Nematode Communities and Soil Health under Climate Change

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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.

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

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][17][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][26][27][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][39][40]. However, the impacts of climate change on nematode abundance and functional groups have not been consensual, displaying significant variation across different studies [41][42][43][44][45].

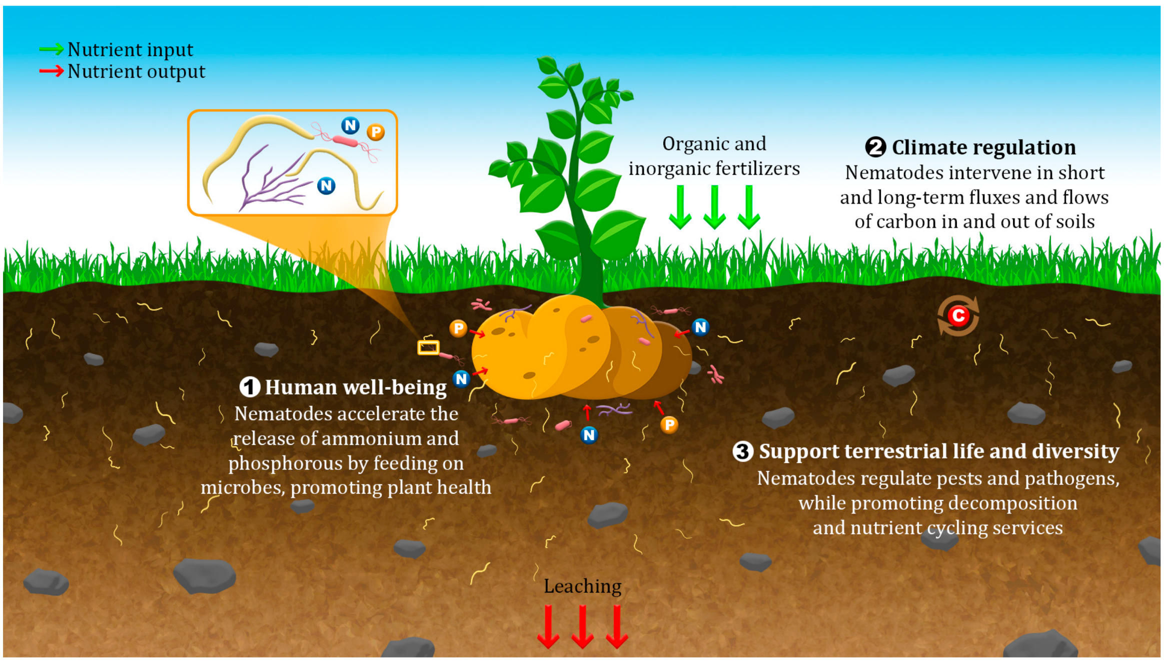

Figure 1. Illustrative representation of the main ecosystem services provided by soil-dwelling nematodes.

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 [46], 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

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 [47], although these confounding effects are not assessed here. 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

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	[50]
	High proportion of plant-parasitic nematodes	[51]
	Decrease in free-living nematode diversity and evenness	[52]
Water scarcity	Reduction in total nematode abundance, and decrease in relative abundance of bacterivores, fungivores, and predators; relative abundance of herbivores unaffected	[53]
	Lower bacterivore and fungivore abundance, marginal increase in omnivores and decrease in fungivores, higher maturity and structure index, and lower prey:predator ratio	[54]

2.3. Land Use

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	[55]
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	[56]
Land use conversion	Negative impacts on soil taxa across a large spatial scale, but agronomic practices limit the climatic constraints on belowground biodiversity	[57]
Monoculture	Increase in fungivores, and decrease in bacterivores, herbivores, and omnivores–predators	[58]
Monoculture, tillage, and manure	Increase in bacterivores and fungivores, and decrease in omnivores–predators	[59]
Vegetation succession	Positive effect on nematode abundance, diversity, complexity of community structure, and diversity-weighted abundance	[60]
Livestock grazing	Decline in bacterivores, herbivores, and omnivores–predators abundance, lower total nematode abundance, and no detrimental effect on fungivore abundance	[61]
Land degradation	Lower nematode trophic diversity	[62]
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	[63]
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	[64]
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	[65]

Factor(s)	Effects on Soil Nematodes	Reference
Spatial distance and environmental filtering	Plant type altered β-diversity of nematodes; spatial turnover was the primary process driving total β-diversity of the nematode community	[66]
Vegetation restoration with varying degrees of degradation	Strong effects on soil nematodes observed under low degradation	[67]
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	[68]
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	[69]
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	[70]

2.4. Nutrient Enrichment

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	[71]
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	[72]
High N deposition	Decrease in most nematode trophic groups and community diversity under understory addition of N compared to canopy addition of N	[73]

Factor(s)	Effects on Soil Nematodes	Reference
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	[74]
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	[75]
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	[76]

2.5. Combined Stressors

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	[77]
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	[78]

Factors	Effects on Soil Nematodes	Reference
Climatic, soil, and historical factors	Current factors, particularly climate, are more influential than historical factors in shaping nematode diversity patterns on a broader scale	[79]
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	[80]
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	[81]
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	[82]
Elevated CO_2 and N, warming, and drought	Increase in nematode density at elevated N and ambient CO_2, and ambient N and elevated CO_2	[83]
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	[84]
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	[85]
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	[86]
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	[87]

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 [88]. 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 [89][90][91]. 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][92]. 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 [93] 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. [94] 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. [95] 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. [96] 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. [97] 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. [98] 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. [99] 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. [100] 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. [101] 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. [102] 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. [103] 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. [104] conducted a field survey on the stability of ecosystems on the Mongolian Plateau. Soil biota diversity, including α-and β-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.

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