



# DIVERSITY AND ECOLOGICAL IMPACT OF PHYTONEMATODES ASSOCIATED WITH CITRUS PLANTS: A COMPREHENSIVE REVIEW

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## ABSTRACT

In order to analyze the functional diversity of soil nematodes, it is necessary to possess a comprehensive understanding of the relationship between biodiversity and ecosystem functioning in both natural and managed terrestrial ecosystems. This review delves into the primary external variables that influence the stability of soil nematode diversity in agricultural production, exploring key approaches to understanding its impact and value. The function of nematode trophic communities is in-depth investigated, with a particular emphasis on two intensively cultivated crops: lime and lemon plants, which represent tropical/subtropical climates. The review underscores the complexity of nematode network analysis for the management of multitrophic interactions and ecosystem restoration during the study period from May 2023 to June 2024, arguing that an interdisciplinary approach is required. The explanation of community shifts is contingent upon an understanding of the evolutionary basis of nematode diversity and its responses to environmental changes at the field level. By combining evolutionary biology, population genetics, and ecology, it is possible to quantify the contribution of nematode fauna to critical soil functions, including carbon transformation, nutrient cycling, insect control, and disease transmission. DNA-based methodologies, in conjunction with key characteristics of nematode diversity, such as trophic groups, life history traits, body size variability, and taxa identities, are essential for the identification of nematode soil ecosystem relationships. In order to establish locally adapted and sustainable management practices, it is imperative to conduct additional experimental studies that focus on nature-based and ecosystem-based solutions.

**Keywords-** *Soil Nematodes; Functional Diversity; Crop Production; Ecosystem Functioning; Biodiversity*

## I. INTRODUCTION

Biological diversity forms the foundation of ecosystem functions and services. However, this diversity faces significant challenges due to human-induced drivers such as climate change, habitat destruction, invasive species, overexploitation, and pollution (Zhang B. et al., 2018). These factors have collectively led to a drastic decline in biodiversity and the degradation of ecosystem services. It is estimated that around 60% of global ecosystem services are either degraded or being used unsustainably (Rawat et al., 2022). Furthermore, more than 75% of Earth's ice-free

land has undergone alterations due to human habitation and land-use changes, highlighting the substantial impact of anthropogenic activities on natural ecosystems (Zhou & Gu, 2024). The conversion of complex natural habitats into simplified agricultural systems, such as croplands, pastures, and permanent plantations, has exacerbated biodiversity loss, particularly in soil ecosystems (Kremen & Merenlender, 2018). Such transformations are especially pronounced in biodiverse but economically poor regions, where agricultural intensification often comes at the expense of ecological integrity (Johns et al., 2013). Conventional agricultural practices characterized

by excessive tillage, inadequate residue management, and overuse of fertilizers and pesticides have contributed significantly to soil degradation, habitat changes, and biodiversity losses (Powelson et al., 2011). Despite these challenges, there is limited knowledge about the impacts of these changes on soil biodiversity, including species loss, community composition shifts, and the associated effects on ecosystem processes such as nutrient cycling and decomposition (Swift et al., 1998).

Nematodes, one of the largest and most diverse phyla in the animal kingdom, play a critical role in soil ecosystems (Admasu Hailu & Admasu Hailu, 2019). These microscopic organisms exhibit remarkable genetic diversity and phenotypic plasticity, enabling them to thrive in a wide range of habitats (Zoubi et al., 2022). In terrestrial ecosystems, nematodes are the most abundant multicellular organisms, often inhabiting the water film around soil aggregates (Coleman et al., 2024). They play a pivotal role in soil food webs, interacting with other soil organisms at various trophic levels (Scheu, 2002). While most nematodes are free-living and contribute to soil health, a subset known as plant-parasitic nematodes (PPNs) spends a significant portion of its life cycle within plant roots, often causing substantial damage to crops (Omran et al., 2023). In the context of citrus plants, particularly lime and lemon, nematodes pose a significant threat to agricultural productivity (Timmer et al., 2003). Citrus plants are economically important crops cultivated globally, and they are highly susceptible to nematode infestations (Tennant et al., n.d.). The most common PPNs associated with citrus plants include species from the genera *Meloidogyne* (root-knot nematodes), *Tylenchulus* (citrus nematodes), and *Pratylenchus* (lesion nematodes) (Abd-Elgawad, 2020). These nematodes not only impair root function but also predispose plants to secondary infections, ultimately reducing yield and fruit quality (Phani et al., 2021).

The ecological influence of nematodes is not limited to their nature as parasites. They are essential to the processes of the soil ecosystem, as they affect the dynamics of microbial communities, the decomposition of organic matter, and the cycling of nutrients (Akhtar & Malik, 2000). The ecological functions, spatial distribution, and community assembly patterns of nematodes are all reflected in their functional diversity, which is particularly noteworthy (Nielsen et al., 2014). New insights into nematode biodiversity and their functional functions in various ecosystems have been provided by recent advancements in molecular techniques, such as next-generation sequencing (NGS) (Ahmed et al., 2016). These instruments have been essential in the identification of nematode species, the comprehension of their distribution patterns, and the

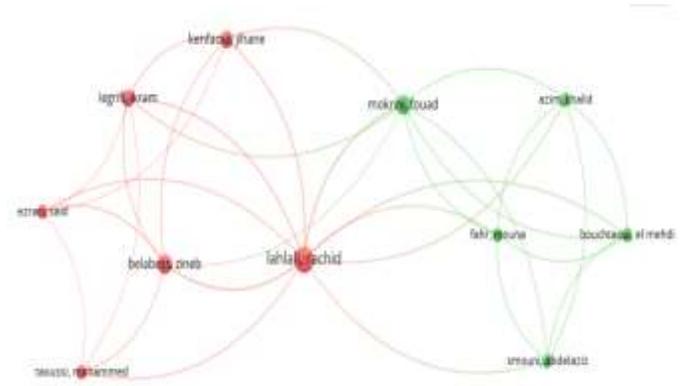
deciphering of their interactions within soil ecosystems (Ferris et al., n.d.). Nematode diversity and community structure are substantially affected by agricultural practices, particularly those implemented in citrus plantations (Porazinska et al., 1999). The transition from natural ecosystems to agricultural landscapes frequently results in a decrease in the functional diversity of nematodes. Intensive agricultural practices, including monoculture, excessive pesticide use, and diminished organic matter inputs, have a detrimental impact on nematode communities (Lazarova et al., 2021). These practices not only diminish the plethora of beneficial nematodes but also establish conditions that encourage the proliferation of PPNs (Karuri, 2022). As a result, it is imperative to implement sustainable agricultural practices that promote soil health and mitigate these effects.

Some strategies that can be employed to suppress PPN populations and increase nematode diversity include cover cropping, organic amendments, and reduced pesticide usage (Abd-Elgawad, 2024). Furthermore, citrus plantations can effectively manage nematode infestations through the implementation of integrated pest management (IPM) strategies that integrate biological, cultural, and chemical control methods. It is imperative to conduct research on the functional diversity of nematodes in citrus ecosystems in order to establish sustainable agricultural practices that maintain ecological integrity while maximizing productivity (Wyckhuys et al., 2024). The objective of this review is to offer a thorough comprehension of the ecological impact and diversity of phytonematodes that are associated with citrus plants, with a particular emphasis on lime and lemon crops. This review emphasizes the necessity of innovative strategies to manage nematode populations while preserving soil biodiversity by analyzing the spatial distribution, functional roles, and effects of agricultural intensification (Van Der Putten et al., 2006). The results emphasize the necessity of incorporating ecological principles into agricultural practices to guarantee the sustainability of citrus production systems (Techen et al., 2020).

## 2. RESEARCH METHOD

A meticulous analysis of 450 academic publications that were specifically focused on the diversity and ecological impact of phytonematodes associated with citrus plants was used to generate insights for this comprehensive review. The selection of papers from reputable periodicals ensured a diverse and robust dataset. The study incorporates data from co-authorship networks, citation metrics, and author contributions to provide a comprehensive perspective during the study period from May 2023 to June 2024. Lahlali Rachid, a central figure with substantial influence and collaboration ability, was

identified as a notable researcher through a comprehensive assessment of the authors' contributions. Citation analysis identified significant works, with nodes such as Lahlali (2022) and Castillo (2007) functioning as citation centers that connect a variety of thematic clusters. Two principal clusters were identified: one commanded by Lahlali and another featuring Mokrini Fouad and Azim Khalid. The collaborative dynamics were exemplified by co-authorship networks. The use of visualization tools to map the collaboration and citation networks emphasized the thematic diversity in the field and the interconnectedness of researchers. A comprehensive understanding of the research landscape is ensured by this structured approach.

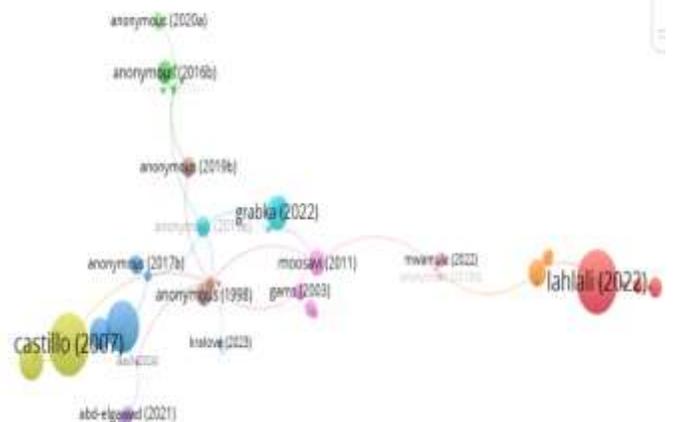


**Figure 1. Collaboration Network of Authors Based on Co-authorship**

The figure.1 depicts a co-authorship network of authors based on shared contributions in academic documents. The nodes represent individual authors, while the edges (links) between them indicate collaborative relationships. The thickness of the edges reflects the strength of collaboration, with thicker edges indicating more significant joint efforts. The colors represent clusters or communities of closely collaborating authors. Lahlali Rachid emerges as a central figure in the network, with strong connections to multiple authors, indicating their pivotal role in facilitating collaborations. The network appears to have two distinct clusters: a red cluster involving authors like Belabess Zineb, Kenfaoui Jihane, and Legrifi Ikram, and a green cluster with authors such as Mokrini Fouad, Azim Khalid, and Smouni Abdelaziz. This suggests thematic or research-oriented groupings. The visualization highlights how central nodes can act as bridges, fostering cross-cluster collaborations and knowledge exchange.

**Table: Author Contributions, Citations, and Total Link Strength**

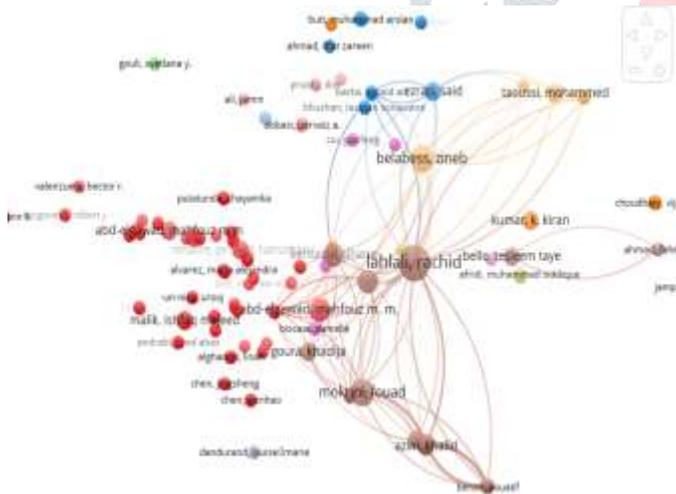
Author	Documents	Citations	Total Link Strength
lahlali, rachid	7	387	26
mokrini, fouad	4	2	17
belabess, zineb	4	385	13
legrifi, ikram	3	7	11
azim, khalid	2	2	10
bouchtaoui, el mehdi	2	2	10
fahr, mouna	2	2	10
kenfaoui, jihane	3	378	10
smouni, abdelaziz	2	2	10
ezrari, said	2	385	7
taoussi, mohammed	2	7	6
boyno, gökhan	2	7	5
demir, semra	2	7	5
durak, emre demirer	2	7	5
ansari, rizwan ali	2	7	3
bello, tesleem taye	2	4	2
fabiya, oluwatoyin adenike	2	4	2
malik, ishfaq majeed	2	2	2



**Figure 2. Citation Network of Authors Based on Document**

The figure.2 represents a citation network, where nodes indicate authors or documents, and edges (links) reflect

citation relationships. Larger nodes signify more influential authors/documents, receiving numerous citations. The thickness and proximity of edges demonstrate the strength and closeness of these citation connections. Colors group authors or documents into clusters, suggesting shared themes, methodologies, or research topics. In this network, Lahlali (2022) stands out as the most prominent node, indicating significant influence within the research domain. Castillo (2007) also appears as a crucial node in a separate cluster, showcasing its enduring impact. These nodes act as citation hubs, connecting various smaller clusters and influencing the network's overall structure. The green cluster around "Anonymous" authors spans multiple years, showing consistent yet less centralized influence. Similarly, Grabka (2022) connects distinct parts of the network, acting as a bridge between clusters like Castillo (2007) and Lahlali (2022). The purple, blue, and yellow clusters illustrate diverse research groups, potentially focusing on distinct thematic areas but contributing to a broader knowledge base. Overall, the visualization reveals key citation flows and connections, identifying influential works while emphasizing the interconnected nature of academic contributions across time and topics.



**Figure 3. Author Collaboration and Citation Network**

The image illustrates an extensive collaboration and citation network among authors, where nodes represent individual authors, and edges signify collaborative relationships or shared citations. Node size reflects the prominence or influence of authors within the network, based on the strength of connections (edges) and the number of collaborations or citations. Different colors cluster authors into thematic or collaborative groups, indicating shared research interests or affiliations. Lahlali Rachid is the central node and appears as the most influential figure in this network, establishing strong connections with numerous authors such as Belabess Zineb, Mokri Fouad, and Azim Khalid. These connections

suggest Lahlali's role as a key hub, facilitating research collaborations across various subfields or topics.

Clusters of nodes, such as those in red, represent tightly knit groups that likely share a common research focus. For example, the red cluster linked to Lahlali Rachid includes Abd-Elgawad Mahfouz M., Malik Ishfaq Majeed, and others, indicating cohesive collaboration patterns within this group. The yellow and blue clusters, connected to authors like Taoussi Mohammed and Belabess Zineb, may signify additional specialized research themes or geographic affiliations. Overall, this visualization highlights the interconnected nature of research networks, the centrality of influential authors, and the thematic or geographic diversity within the broader scholarly community.

### 3. FUNCTIONAL DIVERSITY

Functional diversity plays a vital role in understanding the ecological impact of phytonematodes on citrus plants (Lazarova et al., 2021). The biodiversity–ecosystem functioning relationship emphasizes that ecosystem processes are significantly influenced by the traits of organisms rather than merely their species richness or diversity (Song et al., 2014). Phytonematodes, as soil-dwelling organisms, demonstrate a wide array of functional traits, including physiological, morphological, and behavioral characteristics, that directly or indirectly affect citrus plant health and productivity (Lazarova et al., 2021). These traits influence critical processes such as nutrient cycling, soil structure maintenance, and the regulation of plant health. By adopting a functional trait-based approach, researchers can compare ecological patterns across different ecosystems and better understand the extent to which trait diversity supports ecosystem multifunctionality (Sahu et al., 2017). This approach highlights the resilience of phytonematode communities in citrus ecosystems and their capacity to adapt to environmental disturbances, thus ensuring the continuity of essential ecosystem services (El-Tabakh et al., 2024). Functional diversity within these communities is essential for maintaining balanced interactions and mitigating the negative impacts of certain nematode species on citrus crops.

Ecosystem processes and services, particularly in soil ecosystems, depend heavily on the functional dynamics of soil biota, including phytonematodes (Barrios, 2007). The "functional groups" approach, which has been traditionally employed in ecological studies, may underestimate the influence of the nuanced variations in characteristics within groups on the functioning of the ecosystem (Zoeller et al., 2020). Effect traits that influence ecosystem processes, including the growth, reproduction, and survival of citrus plants, and response traits that

demonstrate their adaptability to environmental changes, are exhibited by phytonematodes (Hussain & Chimhundu, 2023). For example, certain nematode species may improve the availability of soil nutrients by decomposing, while others may pose a hazard by parasitizing citrus roots, resulting in decreased plant vigor (Enyiukwu, D. N., n.d.). Comprehending these functional attributes offers a deeper understanding of their ecological functions and their contributions to soil health (Lehman et al., 2015). This knowledge is essential for the preservation of soil ecosystem services, the management of phytonematode populations in citrus plantations, and the implementation of sustainable agricultural practices. In order to maximize citrus plant health and productivity while reducing ecological risks, researchers and producers can devise targeted strategies by distinguishing between effect and response traits (Lehman et al., 2015).

### 3.1 Nematode Functional Role, Functional Groups and Traits Diversity

Nematodes, a vital component of soil food webs, play a crucial role in soil processes and ecosystem functions. These microscopic organisms contribute significantly to carbon transformation and nutrient cycling through two pathways: the "direct pathway" involving living plant roots and the "indirect pathway" utilizing dead plant residues (J. Wang et al., 2024). Their metabolic and behavioral activities enhance plant growth, primary productivity, and soil health by regulating pest and disease control, as seen in entomopathogenic nematodes

(EPN) (Kallali et al., 2024). Furthermore, nematodes influence soil organic matter decomposition, reinforcing their ecological significance.

Functional groups of nematodes, often categorized based on their feeding behaviors, demonstrate diverse contributions to ecosystem functions (Van Den Hoogen et al., 2019). For example, bacterial and fungal feeders directly excrete organic and inorganic compounds into the soil, promoting nutrient cycling (Kubicek & Druzhinina, 2007). Indirectly, they shape the microbial community's composition and activity, fostering beneficial microbiota while suppressing harmful microorganisms. These microbial feeders can also act as vectors, transferring beneficial or detrimental bacteria and viruses to the rhizosphere (Raaijmakers et al., 2009). The diverse feeding strategies and morphological adaptations of nematodes reflect their evolutionary complexity and ecological roles. Phytonematodes, such as those affecting citrus plants, exhibit species-specific impacts that range from root-level interactions to field-scale influences (Nautiyal & Dion, 2008). Interestingly, phylogenetically distinct taxa can perform convergent functional roles, while closely related taxa may have divergent ecological impacts. Understanding the diversity and ecological roles of nematodes, particularly those associated with citrus plants, requires intensive research to unravel their complex web of ecosystem services and their implications for sustainable agriculture (Y. Zhang et al., 2020).

**Table 1. A schematic list of nematode contributions to main soil functions and services provided by different trophic groups.**

Nematode Trophic Groups	Plant Production	Pests or Pathogens Regulation	Disease Transmission	C and Nutrient Cycling
Bacterial feeders	+/- (vectors of beneficial/harmful bacteria)	+ (feeding on harmful bacteria)		+
Fungal feeders		+ (feeding on pathogenic fungi)		+
Herbivores	+/- (weed control/plant parasitism)		+ (virus vectors)	+
Predators		+ (PPN preying)		+
Omnivorous		+ (PPN preying)		+
Entomopathogens		+ (insect killing)		+

Another representation of nematode functional diversity is related to their life history strategies. A combination of traits (e.g., body size, reproductive potential, longevity, tolerance) have been used to classify nematodes along a

colonizer-persister (c-p) scale (i.e., classification into r- and K-selected species), reflecting the habitat quality, maturity and stability (Bongers, 1999). Non-parasitic nematode families were assigned to five classes. These

range from r-strategists, having short lifecycle, high reproduction rates, high colonization ability and tolerance to stress (c-p 1), to k-strategists, having long lifecycle, very few offspring, low colonization ability and sensitivity to stress (c-p 5) (Bongers, 1990). Based on this classification, the nematode maturity index was developed and extensively tested over three decades. Generally, the c-p ranking is recognized as a functional trait, however it is based on a combination of selected physiological, morphological and behavioral traits. The knowledge on the nematode trophic and life history traits was integrated into a matrix classification of nematode ‘guilds’ (Bongers & Bongers, 1998). The soil food web diagnostic framework was then developed, by providing a weighting system for the presence and abundance of nematode “functional guilds” in relation to enrichment and soil food web structure (Ferris et al., 2001). Nematode communities are mostly surveyed to the genus level and subsequently assigned to feeding and life history groups (at the family level). However, the trophic position and functioning of non-parasitic species continue to be poorly understood, despite their ubiquity and abundance. Moreover, recent studies on *Pristionchus* spp. showed great polyphenisms (alternative phenotypes produced by the same genotype) in mouth morphology, larval development and reproductive or feeding mode (Sommer et al., 2017). Such a nematode phenotypic plasticity allows individuals to adapt easily to changing environments, therefore a great functional diversity can be maintained in the absence of substantial genetic variation (Phillips, 2016). With other experimental studies, these observations indicate that the functional role of nematodes may be highly species-specific (De Mesel et al., 2006) and that certain functions might involve a complex of multiple species with different specific temporal and spatial cues (Sylvain & Wall, 2011). An overlap of functional roles is evident in EPN, as these nematodes are both bacterivores and insect parasites. Although nematodes often represent the dominant eukaryotes in terms of abundance and diversity, most experimental studies used for evaluating their functional role involve a limited number of species. For example, studying the effect of within-trophic level diversity of bacterivorous nematodes and population interactions on nitrogen mineralization, Postma-Blaauw et al. (Postma-Blaauw et al., 2005) found that the life history strategies of the species of the same trophic group significantly affected their communal impact on the soil ecosystem processes. A single nematode species is able to influence the population size of other species that may, in turn, alter the functioning of the system (Trap et al., 2016). How experimental observations can be generalized remains, however, uncertain, in particular if we consider the broad

range of ecosystem types and processes globally present. A better approach to adopt would be to investigate these complex systems through long-term field experiments or in situ studies (Weisser et al., 2017). At first, the functional diversity was assessed mainly as functional group richness (i.e., the number of feeding groups and functional guilds) and their relative abundance. In recent years, the analyses of single or multiple nematode traits were regarded as reliable alternatives to assess the community-level response to disturbances and biodiversity– functions relationships. In terrestrial ecosystems, the functional trait-based approach has been undertaken for nematode assemblages alone (Vonk et al., 2013) or for more complex systems that involve several trophic levels, e.g., bacteria, nematodes and collembolans (Sechi et al., 2017). Body size, measured either at the individual or species level, has been used to evaluate the interaction strengths between consumers and resources (Sechi et al., 2017), and is correlated directly with properties that influence the performance of organisms and communities (Schmitz et al., 2015). The body size/mass spectra of free-living nematodes as response/effect trait metrics alone or in combination with behavior (feeding structure) and life history strategies have been used to evaluate nematode functional diversity (Mulder & Vonk, 2011). The combination of discrete and continuous traits (trophic groups and body size) distribution rather than the functional diversity indices (functional divergence, functional evenness and functional richness) was found to better reveal the soil food web structure and trait-mediated responses of nematode communities to environmental filters in different ecosystem types (Sechi et al., 2018).

### 3.2 Diversity of Phytonematodes in Citrus Ecosystems

Phytonematodes, or plant-parasitic nematodes, represent a significant challenge in citrus cultivation due to their diversity, host-specific adaptations, and varying geographical distributions. Their presence and activity in citrus ecosystems lead to substantial economic losses, prompting extensive research into their taxonomy, biology, and ecological impact. The nematodes affecting citrus plants belong to various genera, including *Meloidogyne* (root-knot nematodes), *Tylenchulus* (citrus nematodes), *Pratylenchus* (lesion nematodes), and *Radopholus* (burrowing nematodes). Each genus includes species that exhibit unique traits impacting their pathogenicity. For example, *Meloidogyne* spp. are known for inducing galls on roots, disrupting the plant's ability to absorb water and nutrients (Williamson & Hussey, 1996). Similarly, *Tylenchulus semipenetrans*, often referred to as

the citrus nematode, is notorious for its impact on citrus yield worldwide (Duncan, 2005).

Recent advancements in molecular and morphological techniques have significantly enhanced nematode identification and taxonomy. DNA barcoding, ITS sequencing, and morphometric analyses provide precise differentiation among nematode species and strains. This increased accuracy enables a better understanding of phytonematode diversity and their ecological roles (Holterman et al., 2006). For example, molecular markers have helped distinguish between cryptic species within the *Meloidogyne* genus, which was previously challenging using morphological methods alone (Blok & Powers, 2009). Phytonematodes exhibit remarkable adaptations that enable them to parasitize citrus plants effectively. Host-specific adaptations often involve complex biochemical signaling pathways between the nematode and the host. For instance, *Meloidogyne* spp. manipulate plant hormonal pathways to establish giant cells, which serve as feeding sites (Bird & Kaloshian, 2003). Similarly, *Tylenchulus semipenetrans* forms syncytia in root tissues, causing extensive damage and impairing nutrient uptake (Duncan, 2005). The specificity of these adaptations indicates co-evolution between nematodes and citrus hosts. Nematodes secrete effectors that modify plant cell functions, promoting their survival while suppressing plant defense mechanisms. These interactions have been the focus of studies aiming to identify resistant citrus cultivars or develop targeted biocontrol strategies (Briar et al., 2016).

The distribution and prevalence of phytonematodes in citrus ecosystems are influenced by environmental and agronomic factors. Tropical and subtropical regions, characterized by favorable climatic conditions for citrus cultivation, often report higher incidences of nematode infestations (Bridge, 1996). For instance, *Meloidogyne* spp. are commonly found in regions with sandy soils, where their mobility and penetration efficiency are enhanced (Van Der Putten et al., 2016). Surveys conducted in citrus-growing regions worldwide reveal variations in nematode prevalence. In the Mediterranean, *Tylenchulus semipenetrans* is the most dominant species, affecting both young and mature citrus orchards (Enyiukwu, D. N., n.d.). In contrast, *Radopholus similis*, known for its aggressive burrowing behavior, poses a significant threat in Southeast Asia and the Americas (De Waele & Elsen, 2007). Understanding these geographical patterns is crucial for designing region-specific management strategies. The increasing impact of global trade and climate change on nematode distribution is another concern. Climate change may alter nematode

survival rates, host-parasite dynamics, and the geographical range of susceptible citrus cultivars (Griffin, 2015). This underscores the importance of continuous monitoring and research to anticipate and mitigate emerging threats. These facets of phytonematode diversity—taxonomy, host-specific adaptations, and geographical distribution—provide a foundation for understanding their ecological impact on citrus ecosystems. Expanding research into these areas, particularly through advanced genomic and ecological tools, will be pivotal in developing sustainable management strategies for citrus nematodes.

#### 4. ECOLOGICAL IMPACT OF PHYTONEMATODES

Phytonematodes, also known as plant-parasitic nematodes (PPNs), are microscopic worms that significantly impact agricultural productivity and sustainability. Their association with citrus plants poses a critical challenge to global citrus industries. This review delves into the ecological impact of phytonematodes, with particular emphasis on their effects on plant health, soil ecology, and interactions with other pathogens. Phytonematodes profoundly affect citrus plant health and productivity by disrupting root systems. These nematodes penetrate root tissues, feeding on the cells and altering root architecture (Nicol et al., 2011). The resultant damage reduces the plant's ability to absorb water and essential nutrients from the soil. Symptoms such as stunted growth, yellowing of leaves (chlorosis), wilting, and reduced fruit yield are common (Chitwood, 2003). For instance, the citrus nematode (*Tylenchulus semipenetrans*) has been extensively documented for its detrimental effects on citrus root systems (Duncan, 2005).

The economic impact of severe nematode infestations is staggering, with losses in the citrus industry alone reaching billions of dollars annually (Jones et al., 2013). Reduced fruit size, poor quality, and lower yields translate directly into diminished profits for growers. Furthermore, the longer-term implications include increased costs for nematicidal and cultural practices aimed at mitigating nematode populations.

Phytonematodes also play a crucial role in shaping soil ecology. Their activity influences microbial communities within the rhizosphere the region of soil directly influenced by root exudates and associated organisms. Parasitic nematodes disrupt the balance of beneficial microorganisms, which in turn affects nutrient cycling (Neher, 2010). Beneficial nematodes contribute to the decomposition of organic matter and the release of nutrients. However, parasitic nematodes, such as root-

knot nematodes (*Meloidogyne spp.*), negatively impact soil health by suppressing beneficial microbial populations (Moens et al., 2009). The cascading effects of nematode activity on soil ecosystems are particularly pronounced in citrus orchards, where intensive cultivation practices often degrade soil quality. Alterations in microbial communities caused by nematodes can lead to soil compaction, reduced organic matter content, and compromised soil fertility (Barker & Koenning, 1998). This underscores the necessity for integrated soil health management practices to sustain long-term citrus productivity.

Phytonematodes often interact synergistically with other pathogens, amplifying their impact on citrus plants. These interactions occur in two primary ways: by predisposing plants to secondary infections and serving as vectors for pathogens. Root damage inflicted by nematodes creates entry points for opportunistic pathogens, including bacteria and fungi (M. A. Back et al., 2002), (M. Back et al., 2006). For example, nematode-infested citrus roots are more susceptible to infections by *Phytophthora spp.*, a genus of oomycetes known to cause root rot and gummosis (Graham & Timmer, n.d.). Moreover, nematodes such as *Xiphinema spp.* and *Longidorus spp.* are vectors for plant viruses. These nematodes transmit viruses by feeding on plant root tissues, leading to systemic infections that further compromise plant health (Taylor, 1972). The combined stress of nematode parasitism and secondary infections often results in significant yield reductions and increased tree mortality.

The ecological impact of phytonematodes extends beyond individual plants and soil health. These nematodes influence the resilience of entire citrus ecosystems by altering plant-microbe interactions and nutrient dynamics. The long-term consequences include reduced biodiversity within citrus orchards and greater vulnerability to environmental stressors, such as drought and soil erosion (Van Der Putten et al., 2006). The global citrus industry faces numerous challenges in managing phytonematodes. Conventional methods, such as chemical nematicides, are effective but pose environmental and health risks (Abd-Elgawad & Askary, 2015). Moreover, the development of nematode-resistant citrus rootstocks is a promising but time-consuming strategy. Integrated pest management (IPM) approaches, which combine cultural practices, biological control agents, and resistant cultivars, are increasingly advocated for sustainable nematode control (Stirling et al., 1992). Phytonematodes represent a significant ecological and economic challenge for citrus production. Their effects on plant health, soil ecology, and interactions with pathogens necessitate a comprehensive understanding to develop effective management strategies. Future research should focus on elucidating the complex interactions between nematodes and other soil organisms, advancing biological control methods, and fostering sustainable agricultural practices. Addressing these challenges will be crucial for ensuring the long-term viability of citrus industries worldwide.

**Table 2. Comparison of Phytonematode Impact on Citrus**

Nematode Species	Primary Host Symptoms	Geographical Distribution	Economic Impact	Management Strategies
<i>Meloidogyne spp.</i>	Root galls, stunted growth	Global	High yield losses	Crop rotation, resistant rootstocks, nematicides
<i>Tylenchulus semipenetrans</i>	Slow decline, reduced vigor	Tropical and subtropical areas	Moderate to high	Soil fumigation, biological control, organic amendments
<i>Pratylenchus spp.</i>	Root lesions, nutrient deficiency symptoms	Widely distributed	Moderate	Resistant cultivars, soil solarization
<i>Helicotylenchus spp.</i>	Root damage, poor growth	Localized	Low to moderate	Improved drainage, organic matter addition

## 5. IMPACT IN HIGH-VALUE CROPS

Citrus crops, as high-value commodities, significantly contribute to the global agricultural economy. The susceptibility of citrus plants to phytonematodes

underscores the importance of understanding their impact on yield and quality. Phytonematodes such as *Tylenchulus semipenetrans*, the citrus nematode, and species of

*Pratylenchus* and *Meloidogyne*, have been extensively studied for their deleterious effects on citrus crops. Their parasitism reduces productivity and increases management costs, posing challenges for sustainable citrus cultivation.

### 5.1 Effects of Lime Cropping Systems on Nematodes

Lime cropping systems offer a unique context to study the interactions between phytonematodes and citrus plants. Lime (*Citrus aurantiifolia*) is particularly vulnerable to nematode infestations, and the cropping system employed plays a pivotal role in determining the diversity and population dynamics of these pests. Research has shown that lime plantations are frequently infested with *Tylenchulus semipenetrans* and *Meloidogyne* species, resulting in stunted growth, yellowing leaves, and reduced fruit yield and quality (Shokoohi & Duncan, 2018). The density and diversity of nematodes in lime cropping systems are influenced by soil properties such as pH, organic matter content, and moisture. Studies by McSorley and Duncan (1995) revealed that acidic soils tend to support higher populations of root-knot nematodes (*Meloidogyne* spp.), whereas neutral to alkaline soils favor the citrus nematode (*T. semipenetrans*). These findings highlight the importance of soil management in mitigating nematode infestations in lime orchards.

Cultural practices, including crop rotation, intercropping, and organic amendments, significantly affect nematode populations in lime cropping systems. For instance, incorporating organic matter, such as compost or green manure, has been shown to suppress nematode populations by enhancing microbial antagonism (Holden-Dye & Walker, 2011). Similarly, intercropping lime with nematode-resistant crops can act as a trap or decoy for nematodes, reducing their impact on lime plants. Chemical nematicides have been a traditional method for controlling nematodes in lime orchards. However, the environmental and health concerns associated with chemical treatments necessitate the exploration of biological alternatives. Biological control agents, such as *Pasteuria penetrans* and nematophagous fungi like *Paecilomyces lilacinus*, have demonstrated efficacy in managing nematode populations in lime systems (Kerry, 2000). These agents disrupt the life cycle of nematodes, reducing their reproductive success and subsequent damage to lime plants.

An integrated approach combining cultural, biological, and chemical methods offers the most sustainable solution for managing nematodes in lime cropping systems. Integrated nematode management (INM) strategies emphasize the use of resistant rootstocks, crop rotation,

and the judicious application of nematicides. According to (Crow & Duncan, 2018), INM practices not only reduce nematode populations but also enhance soil health and promote sustainable lime production. The economic losses caused by phytonematodes in lime cropping systems are substantial. For example, estimated yield reductions due to *T. semipenetrans* range from 15% to 30% in heavily infested orchards (Crow & Duncan, 2018). These losses, coupled with increased management costs, underscore the need for effective control measures. Moreover, the ecological impact of nematode infestations extends beyond the immediate crop losses, as they can alter soil microbial communities and nutrient dynamics. In conclusion, lime cropping systems are particularly susceptible to the adverse effects of phytonematodes. Understanding the interactions between soil properties, nematode diversity, and cultural practices is crucial for developing effective management strategies. By integrating various control measures, it is possible to mitigate the impact of nematodes on lime crops, thereby ensuring their economic viability and ecological sustainability.

### 5.2 Effects of Lemon Cropping Systems on Nematodes

Phytonematodes pose significant threats to high-value crops, including citrus plants, by reducing yield, impairing plant health, and increasing production costs. Among citrus crops, lemons (*Citrus limon*) hold particular importance due to their economic value and widespread cultivation. The interactions between nematodes and lemon cropping systems provide insights into the broader challenges faced by citrus growers. This section delves into the effects of lemon cropping systems on nematode diversity, population dynamics, and their impact on plant health. Lemon cropping systems vary widely depending on geographic location, soil type, and farming practices, each influencing the prevalence and diversity of phytonematodes. Studies by (Nyczepir & Becker, 2015) highlighted that sandy soils, often used in lemon cultivation, are particularly favorable for nematode proliferation. The root-knot nematodes (*Meloidogyne* spp.) and citrus nematodes (*Tylenchulus semipenetrans*) are the most common species infesting lemon orchards, causing root galls, reduced nutrient uptake, and stunted growth. Research by (Sikora et al., 2005) emphasized that monoculture practices in lemon orchards exacerbate nematode problems by continuously providing a suitable host, thus increasing population densities. In contrast, integrated cropping systems that rotate lemon with non-host crops can disrupt nematode life cycles and reduce their populations. However, crop rotation is not always

feasible in commercial lemon orchards due to market demands.

Nematodes affect lemon trees by directly damaging roots and indirectly predisposing plants to secondary infections by pathogens. (Hammam et al., 2021) reported that infestations of root-knot nematodes reduced lemon yields by up to 30% in heavily infested soils. Similarly, citrus nematodes weaken root systems, making trees less resilient to abiotic stress such as drought or nutrient deficiencies. The physiological effects of nematode infestations include impaired water and nutrient transport, resulting in chlorosis, reduced fruit size, and lower fruit quality. Studies by (R. Kumar & Kumar, 2016) showed that nematode-damaged lemon trees exhibit delayed flowering and fruiting, impacting both the quantity and timing of harvests. The presence of phytonematodes in lemon orchards affects soil health by altering microbial communities. According to the work of (Mosca et al., 2024), nematode activity stimulates the growth of pathogenic fungi such as *Fusarium* spp., which further deteriorate root health. Conversely, beneficial microorganisms, including mycorrhizal fungi and rhizobacteria, are often suppressed in nematode-infested soils, reducing the natural resilience of the ecosystem. Studies by (Njeru & Koskey, 2021) demonstrated that organic amendments, such as compost and biofertilizers, could enhance microbial diversity and suppress nematode populations. These practices improve soil structure and nutrient cycling, creating a less hospitable environment for nematodes.

Effective management of nematodes in lemon cropping systems involves an integrated approach combining cultural, biological, and chemical methods. Biological control agents, such as *Pasteuria penetrans* and *Pochonia chlamydosporia*, have shown promise in suppressing nematode populations in lemon orchards (K. K. Kumar & Pervez, 2023). These biocontrol agents infect or parasitize nematodes, reducing their reproductive potential. Cultural practices, including deep plowing, solarization, and cover cropping, can also mitigate nematode damage. According to research by (K.-H. Wang et al., 2006), the use of marigold (*Tagetes* spp.) as an intercrop in lemon orchards reduces nematode populations due to its nematicidal properties. Additionally, resistant lemon rootstocks, such as those developed by (Abd-Elgawad, 2020), offer long-term solutions by limiting nematode reproduction and minimizing damage.

Chemical nematicides remain a common choice for immediate control, but their use is increasingly regulated due to environmental concerns. Studies by (Chen et al., 2020) highlighted that nematicides such as fluopyram

effectively control nematodes in lemon orchards while posing lower risks to non-target organisms compared to traditional chemicals. However, the high cost of nematicides and their potential impact on beneficial soil organisms necessitate careful application. The economic impact of nematode infestations in lemon cropping systems is substantial. According to a study by (Pretorius & Le Roux, 2017), the annual losses attributed to nematode damage in citrus orchards exceed \$1 billion globally. Lemon growers face increased costs due to reduced yields, lower fruit quality, and the need for intensive management practices. The adoption of integrated nematode management strategies can mitigate these losses, but initial investments in biocontrol agents, resistant rootstocks, or organic amendments may deter resource-limited farmers. Governments and agricultural extension services must play a crucial role in promoting sustainable practices and providing financial support to growers.

### 5.3 Effects of Banana Cropping Systems on Nematodes

Bananas (*Musa* spp.) are typically grown in highly commercial, large-scale monoculture plantations. They consist primarily of a single Cavendish genotype and minor variants, while single plantations are usually composed of clones from a single source. This narrow genetic pool represents a major risk for pest and disease outbreaks. Consequently, the banana industry has traditionally relied heavily upon the use of synthetic pesticides to mediate the impact of pests and diseases, including nematodes. As with many tropical crops, bananas are challenged by and susceptible to a range of PPN species. At any one time, they are mostly infected by multiple species [104], which could severely compromise the fruit production and other services provided by plantations. Most studies on nematode assemblages and functional groups' diversity in banana agro systems explored the effects of plant cover composition and diversity changes on regulation of the most common PPN (Djigal et al., 2012). The stability and beneficial ecosystem functions and services (e.g., regulation of weeds, pests or pathogens) of intensively managed agrosystems can be enhanced by increasing plant diversity through cover plants or associated crops. Increasing the cover crop species diversity is expected to enhance plant productivity through increased resource use efficiency (Florence & McGuire, 2020). Multispecies cropping agrosystems perform multiple functions and services other than crop production, increasing soil OM and C sequestration, regulating soil moisture, suppressing weeds, pathogens and pests, retaining N, sustaining higher soil biodiversity, etc. Increasing plant richness tends to

increase pest regulation in the field. The cover plants may control PPN directly, by various self-defense mechanisms and traits (morphological, physical and chemical) and indirectly through soil food web modifications, including changes in the relative abundance between PPN and their predators, e.g., carnivorous nematodes or arthropods (Damour et al., 2015). The abundance of bacterivorous, omnivorous and root-hair feeding nematodes, and the Shannon–Weaver diversity index, tended to increase when a cover crop was introduced between rows (Djigal et al., 2012). However, data showed specific effects of cover crop species, as PPN were less abundant in plots with Poaceae than in those with Fabaceae. Poeydebat et al. (Poeydebat et al., 2017) investigated the processes leading to PPN regulation in banana agrosystems, evaluating the effects of plant richness (crop and non-crop), soil properties (humidity, soil OM, C:N ratio) and nematode trophic groups on multitrophic interactions. Different pest regulation pathways were found, including regulation of *Radopholus similis* by plant community effects, of *Helicotylenchus multicinctus* and *Meloidogyne* spp. by nontrophic interactions with free-living nematodes and of *Pratylenchus coffeae* by both effects. No regulation of PPN by predaceous nematodes was found. Other studies showed that previous crop plants, biochemical characteristics of cover crop litter, management type (conventional vs. organic, mixed vs. monoculture) and the type of organic amendments also applied strongly influenced the nematode assemblages, their trophic interactions and complexity, possibly leading to PPN suppression (Olivares Campos, 2023), (Chauvin et al., 2015). The PPN biology and host adaptation also play a key role in the damage induced. The burrowing nematode, *R. similis*, is the most important PPN of banana, largely as this tends to be the prominent nematode in commercial dessert banana plantations, where close attention is paid to pest management. However, *R. similis* rarely occurs alone but, as an aggressive species, it often overshadows the presence and damage of other nematode species. Other co-occurring species, such as *H. multicinctus* and *Meloidogyne* spp., result in damage beyond that caused by *R. similis* alone (Badra, 1979). In addition, significant differences in the aggressiveness and damage potential of different populations of *R. similis* have been demonstrated, which are themselves differentially affected by host resistance (Plowright et al., 2013). Depending on the geographic location, climate and banana genotype, the nematode diversity may differ substantially. In Africa, for instance, *R. similis* has tended to dominate the nematode communities (and damage) in the East African Highland cooking bananas, at altitudes below 1400 m. Above this altitude, *Pratylenchus goodeyi*,

which is more tolerant of cooler temperatures than *R. similis*, becomes dominant (Coyne, 2009), (Lorenzen et al., 2009). *Helicotylenchus multicinctus* remains ever present across the altitudinal gradients, while *Meloidogyne* spp., *Rotylenchulus* spp., *Rotylenchus* spp. and other *Helicotylenchus* spp., among others, regularly occur (Pokharel et al., 2015). In the hotter lowland areas in East Africa, the nematode community composition has shifted away from *R. similis*, with *Pratylenchus coffeae*, as well as *P. goodeyi*, becoming more prevalent (Luambano et al., 2019). In West Africa, however, where *R. similis* has previously been the dominant nematode pest species, a trend in the rise of *P. coffeae* has been observed (Coyne, 2009). Overall, this demonstrates the continuously dynamic nature of PPN on banana and the need to be aware of this dynamism when developing appropriate management options.

#### 5.4 Nematodes in Apple Crops

Apple (*Malus domestica*) crops are produced in all temperate and subtropical regions of the world and represent the fourth most important fruit crop after citrus, grapes and banana (Hummer & Janick, 2009). EUROSTAT data indicated this crop as the most commonly planted fruit tree in the European Union (EU), with a cultivated area covering 473,500 ha or 37% of the land covered by orchards in 2017. Similar to other agrosystems, apple production systems can provide numerous services or disservices that depend on locality, management type and applied practices (Birkhofer et al., 2019). In addition, apple orchards contribute to services, such as pollination, pest control, soil fertility, nutrient cycling and soil biodiversity conservation in more environment-friendly production systems, when either organic management or novel biodiversity-enhancing practices are used (Samnegård et al., 2019). The trade-offs between provisioning and other ecosystem services and disservices usually arise from the management choices and should be evaluated in terms of the spatial and temporal scales (Rodríguez et al., 2006). Most nematode studies in apple orchards have focused on PPN. However, several recent studies investigated nematode community structure in relation to crop management type or soil management practices (T. Forge et al., 2015). A more comprehensive approach including other soil organisms, such as protozoa (T. A. Forge et al., 2003), AMF (T. Forge et al., 2015) and soil microbes and microfauna (e.g., fungi, bacteria, algae and protozoa), has been used (Pokharel et al., 2015) for studying soil management practices. DNA-based methods were applied too (Kanfra et al., 2018). The community structure and diversity of bacteria, fungi and nematodes, and their relationships from naturally and

conventionally farmed apple orchards, were studied in Japan using denaturing gradient gel electrophoresis (DGGE) (Matsushita et al., 2015). The results indicate that crop type as well as management practices improved the nematode community structure and functional diversity in organic and natural apple orchards, as compared to conventional apple production. However, data relating these results to fruit production and quality were not shown. Studying the functional diversity of nematodes and their relationship with other organisms of the soil food web may help to reveal their contribution to ecosystem services and disservices provided by apple orchards (e.g., pest/disease control vs. apple replant disease, ARD). ARD is common to all major apple growing regions worldwide (Mazzola & Manici, 2012). It affects plant propagation in nurseries and replanted apple orchards reducing plant growth, as well as fruit yield and quality (Winkelmann et al., 2019). Studies on the ARD etiology and soil biology in apple orchards have defined a complex of soil-borne pathogens and parasites as causal agents. In particular, some fungi (*Fusarium* and *Rhizoctonia*), oomycetes (*Phytophthora* and *Pythium*) and nematodes (*Pratylenchus* spp.) have been identified as key causal agents (Tewoldemedhin et al., 2011). Previous research on ARD focused on PPN, mainly *Pratylenchus penetrans* (Dullahide et al., 1994), while the role of free-living nematodes in the disease complex was neglected.

However, a recent study proved the importance of free-living nematodes and their synergetic role to induce ARD (Kanfra et al., 2018). The authors explored the source of the inoculated nematodes (ARD or control soil) and the interaction between ARD nematodes and microbes as factors determining the disease insurgence. They found that when nematode communities extracted from the ARD soil were added to microbes, regardless of their origin, they affected plant growth more severely than treatments without ARD nematodes. The nematodes extracted from control soil in combination with microbes, either from ARD or control soil, did not induce ARD symptoms. The outcomes underline the indirect role of free-living nematodes in transmitting pathogenic microbiota.

### 5.5 Comparative Study of Phytonematodes in Citrus Ecosystems

Phytonematodes, or plant-parasitic nematodes, represent a significant challenge to citrus cultivation worldwide. Their diversity and ecological impacts vary depending on geographical regions, citrus species, and environmental conditions. Below, we present a comparative study of key findings related to the diversity and impact of phytonematodes on citrus plants, focusing on prominent studies.

**Table 3. Comparative Study of Phytonematodes in Citrus Ecosystems**

Author(s)	Year	Phytonematode Species Studied	Geographical Region	Impact on Citrus Plants	Management Strategies Discussed
(Arbor, n.d.)	1999	<i>Tylenchulus semipenetrans</i>	Florida, USA	Caused citrus decline syndrome; reduced fruit yield and quality.	Soil fumigation, resistant rootstocks.
(Shokoohi & Duncan, 2018)	2003	<i>Meloidogyne</i> spp., <i>Pratylenchus</i> spp.	Mediterranean Region	Stunted plant growth, root galls, and reduced water uptake.	Crop rotation, nematicides.
(K. K. Kumar & Arthurs, 2021)	2012	<i>Radopholus similis</i> , <i>Helicotylenchus</i> spp.	India	Root lesions leading to nutrient deficiency symptoms and weakened plant health.	Organic amendments, biocontrol agents.
(Ghaderi & Hosseinvand, 2022)	2017	<i>Tylenchulus semipenetrans</i>	California, USA	Inflicted long-term soil health degradation, causing chronic citrus decline.	Integrated Pest Management (IPM), including biological controls.
(Abd-Elgawad, 2024)	2019	<i>Meloidogyne javanica</i> , <i>Rotylenchulus</i> spp.	China	Severe root damage and reduced resistance to other soil-borne pathogens.	Use of nematode-resistant cultivars and biofumigation.

(Smith et al., 2024)	2020	<i>Pratylenchus coffeae</i> , <i>Rotylenchulus reniformis</i>	Nepal	Induced wilting and leaf chlorosis, drastically affecting citrus productivity.	Neem-based formulations and entomopathogenic fungi.
(Pires et al., 2022)	2022	<i>Heterodera spp.</i> , <i>Aphelenchoides spp.</i>	Brazil	Reduced vigor and susceptibility to environmental stresses, hampering commercial citrus yields.	Biocontrol with microbial antagonists and pheromone traps.

## 6. CONCLUSION

Phytonematodes significantly impact citrus production, with species like *Meloidogyne*, *Tylenchulus*, *Pratylenchus*, and *Radopholus* posing substantial threats to crops such as lemons, limes, bananas, and apples. These nematodes disrupt root function, impair nutrient uptake, and reduce yields, leading to economic losses exceeding billions globally. Lemon cropping systems are particularly vulnerable due to the prevalence of sandy soils and monoculture practices, which exacerbate nematode problems. Similarly, lime systems face challenges from species like *Tylenchulus semipenetrans* and *Meloidogyne*, necessitating integrated approaches combining cultural, biological, and chemical controls.

Banana and apple crops also demonstrate the pervasive threat of nematodes, with *Radopholus similis* dominating banana systems and *Pratylenchus penetrans* contributing to apple replant disease. Sustainable management practices, including crop rotation, resistant rootstocks, organic amendments, and biological control agents, have shown promise in mitigating nematode populations. These strategies not only suppress pests but also enhance soil health and microbial diversity. In conclusion, the adoption of integrated nematode management practices tailored to specific crops and regions is vital for preserving citrus productivity and ensuring long-term agricultural sustainability. Future research should focus on ecosystem-based approaches to optimize pest control while maintaining ecological balance.

## 7. RECOMMENDATION

To mitigate the ecological impact of phytonematodes on citrus plants and promote sustainable citrus production, the following measures are recommended:

1. **Integrated Pest Management (IPM):** Implement biological control using nematode-resistant rootstocks, beneficial microorganisms (e.g., *Paecilomyces lilacinus* and *Pochonia*

*chlamydosporia*), and organic amendments to suppress nematode populations naturally.

2. **Soil Health Management:** Enhance soil fertility and structure through organic mulching, cover cropping, and biofumigation with mustard or marigold plants to reduce nematode infestations.
3. **Early Detection and Monitoring:** Use molecular diagnostic tools and nematode population analysis for early identification of pathogenic species, enabling timely control interventions.
4. **Chemical Control Regulation:** Limit nematicide application to avoid environmental contamination and develop eco-friendly alternatives such as biopesticides and nematode-trapping fungi.
5. **Sustainable Cultivation Practices:** Promote crop rotation with non-host plants and maintain optimal irrigation practices to prevent the proliferation of phytonematodes, ensuring the long-term health of citrus orchards.

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