Review

Soil Nematodes as a Means of Conservation of Soil Predatory Mites for Biocontrol

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Abstract: Numerous lab and field studies have reported the potential of soil predatory mites for the biological control of plant-parasitic nematodes and arthropods pests. Most of these studies have utilized biocontrol agents in augmentative releases, essentially controlling the pest with the released predators. While this may be a valid approach, we hypothesize that conservation of soil mite predators with available, suitable, and accessible free-living nematodes as prey, will provide better agricultural ecosystem performance and long-range sustainability. In this manuscript, we review the relevant studies on soil predatory mite–nematode interactions and highlight their potential for conservation biological control of soil-borne pests. Additionally, we emphasize the importance of implementing environmentally sound soil management practices for the sustainability and conservation of functional soil food webs.

Keywords: Acari; feeding strategy; free-living nematodes; Mesostigmata; Oribatida; plant-parasitic nematodes; Prostigmata; conservation biological control; soil food web

1. Introduction

Biological pest control by natural enemies is a key ecosystem service for soil and plant health. Soil predatory mites feed on a diverse diet making them excellent candidates as biocontrol agents in conservation biocontrol programs in agriculture. However, the contribution of soil microarthropods in regulating pest populations is poorly known [1].

Within mites, Mesostigmata, and especially the family Phytoseiidae, are already widely used for control of above-ground agricultural pests. The most well-known are specialist species, having one prey (e.g., *Phytoseiulus persimilis* Athias-Henriot), while some generalists (e.g., *Amblyseius swirskii* Athias-Henriot) have gained prominence because they can be used for several prey species and also perform well with additional alternative food [2–4]. The same cannot be said for below-ground systems. Despite their known diversity and predatory capacity, only a few soil mite species are used in the biological control of pests, even though below-ground pests, in particular plant-parasitic nematodes, are responsible for severe crop damage in agricultural systems [5]. While soil Mesostigmata mites are mostly generalists, many of them have a preference for free-living nematodes [6–8].

Here we review the trophic interactions between mites and nematodes in soil, how they affect mite fitness and how we can take advantage of these interactions to control plant pests above- as well as below-ground.

1.1. Trophic Interactions in Soil

Soil organisms and the structure and function of their food webs play a key role in nutrient cycling and litter decomposition, soil processes which are crucial for above-ground primary production [9,10]. Their trophic interactions significantly impact the composition and activity of microbial assemblages, and in turn, plant growth and fitness [11]. The microfauna grazers, protists and nematodes, act as regulators by organizing the community

structure and by driving nutrient mineralization of their microbial prey. Moreover, the microfauna releases in mineral forms part of the nutrients captured by grazing [12,13], which for ammonium is estimated at 32–38% of the annual N mineralization in arable soil [14]. Taken together, the multi-trophic interactions in the soil food web are key determinants for plant development and health.

Besides nutrient cycling, another desirable function of a healthy soil is pest suppression. Diverse functions of the soil fauna, such as improving plant resistance and tolerance, are widely acknowledged [15–17], while trophic relationships receive less attention [1,18]. This is mainly due to the fact that predator–prey interactions are difficult to predict in highly diverse soil food webs, settled in a cryptic habitat with a mosaic of abiotic and biotic conditions. Moreover, the two major food chains in soil, the herbivore ("green") and the detritivore ("brown") chains, are traditionally considered as different entities (Figure 1) [19,20], and predators that cross-link these pathways are seldom investigated. However, organisms with a wide diet range, such as predatory mites, have regulatory impact in both the green and brown compartments, and connect carbon and energy transfer in between.
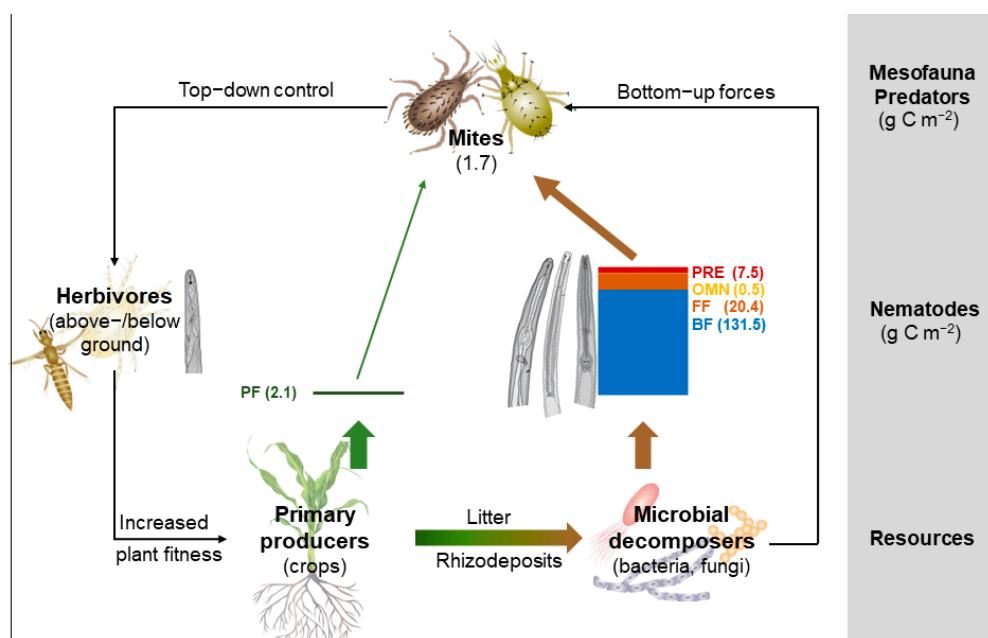

Figure 1. Herbivore (green) and detritivore (brown) food chain in an arable field cropped with maize at 0–10 cm depth. Scheme on C flow and bottom–up and top–down forces in the food web. BF–bacterial feeders, FF–fungal feeders, PF–plant feeders, OMN–omnivores, PRE–predators. Biomass of the soil fauna in brackets in g C m^{-2}, data from Pausch et al. [21].

Microarthropods with their high degree of omnivory and multi-channel feeding across energy sources, are key components of sustainable biological control strategies [18]. In particular, mites function as trophic-level omnivores and form a feeding gradient rather than a discrete trophic group [1]. Generally, biocontrol approaches are designed as top–down control of the prey (pest) by the predator (or parasite). The opposite way, i.e., bottom–up forces along the food chain, leading to increased fitness and improved biocontrol function of a predator, have received very little attention. Only recently, the trophic link between predatory mites and free-living nematodes (FLN) as complementary prey has been shown to improve the efficacy of mites as biocontrol agents [22–24]. This highlights that biological pest control by soil fauna predators should be viewed within the framework of such interactivity.

1.2. Nematodes in Soil Food Webs

Nematodes form one of the largest phyla in the animal kingdom, with more than 25,000 species described to date, and an estimated ≈10 million species [25]. They are the most abundant metazoans, e.g., in soils 3.5–5 million individuals per square meter are common [26]. A recent global survey estimated a total nematode biomass of approximately 0.3 gigatonnes are available as resources for higher predators in surface soils across the world [27]. Soil nematodes are either free-living (FLN) or parasites of plants (PPN) and animals (APN) [28]. The FLN taxa consume bacteria, fungi, protozoa, algae, small rotifers, enchytraeids, as well as other nematodes. Additionally, "facultative root and fungal feeders" change resource depending on availability, and thus display considerable resilience to, e.g., crop removal at harvest [29]. Overall, nematodes have important roles as primary, secondary, and tertiary consumers [30] and, moreover, are prey of the micro- and mesofauna, forming an important node and transition in the soil food web.

With functional groups in both food chains, the herbivore and the detritivore, nematodes can cross-link the pathways of energy and nutrients (Figure 1). In the herbivore food chain, more than 4100 PPN species are responsible for an estimated economic loss to the agricultural sector of nearly $125 billion annually [31]. The detrital food chain comprises the bacterial and fungal grazers and the related decomposition pathways, with the latter pronounced in forest soil due to frequently recalcitrant plant litter [32]. Finally, rhizodeposition fosters microorganisms and the associated bacterial channel, the dominant pathway in arable soils [33]. Taken together, nematodes are widely involved in ecosystem-level processes such as soil energy flow and nutrient cycling (e.g., [34,35]).

Their high abundance, species, and trophic diversity make nematodes good indicators of food web conditions [36–38]. Nematode life history traits and trophic groups provide a framework of indices to determine food web disturbance, succession, carbon pathways, enrichment, and structure [37]. Further, to assign the magnitude of ecosystem response, Ferris [39] established "metabolic footprints" as functional attributes by integrating nematode body mass and activity (i.e., respiration). These approaches are used, e.g., as functional descriptors of land use [40] or as models towards identifying sustainable soil health management [41]. Comparable to the famous model *Caenorhabditis elegans*, nematode trophic networks have developed into a model providing insights into the nature of ecosystem functions and services as well as soil and plant health [42,43].

1.3. Mites in Soil Food Webs

Mites are one of the most abundant groups of the mesofauna (reaching up to 85% of the soil invertebrate fauna: [44]), and are also diverse, with numerous species mainly from Mesostigmata, Oribatida and Prostigmata [45–48]. Mites are characterized by the trophic levels they occupy, the multiplicity of reproductive strategies they exhibit, and their diverse forms of dispersal [45,49]. Due to their importance in edaphic processes and their response to perturbation, e.g., in agricultural systems [50], mites have been used as indicators of environmental disturbance, particularly taxa of Oribatida (excluding the Astigmatina cohort) [51,52] and Mesostigmata [53–55].

Edaphic Mesostigmata are an abundant and diverse group, universally present in soil. Although fungal and detritivorous species are known, these mites are largely predators of other invertebrates, including plant pests [6,45,46,56–58]. Many species, especially the sub-orders Dermanyssina and Parasitina, are considered aggressive predators that have very active prey-seeking behavior in leaf litter and soil pores [47]. Soil surface- and litter-dwelling Mesostigmata are large, generally well-sclerotized, and predators of arthropods, whereas taxa inhabiting greater soil depths are relatively small, poorly sclerotized and mainly feed on small invertebrates such as nematodes [45,59].

Oribatid mites have been recognized as a characteristic soil group due to their high abundance, juvenile polymorphism and slow reproduction. In addition, oribatids are an important group involved in several processes occurring in the soil, such as decomposition of organic matter, control of microorganism and nematode populations, and facilitation of

microbial colonization [45,60,61]. Oribatids are sensitive to changes in soil ecological quality, as has been proven by studies such as Maraun et al. [61], Arroyo and Iturrondobeitia [62], Minor and Cianciolo [63], Illig et al. [64], Kardol et al. [65] and Nielsen et al. [66]. Oribatids are the dominant group in the upper soil layers and reach up to 150 species in a single location [67], and between 50,000 and 500,000 individuals per square meter [45].

The soil Prostigmata group is composed of species that are predators of other arthropods and nematodes, but also fungivores. These mites are quite abundant in some ecosystems and their population can grow rapidly [45,68,69].

2. What Has Prevented the Broader Use of Soil Predatory Mites and Why Should This Change in the near Future?

To date there are several reasons for the limited use of soil predatory mites in agricultural systems for the control of soil pests: (1) Pre-plant soil sterilization by fumigation, solar energy or steam as well as pesticides applied to the soil are still recommended [70,71]. (2) Agricultural soils lack structure and conditions limit the mobility and ability of mites to forage for prey [72], and they are deficient in organic matter [73], which supports soil biota growth. (3) Only limited species of predatory mites are commercially available (Table 1), and distributing novel generalist biocontrol agents (BCAs) across borders is becoming more and more problematic due to legislation requiring specific risk assessments for each species [74]. (4) The effect of prey species' suitability on life table parameters are usually tested separately for each prey, but predator fitness is likely to be better when different prey types are offered together [22]. (5) Identification of species must be performed by experts in soil predatory mite taxonomy, an expertise in shortage on a global scale [75]. (6) Knowledge is lacking on the predation capacity of predatory mites in agricultural soils with given abiotic and biotic attributes, because most studies are conducted in artificial laboratory set-ups. Of the 177 publications we reviewed with reports of trophic relationships between mites and nematodes, 149 were exclusively laboratory experiments, especially in Petri dishes; 17 were conducted in potted plants either in the laboratory or in greenhouses; and only 24 included observations or experiments in the field (Table S1).

While soil sterilization is still being used, mostly in conventional agriculture, for the control of soil pests, this cannot be considered to be a sustainable solution as it needs to be routinely repeated and negatively impacts soil diversity [76]. Additionally, pesticides applied to the soil pose a potential hazard to the beneficial soil meso- and macrofauna [77]. However, the availability of these pesticides is decreasing as registrations are being reviewed and revoked by the respective authorities [78–80].

Similar to the scientific and public awareness of the need for the reduction of pesticide use [81,82], there are initiatives across the globe, all with the common objective of caring for soils [83], aimed at enhancing soil fertility and preserving and conserving soil biodiversity [84] including: the EU Soil and Biodiversity Strategies, EU Soil Observatory, FAO UN Global Soil Partnership (GSP), the Intergovernmental Technical Panel on Soils (ITPS), the Convention on Biological Diversity (CBD) and the Global Soil Biodiversity Initiative (GSBI). Ultimately, these initiatives will lead to environmentally friendly soil practices, supporting functional soil food webs capable of providing the necessary ecosystem services.

The drawback of a low number of commercialized species and the legislation required for registering new species will likely continue to restrict their use for augmentative biological control. However, these limitations do not apply to the use of known and novel BCAs in conservation biological control programs. This is especially true when soil amendments, such as cover crops [85,86] and various composts [87,88], are utilized for enhancing abiotic and biotic soil attributes pertaining to the conservation of multiple species of arthropods and FLN.

Finally, embracing soil biodiversity for the conservation biological control of soil pests is challenging because it requires specialized taxonomists, an expertise that is in short supply across the globe. In recent studies [89,90], we have met this challenge by applying an integrative taxonomic approach, utilizing the Barcode of Life Database system (BOLD)

platform. This entailed a combined effort where agronomists and/or ecologists were responsible for collecting and extracting samples, specialized personnel for DNA barcoding and expert taxonomists for morphological identification. These studies contributed novel sequences of expertly identified soil predatory mites to BOLD and provided new information on the species diversity of soil mites in farming systems.

Table 1. Soil mites commercialized for biological control (modified after Van Lenteren [91] and Knapp et al. [92]).

Species	Target	Region of Application	First Commercial Use
Androlaelaps casalis (Berlese, 1887)	*Dermanyssus*	Europe	2012
Stratiolaelaps miles (Berlese, 1882)	Sciaridae	Europe, North America, Asia, Aus/NZ	1995
Stratiolaelaps scimitus (Womersley, 1956)	Sciaridae, thrips	Europe, Latin America	1990
Gaeolaelaps aculeifer (Canestrini, 1884)	Diptera, thrips, mites	Europe, North Africa, North America, Asia, Aus/NZ	1995
Gaeolaelaps gillespiei Beaulieu	Sciaridae, thrips	North America (Canada)	2009
Macrocheles robustulus (Berlese, 1904)	Diptera, thrips, Lepidoptera?	Europe	2010
Pergamasus quisquiliarum (Canestrini, 1882)	Symphyla	Europe	2000
Cheyletus eruditus (Schrank, 1781)	*Dermanyssus*, pests of stored products	Europe	1985

3. Nematophagous Mites

Despite the large number of published studies showing interactions between mites and nematodes (177 publications, Table S1; mostly in laboratory experiments), the understanding of this interaction is still neglected, as stated by Walter and Proctor [47]. According to these authors, there are two main reasons for the lack of study. The first is related to the conception that mites are restricted to air-filled soil pore spaces, while nematodes are restricted to water-filled pore spaces, limiting their encounter and interaction. However, this argument is not entirely accurate, because it is known that nematodes can move between air-filled pore spaces, as well as that some mites are able to extend their chelicerae into water films to extract nematodes. The second mis-assumption is that the size and soft elongated body of nematodes allows them to enter small soil pores, not accessible for large mites with sclerotized and inflexible shields. However, nematophagous mites, such as many Rhodacaridae [8] and several Ascidae [93], have an elongated and flexible body, allowing them to move through small spaces, or have chelicerae capable of reaching these small pores [47,94] (for details see Section 5.2).

3.1. Oribatida (Non-Astigmatina)

Few studies have been conducted on the interaction between Oribatida and nematodes. Of the 177 references reviewed, only 13 studies investigated Oribatida (Table S1), which corresponds to approximately 60 species or morphospecies of Oribatida, related to about 20 species of nematodes or mixtures of different nematodes. The first studies showing a relationship between Oribatida and nematodes were conducted by Rockett and Woodring [95,96] who observed *Pergalumna* (*P.*) *emarginata* (Banks) (cited as *Pergalumna omniphagous* Rockett and Woodring) feeding on a FLN and a PPN. Based on their observations, these authors suggested that oribatids could be an important regulating factor for nematode populations. Following these studies, nematode consumption was shown for various oribatids, yet only in a few cases (e.g., [6,97–99]) species were reported to have succeeded in developing on a nematode-based diet. As for the type of nematodes, most studies reveal FLN as an important prey, but feeding and reproduction on PPNs and APNs

takes place too (Table S1). Recently, DNA gut content analyses revealed FLN as a frequent diet of 14 Oribatida species in forest soil [100–102] (see Section 4). This indicates that nematodes are part of the diet in the field, despite the availability of other resources.

3.2. Astigmatina

While Astigmatina is a group of mites that is not well-represented in soil, Acaridae may be especially abundant in leaf litter and the upper soil layers rich in organic matter [68]. Although scarce (19 out of 177 published studies reviewed), there are some reports of nematophagy. The first mention of this interaction was made by Karg [103], reporting eleven- and five-times higher populations of *Rhizoglyphus echinopus* (Fumouze and Robin) and *Tyrophagus similis* Volgin (cited as *Tyrophagus dimidiatus* (Hermann), *Tyrophagus infestans* Berlese), respectively, in fields contaminated with *Globodera rostochiensis* (Wollenweber) Skarbilovich (cited as *Heterodera rostochiensis* Wollenweber) compared to non-infested fields. Even though no direct trophic relationship between nematode populations and Astigmatina was established in this study, it is possible that the mites may have increased their populations because of the large availability of nematodes as food source. *Tyrophagus similis* was later reported as a consumer also of FLN [97,98], while *R. echinopus* has only been reported as a consumer of PPNs [104]. The latter is also true for *Rhizoglyphus robini* Claparede, where *Meloidogyne incognita* (Kofoid and White) Chitwood was observed as prey [105]. The latter two species are considered important soil-dwelling pests of plants such as bulbs [106] that under special conditions can have a regulating effect on soil nematodes [68]. The Astigmatina species with the most reports of nematophagy is *Tyrophagus putrescentiae* (Schrank), using 14 different species of FLNs [107,108], 17 species of PPNs [108–111] and one species of APN [112] as prey. Moreover, *Sancassania* species are consumers of entomopathogenic nematodes, reducing their populations in the field [113].

The effect of a nematode-based diet compared to other diets has not been extensively studied for Astigmatina species. There are only reports for *Sancassania manure* (Eraky & Osman) and *Sancassania* sp. (cited as *Caloglyphus* sp.). In the first case, fecundity was higher with an unidentified yeast and cheese, than with *Meloidogyne* sp. [114]. For *Sancassania* sp., a slight delay in development was observed when feeding on *Cephalobus* sp. compared to an unidentified yeast [115]. Further experiments are needed to determine whether a mixed diet including nematodes can be beneficial for these mites.

3.3. Prostigmata

For Prostigmata only 11 publications recorded consumption of nematodes (Table S1). More studies have been performed, but the results show that this mite group does not seem to have a nematophagous habit for the most part. A total of 16 species, mainly of the family Cunaxidae, are reported to consume nematodes, with most able to be reared or developed on nematode-based diets [116–120]. Walter [7] found that several species of Eupodidae are capable of feeding on nematodes, but at low frequency and with a preference for microphytes.

Comparison of the effect of a nematode-based diet and other diets on mite fitness has only been conducted for *Cunaxa capreolus* (Berlese) and *Pulaeus pseudominutus* (Shiba). The fecundity of *C. capreolus* was higher when feeding on J2 of *M. incognita* than when feeding on J2 of *Tylenchulus semipenetrans* Cobb [120] and was higher when feeding on the colembolan *Entomobrya musatica* Stach than on the nematode *Mesorhabditis scanica* (Allgén) Sudhaus (cited as *Rhabditis scanica* Allgén) [119]. In the case of *P. pseudominutus*, no differences in fecundity were observed when mites were fed with the fungi *Fusarium oxysporum* Schltdl. and *Pythium spinosum* Sawada compared to the nematode *Rhabditella muscicola* Andrássy [118]. As with Oribatida, further studies are needed to establish the relationship these mites have with nematodes in the soil and how this interaction may be beneficial in the control of other organisms, including plant pests.

3.4. Endeostigmata

In the suborder Endeostigmata, nematophagous mites have been reported [6,47,121] in five species belonging to two families (Table S1). Most studies with these mites have been conducted with FLN; however, *Alicorhagia fragilis* Berlese and *Alycus roseus* Koch were shown to consume the entomopathogenic nematode *Steinernema feltiae* (Filipjev) Wouts, Mráček, Gerdin and Bedding. For most of the reported species of this family, reproduction and development have been observed with a nematode-based diet.

3.5. Mesostigmata

Mesostigmata is the group with the most studies (148 publications out of 177 reviewed) of interactions with nematodes (Table S1). However, only four were conducted on communities of mites and not on a specific species. In these studies, either nematode consumption was observed [47] or that the presence of these predatory mites coincided with the reduction of PPNs [105,122,123] (cited by [124]). Among these studies, Stirling [105] reported that Mesostigmata mites were present in all sawdust-based amendments added to pots in field and greenhouse, which coincided with a reduction in *M. incognita* density and a reduction in root galls compared to sterilized soil and sand.

3.5.1. Gamasina

Within Gamasina, nematophagy has been reported in 250 species within 19 families, by 134 studies performed with about 106 different species of nematodes, 19 unidentified nematodes and several species mixtures (Figure 2, Table S1). Azevedo et al. [125], Castilho et al. [8], McMurtry et al. [126], Moreira and Moraes [127], and Moraes et al. [93] reviewed the dietary habits (including nematodes) up to 2015 for Gamasina mites including Ascidae, Blattisociidae, Digamasellidae, Eviphididae, Heatherellidae, Laelapidae, Leptolaelapidae, Macrochelidae, Melicharidae, Ologamasidae, Parasitidae, Parholaspididae, Phytoseiidae, and Rhodacaridae.
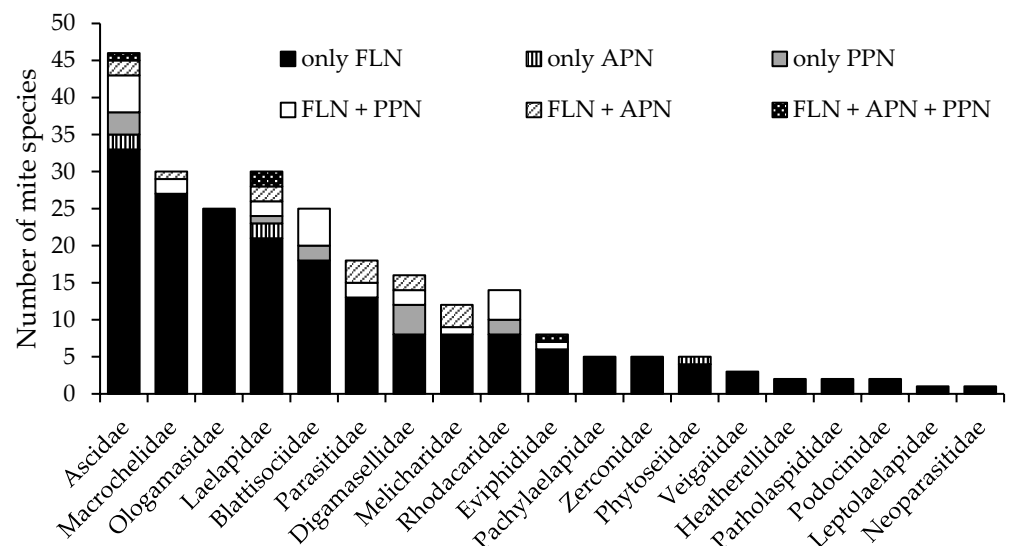

Figure 2. Number of mite species per family of Gamasina (Mesostigmata) reported consuming nematodes. APN = animal parasitic nematodes, FLN = free-living nematodes, PPN = plant parasitic nematodes.

The family with the highest number of nematophagous species is Ascidae (46 species, Figure 2). Species in this family consume FLNs, APNs and PPNs. The ascid species consuming the most nematode species is *Gamasellodes vermivorax* Walter (11 FLN species, two PPN species, two APN species, one species of unidentified nematode and four mixtures of different nematodes), followed by *Protogamasellus mica* (Athias-Henriot) (nine FLN species, five PPN species, one species of unidentified nematode and four mixtures of different nematodes). Generally, reproduction and development have been observed with

a nematode-based diet, and in several cases, reproductive parameters have been better with FLNs than with PPNs [128,129]. The few comparisons of nematode prey with other diets showed that effects depended on the mite species. While in some cases shorter development times were reported with a nematode diet (e.g., *G. vermivorax*; [7,130]), in others higher fecundity occurred with other diets (e.g., *Arctoseius cetratus* (Sellnick) [131]; *Protogamasellus minutus* Nasr [132]; *Protogamasellus similis* Genis, Loots and Ryke [133]). In the greenhouse, the colonization of Ascidae species has been observed on PPN-infested pots ([117,134]) and also reduction of both FLN and PPN populations when, e.g., *P. mica* were present [135]. Several species of this family are considered to belong to the small-pore nematophagous guild because of their size and body shape [6,47,59] (see Section 5.2).

Laelapidae and Macrochelidae are the families with the second-highest number of nematophagous species (both with 30 species, Figure 2). For both families, most of the reports involve FLN. However, there are more reports of species consuming APN and PPN in Laelapidae than in Macrochelidae (Table S1, Figure 2).

Laelapidae is well-represented in soil and leaf litter, although it is also found in association with animals [136]. *Cosmolaelaps indicus* Bhattacharyya (cited as *Hypoaspis calcuttaensis* Bhattacharyya) consumed many different nematodes (16 FLN species, 17 PPN species) [137] (Table S1), followed by *Gaeolaelaps aculeifer* (Canestrini) (cited as *Hypoaspis aculeifer* Canestrini) (four species of FLN, five species of PPN, two species of APN, two species of unidentified nematodes and two mixes of FLN and PPN). The latter is a commercially produced species for the control of agricultural pests that have at least part of their life cycle in the soil [136]. Several field studies and greenhouse experiments for PPN control have been conducted with the commercially available species *G. aculeifer, Stratiolaelaps miles* (Berlese) and *Stratiolaelaps scimitus* Womersley demonstrating reductions in nematode abundances [24,138–141].

Comparison of a nematode-based diet with other diets has been conducted in species such as *Cosmolaelaps claviger* (Berlese) [142], *Cosmolaelaps jaboticabalensis* Moreira, Klompen & Moraes [143], *Cosmolaelaps simplex* Berlese [144], *Cosmolaelaps vacuus* (Michael) (cited as *Hypoaspis (Cosmolaelaps) vacua* (Michael)) [7,130], *G. aculeifer* [145–147], *Gaeolaelaps oreithyiae* Walter and Oliver [148], *S. miles* [149], and *S. scimitus* (Figure 3) [24,141]. In many cases, a positive effect on the reproductive parameters and developmental times of mite species has been observed with a nematode-based diet, especially FLN (e.g., [7,130,143,146–148]). On one hand, such positive effects of a nematode-based diet can hamper predation on a target pest, e.g., *Frankliniella occidentalis* (Pergande), an insect pest of great importance in various crops [143]. On the other hand, a study by Azevedo et al. [24] shows that the effect of FLN as supplementary food can result in a decrease in damage caused by pests such as root-knot nematode, *M. incognita,* likely mediated by an increased predator fitness.

Macrochelidae is a family especially associated with temporary habitats such as excreta and decaying animals, so efforts to use this family as a biological control agent have largely focused on pest organisms associated with these environments such as different species of flies [125]. It is also in these habitats, or on substrates simulating these environments, that the trophic relationship with nematodes, especially FLN, has been observed (Table S1). *Macrocheles muscaedomesticae* (Scopoli) consumed most nematode species (11 FLN species, one PPN species and four unidentified FLN species), followed by *Glyptholaspis confusa* (Foà) (five FLN species). For many mites in this family, reproduction and development have been observed on a nematode-based diet. Also, the comparison with other diets was performed and in several cases preference or higher fecundity has been found when mites feed on fly eggs or larvae (e.g., [150–153]). However, higher fecundity has been observed also with nematode diets (e.g., [150,154,155]) and even the addition of nematodes to other diets has led to higher reproduction (e.g., [154,156,157]). Although there may be a decrease in predation of the target pest with nematodes as an alternative diet, mite fecundity increases [23,154]. Ultimately, such a higher predator population can control the pest of interest in the medium to long term [23]. Another important point to consider is that adults of several species of this family seem to prefer fly eggs or larvae for feeding,

but in immature stages the preference may be towards nematodes (e.g., [156–158]). This suggests that a diverse diet including nematodes may favor the pre-adult development and sustainability of Macrochelidae to perform as BCAs (see also Section 5.1).
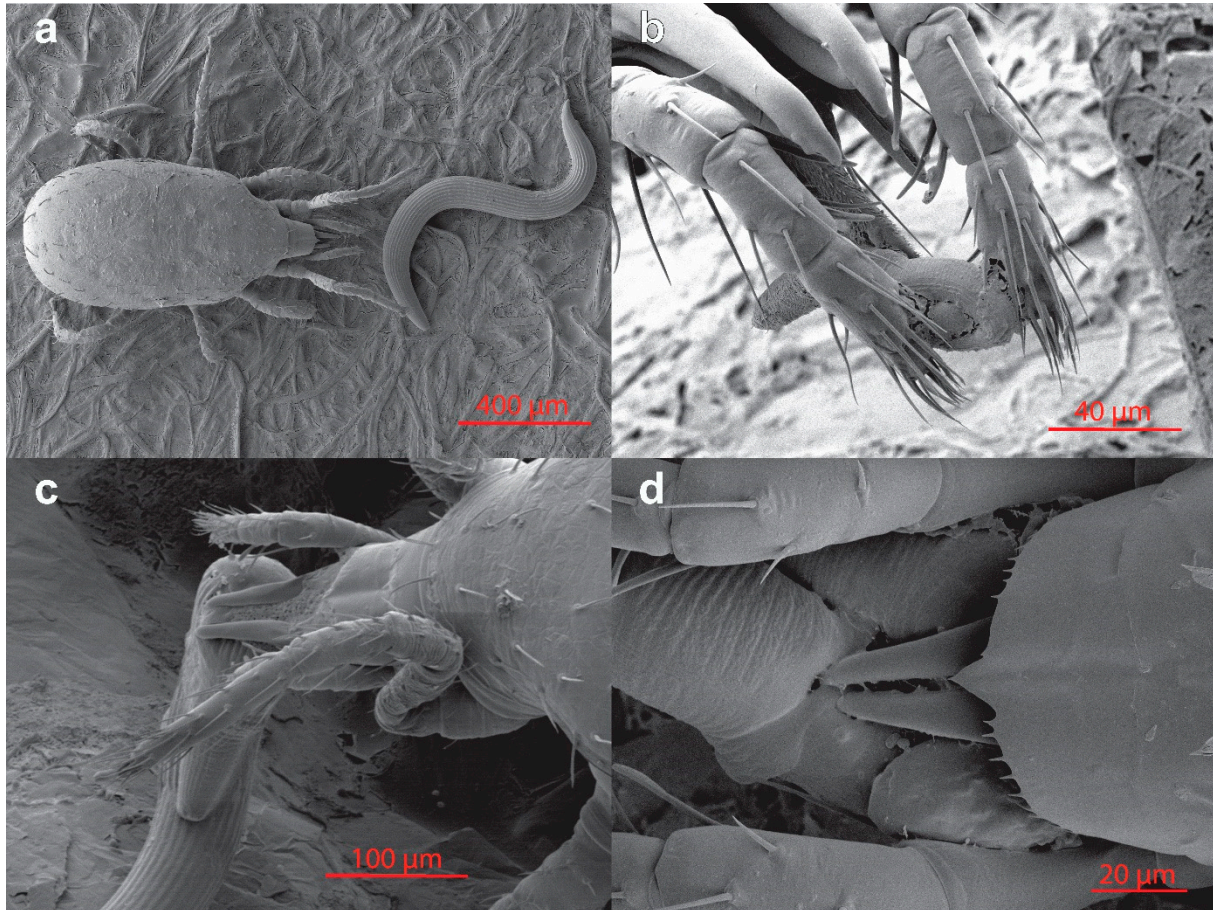

Figure 3. Low temperature scanning electron microscope images of *Stratiolaelaps scimitus* Womersley sensing and feeding nematodes. (**a**) Adult female senses the free-living nematode *Pristionchus aerivorus* (Cobb in Merrill and Ford) Chitwood by touching the nematode with the tarsus of leg I. (**b**) Adult female grasping a J2 of the root-knot nematode *Meloidogyne incognita* (Kofoid and White) between palps just at the level of the apotele. (**c**) Immature holding *P. aerivorus* with its chelicerae and initiating the feeding process. (**d**) Close-up of the mite gnathosoma in dorsal view of an adult female holding between the chelicera and feeding on the free-living nematode *Mesorhabditis inarimensis* (Meyl) Dougherty. Images: Joe Mowery, Gary Bauchan, Ron Ochoa, Lynn Carta, Eric Palevsky.

In Ologamasidae and Blattisociidae, 25 species have been shown to consume nematodes for each family (Figure 2, Table S1). For Ologamasidae only FLN consumption was observed (e.g., [115,159,160]), while for Blattisociidae predation on both FLN and PPN was reported (Table S1). For the latter, a nematode-based diet was also compared to other diets. For *Lasioseius africanus* Nasr [161], *Lasioseius berlesei* (Oudemans) [134], and *Lasioseius floridensis* Berlese [162], higher fecundity occurred with a nematode diet compared to other food resources. However, in other species such as *Lasioseius queenslandicus* (Womersley) (cited as *Lasioseius athiasae* Nawar & Nasr) higher fecundity has been observed with other diets [163,164]. In experiments with PPN, species such as *Blattisocius dolichus* Ma [124,165] and *Lasioseius penicilliger* Berlese [138] have been observed to reduce nematode populations.

In the case of Parasitidae, 18 nematophagous species have been reported (Figure 2). The species consuming the highest number of nematode species is *Pergamasus septentrionalis* (Oudemans) (four FLN species and two APN species) [100–102]. When comparing a nematode-based diet with others, higher fecundity with nematodes has been

observed in *Parasitus bituberosus* Karg [22,166], and *Porrhostaspis lunulata* Müller [167]. Rueda-Ramírez et al. [22] further showed that daily oviposition was 1.4 times higher when the target prey, *F. occidentalis*, was mixed with the FLN *Rhabditella axei* (Cobbold), than with a solely nematode diet. In this family, as in Macrochelidae, a varied diet seems important as it has been observed that immature stages may prefer nematodes, while feeding behavior may be different in the adult stage [22,158].

Diagamasellidae, Rhodacaridae and Melicharidae have reports of 16, 14 and 12 nematophagous species, respectively (Figure 2, Table S1). Diagamasellidae and Melicharidae were shown to feed on APN, FLN, and PPN, while in Rhodacaridae there are only reports of consumption of FLN and PPN. This is not unusual as species of the first two families are associated with animals, especially arthropods, while Rhodacaridae mostly inhabit soil [8]. In the latter family several species are considered generalist predators, but they reproduce and develop very well on a nematode-based diet [6,59,168]. Moreover, their shape and size give them the ability to reach spaces in the soil where nematodes are present, comparable to Ascidae (see Section 5.2) [6,47,59]. In these three families, species capable of developing and reproducing on a nematode-based diet have been observed, which in several cases, had a more positive effect on the reproductive parameters of the mite population than other diets (Table S1).

For Eviphididae, only eight nematophagous species have been reported (Figure 2, Table S1) despite being considered a family with commonly nematode specialist species [6,7,47], which may be because this family is relatively small (about 108 species) [169] compared to Macrochelidae and Laelapidae, or owing to the few studies conducted (12 publications). For most, reproduction (e.g., [170,171]), development (e.g., [6,7]) or preference for nematodes (e.g., [7,145]; Table S1) has been observed. In the case of *Alliphis siculus* (Oudemans), populations increase in fields contaminated with PPN [145,172] and the addition of nematodes to the diet considerably increases their abundance [173]. Eviphididae is a family that seems to be closely related to nematodes, suggesting their regulatory potential on populations of these organisms.

Other families (see Figure 2) have fewer reports of nematophagous species (five or less), possibly because they are less common or less-studied families, e.g., Zerconidae, or due to different feeding preferences e.g., Veigaiidae [6,8,59]. Among these, Zerconidae deserve highlighting, as species specialized in consuming nematodes have been reported [7] and, moreover, in microcosm experiments their presence coincides with low nematode populations [174].

3.5.2. Uropodina

Within Uropodina, nematophagy was shown in 15 species within 5 families (15 publications; Table S1). The family with the most species reported is Uropodidae, with *Uropoda cassidea* (Hermann) consuming the most nematode species in this group (six FLN species and one APN species). Reports of the nematophagy of *U. cassidea*, as well as that of *Trachytes aegrota* (Koch), are based on the detection of nematode genetic material in the gut of the mites [100–102]. Other studies have shown that different uropodid species prefer nematodes (e.g., [152,158,175]) and that addition of nematodes in the diet may increase reproduction (e.g., [176,177]).

3.5.3. Other Mesostigmata Groups

Nematophagy has also been reported in one species of Microgyniina, four species of Sejida and ten species of Trigynaspida (Table S1). Further studies are needed to better understand the effect of nematodes on different biological parameters of these mites.

4. Nematodes as a Food Source for Mites in Ecosystems

Nematodes serve as a diet for many predatory soil animals, particularly other nematodes [28,178] as well as several groups of arthropods such as Acari, Coleoptera, Collembola, and Symphyla [59,174,179,180] (for mites see Section 3). Although early soil food web mod-

els assigned mites as top predators [181] (Figure 1), the trophic link to nematodes has not received attention for a long time, with exception of Mesostigmata, as worm-like prey was indicated by their mouthpart morphology [58,182,183].

A suite of advanced methodological approaches now provides deeper insight into mite feeding behavior in the field. Using stable isotopes (^{15}N/^{14}N) Schneider et al. [184] showed the first evidence that oribatid mites span over four trophic levels, from phycophages over primary and secondary decomposers to carnivores. The combination of ^{15}N isotopic signals from forest soil mesostigmatids and oribatids, with data from laboratory feeding experiments, further pointed to a central role in regulating the population dynamics of the microfauna [185]. Finally, Klarner et al. [186] integrated the variation in ^{13}C/^{12}C and ^{15}N/^{14}N of 40 mesostigmatid mites from an old growth beech forest soil, which revealed that the diet of the dominant species consisted in large part of nematode prey.

A more fine-tuned approach is molecular gut content analysis, which characterizes feeding interactions at a high level of taxonomic resolution [187]. Heidemann et al. [100] established the first primers for binary trophic links between nematodes and mites in laboratory no-choice experiments. Subsequently, for forest soil food webs, nematode predation was assigned for species in Uropodina, Gamasina, and Oribatida [102]. Thus, FLN form an important prey for mites, also in groups commonly regarded as detritivores such as Oribatida. In a follow up study, Heidemann et al. [101] showed that nematode consumption by mites differed due to microhabitat, i.e., litter, grass, and moss, indicating distinct trophic niches in this predator–prey interaction.

This considerable top–down control of predatory and omnivore mites on nematodes can impose biocontrol on PPN in the rhizosphere [123,188], but also affect bacterial and fungal feeders (up to 50% less biomass [189]) and the activity of their microbial resources [180]. This trophic linkage even results in the fact that ecological indices based on nematode community structure (see Section 1.2) are reliable predictors of the trophic composition and functional characteristics of soil mite assemblages [50]. For example, bacterial-feeding and predatory nematodes, together with predatory mites, were associated with high food web enrichment and structure. This highlights the close relationship between nematodes and mites in soil ecosystems.

5. Variables Important for Trophic Interactions

5.1. Nematodes as an Important Source of Fatty Acids in Soil Food Webs

Nutritional quality is a key determinant for population development in soil microarthropods and can affect, e.g., fitness traits such as body mass [190], offspring and longevity [146] or even male reproductive behavior and mating success [191]. Using the oribatid *Archegozetes longisetosus* as model, Brückner et al. [192] showed that diet quality affected nine different traits related to life history, morphology, and exocrine gland chemistry. These effects were mainly based on element stoichiometry in the diet, with offspring correlated to the C/N ratio, while body mass was linked to the C/P ratio [193]. To avoid nutritional imbalances active prey mixing is common, also in predatory mites [194]. For mass rearing of mites as BCAs, dietary supplements as well as improved prey quality were shown to have beneficial impact on biocontrol parameters, i.e., the robustness of the predatory mite population via its target pest [195,196].

For a long time, soil microarthropods were assumed to optimize food intake by selection according to C/N ratio [192,197,198], while other nutrients were rarely taken into account. Only recently, the lipid composition of the diet was established, in particular the content of ω3 long-chain polyunsaturated fatty acids (ω3 LC-PUFA). Eicosapentaenoic acid (EPA, 20:5 ω3) and docosahexaenoic acid (DHA, 22:6 ω3) are considered as semi-essential biomolecules in food webs, due to their key physiological functions in many animals [199]. However, ω3 LC-PUFAs are not widely available in terrestrial food webs [200]. Early work reports the synthesis of EPA in four species of the FLN *Caenorhabditis* [201,202] as well as EPA occurrence in *Turbatix aceti* [203]. Recently, the ability to synthesize EPA was described

in the taxa *Panagrolaimus* and *Mesorhabditis* [204]. This suggests nematodes are an important source for ω3 LC-PUFA in the soil food web.

Mites are known to perform the initial step of PUFA biosynthesis, the desaturation from oleic acid to linoleic acid [205,206]. Experiments with ^{13}C glucose as substrate showed that linoleic acid is stably converted into 6,9, heptadecadiene, a major secretory component [207]. To date, in the few lipid patterns available for mites, no ω3 LC-PUFAs are reported for body lipids, oil glands or cuticular surface [208–210]. That the provision of EPA and DHA by nematode prey enhances consumers' life cycle, health, and fitness, was shown for Collembola [211]. Similarly, nematodes can provide these nutritionally valuable biomolecules to their major predators, the mites, fostering overall fitness and thereby biocontrol function.

5.2. Size Matters?

At the micro-scale, soil structure constrains food accessibility. As stated by Walter and Ikonnen [59] and observed by other authors [8,212] small Rhodacaridae-type mites (species of Ascidae, Digamasellidae and Rhodacaridae, especially) have a small, elongated body with a split dorsal shield and a flexibility that allows them to access deeper soil layers. There, they can reach depths [8,59] or pore spaces [47] populated by nematodes and feed on them. These mites were assigned by Walter and Ikonnen [59] as the nematophagous small-pore guild (Figure 4a).
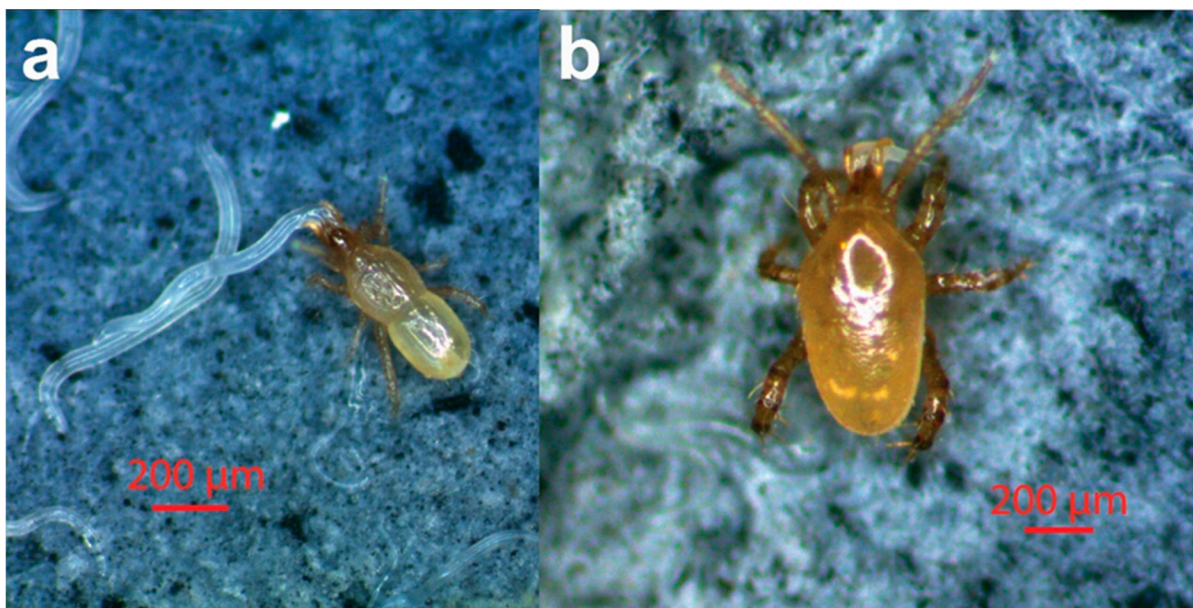

Figure 4. (**a**) Adult female of *Protogamasellopsis zaheri* Abo-Shnaf, Castilho and Moraes (Mesostigmata: Rhodacaridae) from the small-pore guild feeding on the free-living nematode *Acrobeloides* sp. (**b**) Adult female *Gaeolaelaps aculeifer* (Canestrini) (Mesostigmata: Laelapidae) feeding on the free-living nematode *Panagrellus* sp.

Besides the many reports of nematode preference and ability to control populations in the small-pore nematophagous guild (see Table S1), also larger mites (Laelapidae, Macrochelidae, and Parasitidae, especially, Figure 4b) voraciously feed on nematodes (e.g., [22,23,150,155]). It can be assumed that medium-to-large sized mites, mostly inhabiting the upper soil layers, predominantly feed on nematode populations associated with the organic matter present (e.g., all trophic groups of FLN and PPN, attacking the roots of young plants), whereas smaller mites accessing greater depths and small pores mainly feed on nematodes that occupy these spaces (e.g., bacterial- and fungal-feeding FLN and juvenile PPN).

Size and shape may confer the ability of certain mites to reach spaces where nematodes are present in the soil. However, this is not always associated with being exclusively nematophagous. For example, Walter et al. [6] found several species of Rhodacaridae-type mites (e.g., *Gamasellodes vermivorax* Walter and *Rhodacarellus silesiacus* Willmann) that, although they fed and developed very well on nematodes, they also fed on other prey such as Collembola and mites. These same authors classified some species of Eviphididae (Mesostigmata) and Endeostigmata, whose body format is not slender and without a divided dorsal shield, as nematode specialists. This food flexibility within guilds or morphotypes of mites can be viewed as an adaptation to the accessibility of nematode resources in the soil matrix.

6. Enhancing Conservation and Efficacy of Soil Acarine Biocontrol Agents (ABA)

Beretta et al. [4] recently reviewed the use of soil predatory mites, mostly applied as augmentative biological control agents for the control of edaphic stages of thrips, flies, mites, and PPN in greenhouse and screenhouse systems. While a considerable number of studies were cited, most were conducted on the two commercially available laelapid species, *G. aculeifer* and *S. scimitus* (Table 1). To improve the efficacy and establishment of augmentatively released soil predatory mites, the authors encouraged the provisioning of alternative foods and the addition of soil mulches. For many greenhouse systems these approaches are certainly valid since they are often soilless. In contrast to augmentative biological control in such protected agrosystems, conservation biological control in outdoors cropping systems promotes the 'modification of the environment or existing practices to protect and enhance specific natural enemies or other organisms to reduce the effect of pests' [213].

Ecofriendly soil management of abiotic and biotic parameters is crucial for the conservation of ABA. Abiotic interrelated physical attributes such as soil structure, texture, and water content [214] can be limiting factors for ABA foraging and survival [72] (see also Section 5.2). Abiotic soil attributes, especially soil organic matter, are essential for the growth of microbiota, upon which free-living nematodes graze [215,216], the latter serving as essential prey (as discussed above) for many soil predatory mite species. Conservation agriculture, promoted by the FAO as an ecofriendly approach, includes three principles: minimum mechanical soil disturbance, permanent soil organic cover, and species diversification [217]. Compared to the conventional practices of tillage, bare soil between crops and minimal crop rotation, conservation agriculture provides a solid foundation for re-generating functional soil food webs. Minimal mechanical soil disturbances help to conserve and preserve soil structure and texture, while permanent soil organic cover generates soil organic matter, moderates temperatures and retains soil moisture. Finally, species diversification by crop rotation [218] and the introduction of service crops [219] enhances soil microbiota biodiversity.

In a study conducted in a Long Term Research Agricultural Systems (LTRAS) project (12 years after it was established), the abundance of bacterial-feeding and predatory nematodes, as well as predatory and omnivorous mites, were greater in organic plots, predominantly under no till, and lowest in the conventional standard tillage [50]. In contrast, in a more recent study in olives and vineyards in semi-arid Mediterranean agroecosystems in Spain, the soil food webs of the organic and conventional systems were degraded, with similar low structure and enrichment nematode indices [220]. The authors suggested that organic management in itself is not enough and that soil conservation practices such as reduced tillage and cover cropping are necessary to enhance agroecosystem sustainability. Wang et al. [221] evaluated in a two-year study the effects of strip till cover cropping. In the second year, yield was significantly higher in the sun hemp cover crop treatment, as were the nematode structure index and abundance of predatory mites. In a long-term field study assessing the effects of tillage and cover crop over 16 years, management systems using cover crops strongly enhanced the nematode assemblages in the field soil [222]. Recently, using a soil amendment, Udalova et al. [223] demonstrated that the addition of

insect-compost enhanced the abundance of bacteriophagous, polyphagous, and predatory nematodes, and reduced root-knot nematodes, *M. incognita*, in tomato.

Just as many soil amendment studies focused on nematodes (some cited above) have not monitored mite communities, likewise, several mite studies have not taken into account FLN. Messelink and Kogel [224] applied a biowaste compost for the introduction of predatory mites and Grosman et al. [225] used a mulch layer and the provisioning of Astigmatina prey to enhance establishment, abundance and performance of the predatory mites *Macrocheles robustulus* and *Gaeolaelaps aculeifer*. Esteca et al. [226] applied dehydrated coffee husk and pulp as a mulch for the conservation biological control of *Tetranychus urticae*. In all three cases, these soil amendments probably altered FLN abundances, which could have in turn affected predatory mite populations and biocontrol efficacy (Figure 5).
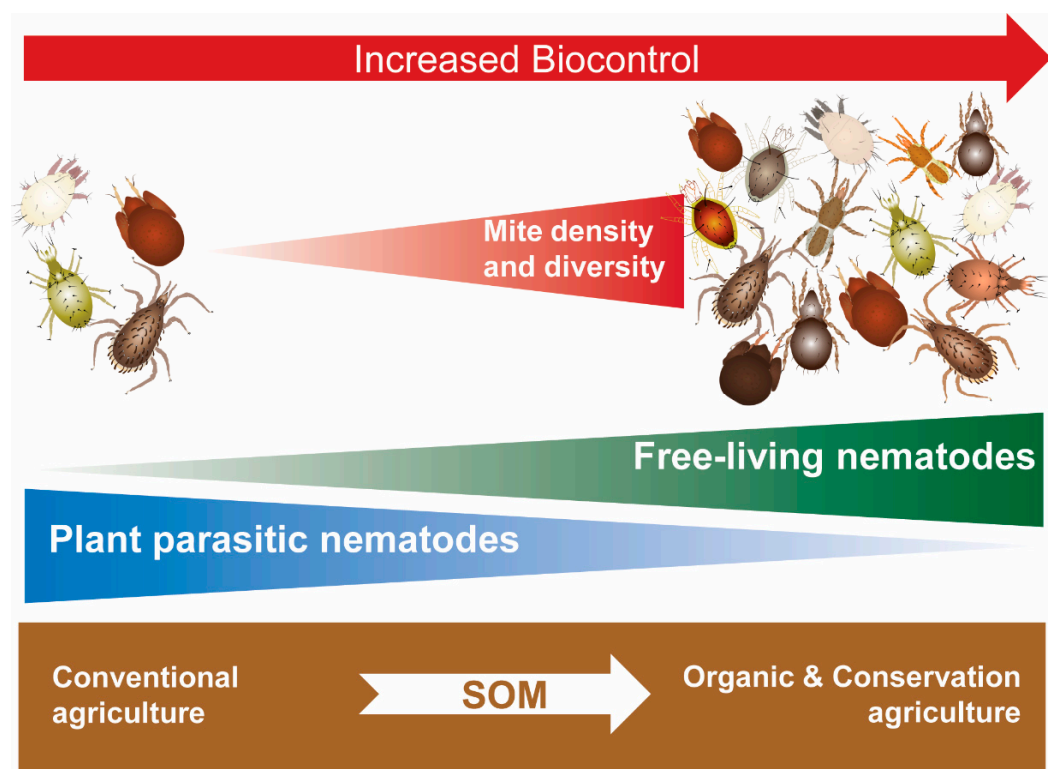

Figure 5. Schematic illustration of our hypothesis: conservation of soil mite predators with available, suitable, and accessible free-living nematodes as prey will provide better agricultural ecosystem performance and long-range sustainability.

The time and taxonomic skills required to morphologically identify mesofauna communities from soil samples are most likely the reasons why soil amendment manuscripts are usually focused on either mites or nematodes, but not both. Future studies on the effects of soil conservation practices on ecosystem services could consider using metabarcoding of soil samples, which have recently been used for identifying mite [227] and nematode communities [228].

7. Future Research Needed

Although numerous studies have been published on soil mite–nematode interactions, most have been conducted in the lab in small arenas with a single species of mite and nematode, assessing the effects on mite fitness and/or nematode control (Table S1). An important next step is to transfer laboratory research to semi-field and field conditions. Modern molecular approaches can support this in both taxonomic (i.e., barcoding) and ecological (i.e., gut content analyses) studies, allowing for a more realistic picture of the trophic linkages between mites and nematodes and its significance for biological control.

Future research should study soil mite and nematode assemblages in different cropping systems, soils, and climate zones. Soil degradation is recognized as a global threat and soil organic matter depletion is a significant factor in this. Novel conservation soil management strategies will aim at increasing soil organic matter and reducing soil erosion and compaction. Future research should assess how these management strategies will improve soil health and biodiversity, which largely include mites and nematodes. Harnessing the local biodiversity can favor the increase and sustainability of biological control agents and favor the restoration of soil food webs (Figure 5). Strategies may include the use of organic amendments derived from animal feed production and or composting, which increase the accumulation of soil organic matter and in turn foster soil life as well as biocontrol.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/agronomy13010032/s1, Table S1: Reports of mite species per group and family reported consuming nematodes [229–324].

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