosystems. Nematode diversity and richness were highest at abundant levels of nutrients, but decreased as nutrient availability declined. To determine how a temperate forest's soil nematode community respond to N deposition and/or reduced water availability, Wang et al. [87] carried out a 10-year manipulative experiment by applying N to the soil, while reducing water availability. The soil nematode community composition significantly changed in response to N deposition and/or water availability in a temperate forest. In fact, the standalone addition of N and in combination with reduced water input negatively impacted the soil nematode community by significantly reducing both abundance and diversity. On the other hand, precipitation reduction only had a significant effect on the abundance parameter. Indeed, the effects of N addition and reduced water input on soil nematode communities were synergistic at higher trophic levels. However, the sole addition of N was more detrimental to the soil nematode community. To evaluate the effect of returning agricultural residues on the soil food web, Li et al. [88] undertook a 16-year field experiment using six fertilization practices. Applying agricultural residues promoted and increased belowground microbial biomass and diversity, soil co-occurrence network complexity, and ecosystem multifunctionality compared to using chemical fertilizers alone.

In general, the greater the number of disturbances, whether directly or indirectly caused by human activities, the longer the recovery time for the system and the greater the impact on soil nematode communities, which compromises their benefits to humankind. Although manipulative studies in experimental units research has been elucidating the impacts of each independent factor individually, observational studies in actual ecosystems suggest strong interactive effects among them. It is therefore anticipated that a large sampling effort at appropriate scales, combined with an in-depth local and remote-sensing characterization of sampled ecosystems can provide key knowledge that can be translated into management and policies for climate change adaptation and mitigation. The combined effect of multiple stressors on nematode communities is summarized in Table 5.

**Table 5.** Effects of multiple factors on soil nematode communities.

Factors	Effects on Soil Nematodes	Reference
Soil moisture, P addition, and aboveground vegetation	Plant type and water availability had a greater impact on nematode abundance and community composition; drought was detrimental to the total density of nematodes and functional guilds; bacterivores, herbivores, and omnivores were significantly more abundant in soils with legumes	[78]
Biotic (microbial biomass and competition) and abiotic variables (moisture, salinity, and elevation)	Spatial segregation between two competing bacterivore species, with contrasting responses to abiotic factors: one best adapted to high salinity, lower temperatures, and low moisture environments, while the other thrives at higher temperatures, higher soil moisture, and lower salinity	[79]
Climatic, soil, and historical factors	Current factors, particularly climate, are more influential than historical factors in shaping nematode diversity patterns on a broader scale	[80]

Table 5. Cont.

Factors	Effects on Soil Nematodes	Reference
Liming treatments	Interacting nematode and microbial communities minimally impacted by liming, with an increase in omnivores and predators, who keep bacterivores under control; stronger interaction in the presence of an abundant microbial community	[81]
Increasing aridity across a large spatial scale	Decline in total and relative nematode abundance of each functional guild under increasing aridity; taxonomic richness of total nematode community and functional guilds decreased under moisture scarcity; at the dry end of the aridity gradient, richness of bacterivores was higher, while herbivores declined steadily; richness of fungivores and omnivores–predators remained relatively stable up to a certain point, before dropping steeply	[82]
Drought and fertilization	Drought favored bacterivores and fungivores, and likely had detrimental effects on higher trophic levels; fertilization caused a prominent increase in bacterivores and an equally significant drop in fungivores	[83]
Elevated CO <sub>2</sub> and N, warming, and drought	Increase in nematode density at elevated N and ambient CO <sub>2</sub> , and ambient N and elevated CO <sub>2</sub>	[84]
Warming and precipitation	Decrease in nematode abundance, especially of bacterivores and herbivores (with minor effects on fungivores), under artificial warming, but the nematode community diversity and functions remained stable; decrease in nematode abundance, especially of bacterivores and omnivores–predators, under reduced precipitation, with fungivores and herbivores relatively insensitive to water stress; increase in nematode abundance and community diversity with water availability	[85]
Ecological and edaphic factors	Reduced nematode abundance and diversity with increasing altitude, with bacterivores consistently the dominant group; nematode diversity was mostly influenced by temperature and moisture; decrease in nematode abundance with increasing soil acidity; nematode diversity and richness were directly proportional to nutrient (N and P) levels	[86]
N deposition under reduced water availability	Reduced nematode abundance and diversity under N addition and reduced water input; synergistic effects of N addition and reduced water input on soil nematode communities at higher trophic levels; sole addition of N was more detrimental to the nematode community	[87]
Returning agricultural residues	Nematode diversity was lower in treatments with conventional chemical NPK fertilizers; positive correlation between omnivore–predator abundance and ecosystem multifunctionality and soil fertility	[88]

### 3. Nematode Contributions to Soil Health

The adaptability of nematodes, as evidenced by frequent shifts in habitat transition, along with their ability to withstand environmental changes, has significant implications for soil functions on a global scale. Indeed, the ability of nematode functional guilds to perform ecosystem services depends on the soil condition [25] that can be measured according to their metabolic footprints [89]. However, land use (including soil properties), agricultural management practices, and climate all contribute to shaping nematode communities and, thus, affect nematode contributions to soil health through modification of their abundance, functional groups, and metabolic footprints, leading to shifts in ecosystem processes and services [90–92]. According to the most comprehensive dataset on abundance and functional group composition reported to date,  $4.40 \pm 0.643 \times 10^{20}$  nematodes are estimated to inhabit the topsoil across the globe [28,93]. Among these,  $1.92 \pm 0.208 \times 10^{20}$  are bacterivores,  $1.25 \pm 0.114 \times 10^{20}$  herbivores,  $0.64 \pm 0.065 \times 10^{20}$  fungivores,  $0.39 \pm 0.046 \times 10^{20}$  omnivores, and  $0.20 \pm 0.031 \times 10^{20}$  predators, amounting to an estimated biomass of 0.3 gigatonnes (Gt) and representing 82% of the total human biomass on the planet. Nematodes are especially abundant in regions of the world that are more susceptible to the detrimental effects of climate change, like boreal forests and

tundra. During the growing season, soil-dwelling nematodes may account for a C turnover of 0.14 Gt C per month, and although these are approximations of their metabolic footprint, this is strong evidence that nematodes are major players in soil C sequestration. Furthermore, they are direct intervenors in ecosystem services such as litter decomposition, nutrient cycling, and plant nutrient uptake. Indeed, understanding the susceptibilities and ecological preferences of soil nematodes can help predict changes in ecosystem services. To determine which factors best explain a soil health trait, Martin et al. [31] explored the incorporation of nematode communities in the assessment of belowground biota by using an exploratory factor analysis of permanganate oxidizable C, soil protein, and mineralizable C, based on data from two longstanding experiments across many different fields. Fungivores were found to be highly integrated with soil biological health indicators of permanganate oxidizable C and acid phosphatase, suggesting that this functional guild may be essential for supplying essential ecosystem services, especially C cycling and P mineralization. To determine the metabolic footprint and soil food web complexity across two ecosystems in Kenya, Karuri [94] collected soil samples and assessed the nematode community structure. Nematode functional group abundance differed between the two systems, with tea fields recording a significantly higher number of *c-p* 2 nematodes while the *c-p* 3 category was greater in the forest. This resulted in a greater predator footprint in the tropical forest, possibly contributing to a slightly more structured state as indicated by the functional metabolic footprint. Overall, the tropical forest had a higher abundance of nematode genera compared to the tea field, but the latter yielded a high density of *c-p* 2 nematodes (mainly bacterivores and fungivores) that are best suited to survive in unfavorable conditions. This study underlines that the conversion of this natural ecosystem to tea fields affected the nematode community structure and compromised the food web complexity, with a reduced predator footprint and increased herbivory disservice. In an attempt to shed light on how microbe-feeding nematodes impact plant performance in low P soils, Jiang et al. [95] designed a series of experiments in natural and sterilized soils with wheat. The presence of nematodes enriched bacterial community structure for certain groups, while also strengthening microbial connectance. Phosphate-solubilizing bacteria facilitated P cycling and were responsible for these changes in microbiome structure, but this enhancement varied according to nematode feeding behavior: nematodes that had weaker feeding intensity were found to support a greater abundance of phosphate-solubilizing bacteria and lead to better plant performance in comparison to nematodes with greater feeding intensity. Nevertheless, this work provides insight into how soil nematodes contribute to shaping bacterial communities and increasing P bioavailability, by interacting with phosphate-solubilizing bacteria, thus enhancing plant performance and providing key ecosystem services. Likewise, Zheng et al. [96] conducted a 7-year field experiment to understand how nematode predation influences P availability and cycling. The addition of nematodes, along with chemical and organic fertilizers, led to a significant improvement in the nutrient availability in the rhizosphere. This increase in N availability suggests that nematode predation may have caused shifts in C/N ratios. Nematode feeding on specific microbial taxa induced changes in the overall community structure. On the whole, these results highlight the importance of nematode predation in shaping the rhizosphere microbiome community and inducing microbially mediated mechanisms of competitive interaction, by enhancing P availability in the rhizosphere.

A stable and diverse soil nematode community secures efficient decomposition, leading to more nutrient mineralization that readily become available to plants, thus reducing the need for fertilizer application. Moreover, a natural regulation of pests and diseases performed by soil nematodes will reduce our dependence on pesticides. Ultimately, with reduced farmer intervention and corresponding anthropogenic impact, systems will be less disturbed and soils healthier.

#### 4. How Nematodes Promote Soil Resilience

As highly adaptable animals, with diverse roles in ecosystem functioning, the physiological and life history traits of nematodes make them less susceptible to environmental changes compared to larger fauna higher-up in the food web. Indeed, these characteristics could prove useful for the resistance and resilience of soils to natural and anthropogenic changes.

To better comprehend the role of bacterivores in maintaining functional stability of ecosystems under disturbance, Chen et al. [97] studied their contributions to promoting soil resistance and resilience under copper and heat stress. The relative shifts in two dominant bacterivore genera, *Acrobeloides* and *Protorhabditis*, responded differently to disturbance. *Protorhabditis* exhibited greater resistance and resilience to copper stress compared to *Acrobeloides*, while both genera displayed higher resilience only by the end of the experiment under heat stress. Indeed, bacterivores showed a positive effect on soil resilience under thermal stress starting at 28 days. The increase in relative abundance of bacterivores did not significantly affect soil resistance in terms of microbiota but it improved soil resilience to copper stress. The differences in responses of soil function to disturbance highlight the role of bacteria-feeding nematodes in promoting ecosystem stability under stress. To determine the effects of soil properties, rainfall, and temperature on soil nematodes, da Silva et al. [98] analyzed the changes in nematode community structure under contrasting types of land use in a seasonally dry tropical forest in Brazil. Nematofauna composition in the secondary forest differed in abundance and richness compared to agricultural systems, being expectedly higher in the former and lower in the latter, with bacterivores and omnivore–predators more susceptible to the type of land use. The variation in taxonomic composition among the studied sites was strongly related to soil properties, monthly mean rainfall, and temperature, which accounted for 65.42% of the total variation. These results further indicate that anthropogenic activities, expressed by the conversion of native vegetation to cropping systems, which modify soil characteristics, as well as climate variables, negatively affect the structure and composition of nematode communities. Nevertheless, changes in nematode community composition and structure can be reversed by allowing the fields to undergo secondary forest regeneration after abandonment. Seeking to identify the major ecological predictors of soil invertebrate diversity, Bastida et al. [99] surveyed 83 locations in six continents, from polar to arid climates, to study three soil invertebrates: nematodes, arachnids, and rotifers. Different ecosystem types such as forest, grasslands, and shrublands were included in the survey and nematodes were the most abundant, accounting for 43% of all taxa surveyed. Aridity was detrimental to the diversity of nematodes, whereas forest, plant richness, and annual net primary productivity were positively correlated. These findings exposed potential vulnerabilities of soil invertebrates to climate change in locations where hotter temperatures may occur in the future. Moreover, deforestation processes and increase in aridity may reduce nematode diversity, providing evidence of the importance of vegetation and climate for the diversity of soil invertebrates. Considering an increasing likelihood of extreme climatic events, Majdi et al. [100] exposed five species of free-living bacterivorous nematodes to a wide range of temperatures under controlled conditions, and their population growth rates and body-size distributions were measured. Body size at maturity was inversely proportional to temperature, mature females were laying a smaller number of eggs at higher temperatures, and a prevalence of early juvenile stages resulted in reduced body-mass structure with increasing temperature. Additionally, closely related species like *Plectus acuminatus* and *P. cf. velox* had very different thermal tolerance ranges, with the population growth of most tested species declining between 25 and 30 °C, and *A. nanus* exhibiting the broadest thermal tolerance range. This study demonstrated how thermic stress can induce changes in the growth and size–structure of bacterivores. To investigate the community-weighted mean body mass of soil nematodes, Andriuzzi et al. [101] studied the role of water availability in the body size of these invertebrates across a gradient of precipitation in North American grasslands, ranging from arid to semiarid and mesic conditions. An increase in nematode community-weighted mean mass from



arid to mesic conditions was observed, but no effects were reported at the arid site. When grouping community-weighted mean mass by feeding habits, only plant-parasitic nematodes showed a positive response to water input in semiarid and mesic conditions. This suggests that aridity acts as a buffer against large-bodied nematodes, limiting community body size shifts in response to extreme events, either drought or rainfall. Aiming to study the latitudinal variation in soil nematode communities under climate warming-related range-expanding and native plants, Wilschut et al. [102] showed that the composition of soil nematode communities changes across a latitudinal gradient, but not their richness or abundance, with plant species identity (both range-expanding and native plant species) being the strongest predictor of this shift. These findings further indicate that this variation is less dependent on soil characteristics, such as pH and soil moisture. In addition, plant species that expand their range due to climate warming may experience advantages by being free from nematode herbivory in their new habitat. A plant removal experiment was set up by Wang et al. [103] to better understand how dominant vegetation changes impact nematode assemblages. Edaphic properties, especially soil C and N content, were the primary drivers of nematode community structure and community-weighted mean biomass, with no observable short-term effects resulting from vegetation removal. However, long-term effects on nematode assemblages are expectable due to nutrient flow mediated by shifts in vegetation composition. To characterize and explore the relationship between soil biota and plant diversity and productivity, Bennett et al. [104] carried out a long-term experiment. Plant species richness had a positive effect on fungi, including increased arbuscular mycorrhizal fungi, while reducing plant-parasitic nematodes. Overall, soil biota resistance to disturbance increased with plant diversity, highlighting the importance of plant species richness for belowground communities. To evaluate the impacts of various measures of trophic diversity, climate, and soil environmental factors across three spatial scales, Wu et al. [105] conducted a field survey on the stability of ecosystems on the Mongolian Plateau. Soil biota diversity, including  $\alpha$ - and  $\beta$ -diversity, positively contributed to ecosystem stability, with soil nematode diversity and trophic groups associated with higher ecosystem stability. The relatively low abundance of herbivores may have contributed to enhanced plant performance by increasing root exudation, which stimulated microbial activity and nutrient availability. The positive association of soil biota diversity with ecosystem stability was similar to that of plant diversity in some cases. Similarly, an increase in the abundance of higher trophic levels such as omnivores–predators and microbial-feeding nematodes may have resulted in improved nutrient transfer to plants, leading to enhanced plant productivity and maintaining ecosystem stability through top–down effects.

Severe anthropogenic impacts often lead to simplified soil food webs, with limited top–down control by omnivores–predators, ultimately compromising ecosystem functioning and impairing their natural ability to mitigate the effects of climate change. It is therefore crucial to restore the complexity of soil food webs to enhance soil resilience to climate change.

## 5. Future Prospects

In decades to come, artificial intelligence and other digital technologies will surely be part of the solution to address some of the environmental challenges we face, but they also bring along new problems due to the physical infrastructures they require, with an associated environmental footprint that is often overlooked [106,107].

Some of the major hurdles that modern society faces are land use conversion and land use intensity, which significantly affect soil biodiversity and functions. Nevertheless, nematode community structure can be used as a bioindicator and provide insights on the overall soil health, and sustainable agroecological practices are a good way to promote their presence in degraded soils. Indeed, as key contributors to soil quality, a diverse community of beneficial nematodes can help with soil remediation and ecosystem functioning restoration, by enhancing soil organic C, increasing decomposition services, and keeping pests and pathogens under control.

On the one hand, conventional practices have a swift impact on the selection of plant-parasitic nematodes, and it is crucial to reduce nematode herbivory in agroecosystems. However, managing plant-parasitic nematodes under global change is, in itself, challenging. As polyphagous organisms, natural selection will most likely push herbivorous nematodes to adapt to new conditions, so current management options may not suffice [108]. Instead, we should focus on reducing crop loss and enhancing ecosystem services, both of which will work in our favor, and implement adaptive management strategies against plant-parasitic nematodes, to keep them below damaging thresholds [109]. On the other hand, conservation agriculture and organic farming can improve the abundance and biomass of soil taxa, while stimulating the activity of beneficial nematodes and positively shifting the structure of the soil food web [110]. Sustainably managing biodiversity to provide essential services can offer significant benefits to producers while minimizing our environmental impact. To achieve this, it is important to promote nematode decomposition services, which will reduce our dependence on mineral fertilizers. Mineral fertilizers have been used extensively due to their rather direct availability to plants, but they are not adequate substrates for decomposition food chains in the soil food web. The addition of organic matter, combined with reduced tillage so as to avoid disturbance to the soil food web, can provide a large number of heterogeneous resources to decomposers, thus sustaining longer, more complex food chains, that increase the self-regulation and stability of the soil food web [47,111]. The increased food web structure thus obtained is thought to enhance the natural regulation of soilborne pests and diseases, including that of plant-parasitic nematodes, thus supplying an important regulation ecosystem service to agroecosystems, and reducing the dependence on chemical pesticides [112]. Moreover, through their regulatory role in the decomposer community, bacterial- and fungal-feeding nematodes have the capacity to increase resource partitioning, substrate-use efficiency, and nutrient mineralization by bacteria and fungi, thus contributing to plant nutrition whilst promoting C sequestration [113]. Finally, increasing crop diversity, either in space (intercropping, polycropping) or in time (rotation) may be able to dilute herbivory and antagonism by specialist organisms—a well-described soil-feedback mechanism that leads to overyielding or increased plant productivity [114]. The shift in the paradigm of agricultural management brought about by agroecology, with a holistic view that comprehends interactions among agroecosystem components, has a sound scientific basis and, in their sixth and latest report, the IPCC recommends its implementation with a high confidence that it can contribute to resilience and climate change mitigation [115]. However, in opposition to the effects and mechanisms of fertilizer and pesticide use that have been well documented over recent decades, the effects of agroecological practices such as organic matter addition, low tillage, and increasing crop diversity lack research in real agroecosystems, to ensure they achieve positive outcomes in a wide range of agroecosystem types.

Lastly, in order to tackle greenhouse gas emissions and increase resilience to climate change, it is imperative to adopt sustainable agroecological practices that are plant beneficial, thus increasing the link between soil biodiversity and ecosystem functions, and enhancing trophic interactions that bolster the stability of soils and their resilience to climate extremes [116,117]. Likewise, by recognizing free-living nematodes as plant-promoting agents, we could harness their potential to our benefit by promoting their presence, thus catalyzing decomposition services, while improving plant performance and increasing soil C sequestration. By promoting diverse nematode communities, we will be contributing to soil health, and by achieving a well-balanced and well-managed system, it is possible to increase productivity, guarantee food security, and reduce the yield gap, with a limited human footprint on the environment.

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