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Systematic review and meta-analysis

Ecosystem functions supported by soil bacterivorous nematodes

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ABSTRACT

Nematodes provide essential ecosystem functions, yet their specific contributions remain insufficiently quantified. Among them, bacterivorous nematodes (BN) are abundant and functionally diverse, but their ecological roles are often overlooked. Here, we combine a comprehensive literature review with a *meta*-analysis to assess the contribution of BN to terrestrial ecosystem functions from controlled experiments. Across 1131 effect sizes, our *meta*-analysis shows that BN significantly promote key soil processes: they increase microbial biomass by 20%, microbial respiration by 31%, and enhance nutrient cycling, raising soil-available N and P by 21% and 17%, respectively. They regulate bacterial community composition through selective feeding and dispersal, and can stimulate enzymatic activities compared to soil without BN. BN also improve shoot and total biomass by 19% and 13%, shoot N amount by 22%, and root N amount by 35%. In addition, BN influence root morphological traits (e.g., lengths, branching) and can modulate mutualistic interactions, particularly with mycorrhizae and rhizobia. Finally, BN can also contribute to the degradation of soil contaminants, the regulation of pathogens, and carbon sequestration. However, these effects are modulated by several factors; they vary widely with nematode species, life-history strategy, soil nutrient status (especially soil C:N ratio and P availability), and experiment duration. We discuss underlying mechanisms, including consumer-driven nutrient recycling and microbial stimulation, and identify major research gaps in the functional ecology of soil BN. Our synthesis highlights BN as pivotal players in soil functioning and calls for broader recognition of their roles in sustainable agroecosystem management.

1. Introduction

Soil harbors about 59 % of the world's biodiversity (Anthony et al., 2023), including over one million species and billions of organisms belonging to bacteria, fungi, protists, nematodes, mites, insects and earthworms (Bardgett and van der Putten, 2014). These organisms perform crucial ecosystem functions and services through complex interactions, such as nutrient and water cycling, soil formation or climate regulation (Creamer et al., 2022; Delgado-Baquerizo et al., 2020; Lavelle et al., 2006). Additionally, soil life impacts aboveground processes (Bardgett and Cook, 1998), supports plant growth and nutrition in terrestrial environments, and enhances the resilience of soils against numerous threats (Tibbett et al., 2020). Developing a comprehensive, precise and up-to-date understanding of the multiple roles played by soil organisms, including improved parameterization of models for soil nutrient cycling and soil-derived greenhouse gas emissions, is essential for accurately predicting and effectively mitigating the impacts of global changes on ecosystem functions and services.

Nematodes, with their large taxonomic diversity (Hodda, 2022c) and wide range of functional features (Hodda, 2022b; Yeates et al., 1993; Zhang et al., 2024), are among the soil organisms that require a comprehensive exploration of their ecological roles to harness their potential in mitigating global changes on ecosystems functions. Nematodes alone are estimated to account for approximately one million species, with about 43–50 % of this diversity dwelling in soils (Anthony et al., 2023). These microscopic worms are widely distributed throughout the world (Van Den Hoogen et al., 2019), and exhibit a remarkable local species diversity and abundance (Nielsen et al., 2014), positioning them as one of the most abundant groups of organisms (Van Den Hoogen et al., 2019). Additionally, they have developed different feeding strategies, i.e., herbivorous, bacterivorous, fungivorous, omnivorous and predators, allowing them to occupy different trophic levels within the soil-food web (Hodda, 2022b; Yeates et al., 1993).

Among the five trophic groups, bacterivorous nematodes "BN" (Box 1) are often the dominant feeding strategy, composing up to 60–80 % of the total nematode abundance, except in forest ecosystems, where

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fungivores may dominate, and in agricultural fields, where herbivores can represent the major group (Van Den Hoogen et al., 2019). This proportion can reach up to 90–99 % in soils where microbial activity is high (Griffiths, 1994). BN exhibit variable alpha taxonomic richness from low values in disturbed crop soils up to 10 genera in mature ecosystems (Ettema, 1998; Hu et al., 2014; Nielsen et al., 2014). Notably, BN has particular features with significant functional implications that are not presented in the other feeding strategies. For instance, after a severe soil disturbance, the first colonizer nematodes are bacterivorous enrichment opportunists, which provide the primary prey base for larger nematodes and other predators, thereby facilitating the establishment of bigger organisms in the soil food web (Bongers, 1990; Ferris and Bongers, 2006; Ferris et al., 2001; Potapov et al., 2021). Their importance is also underlined from a phylogenetic perspective since they represented ~27 % and ~65 % of all nematode taxa and all nematode terrestrial taxa, respectively (Hodda, 2022a; Hodda, 2022b).

The ecological importance of BN for ecosystem functioning has already been reviewed (Lang et al., 2023; Mezeli et al., 2020; Trap et al., 2016). However, the literature has examined the role of BN as a part of a broader range of organisms, either with mesofauna (Lang et al., 2023), protist (Trap et al., 2016), diverse soil organisms (Mezeli et al., 2020), or with all nematode trophic groups (Ferris, 2010; Yeates, 2003), making it difficult to quantify the global contribution of BN to ecosystem functioning. In addition, this literature mostly focused on specific functions without providing a comprehensive exhaustive overview of the roles of BN.

To fill these gaps, we conducted a systematic review supplemented by a *meta*-analysis to provide a reliable synthesis of available observations, trends, discrepancies and gaps on the ecological roles of soil BN on terrestrial ecosystem functions. Our overarching research question was: what are the functions of BN in soils? The *meta*-analysis is based on experiments carried out under controlled laboratory conditions, emphasizing the causal effects of the presence of BN on numerous soil biological properties and functions and plant growth and nutrition. We also aimed to provide research perspectives that we believe are especially promising to enhance our understanding on this topic.

2. Methods

2.1. Global approach

We conducted a systematic review and a *meta*-analysis using a reproducible process to search the literature on this topic (Puissant et al., 2021). By combining a literature review with *meta*-analysis, we integrated qualitative insights with quantitative data to estimate the effects of the presence of BN on specific soil functions. This approach ensures a robust and comprehensive examination of the available knowledge on the role of soil BN in ecosystem functions.

We applied the Common International Classification of Ecosystem Services (CICES) version 5.1 to systematically categorize the ecological

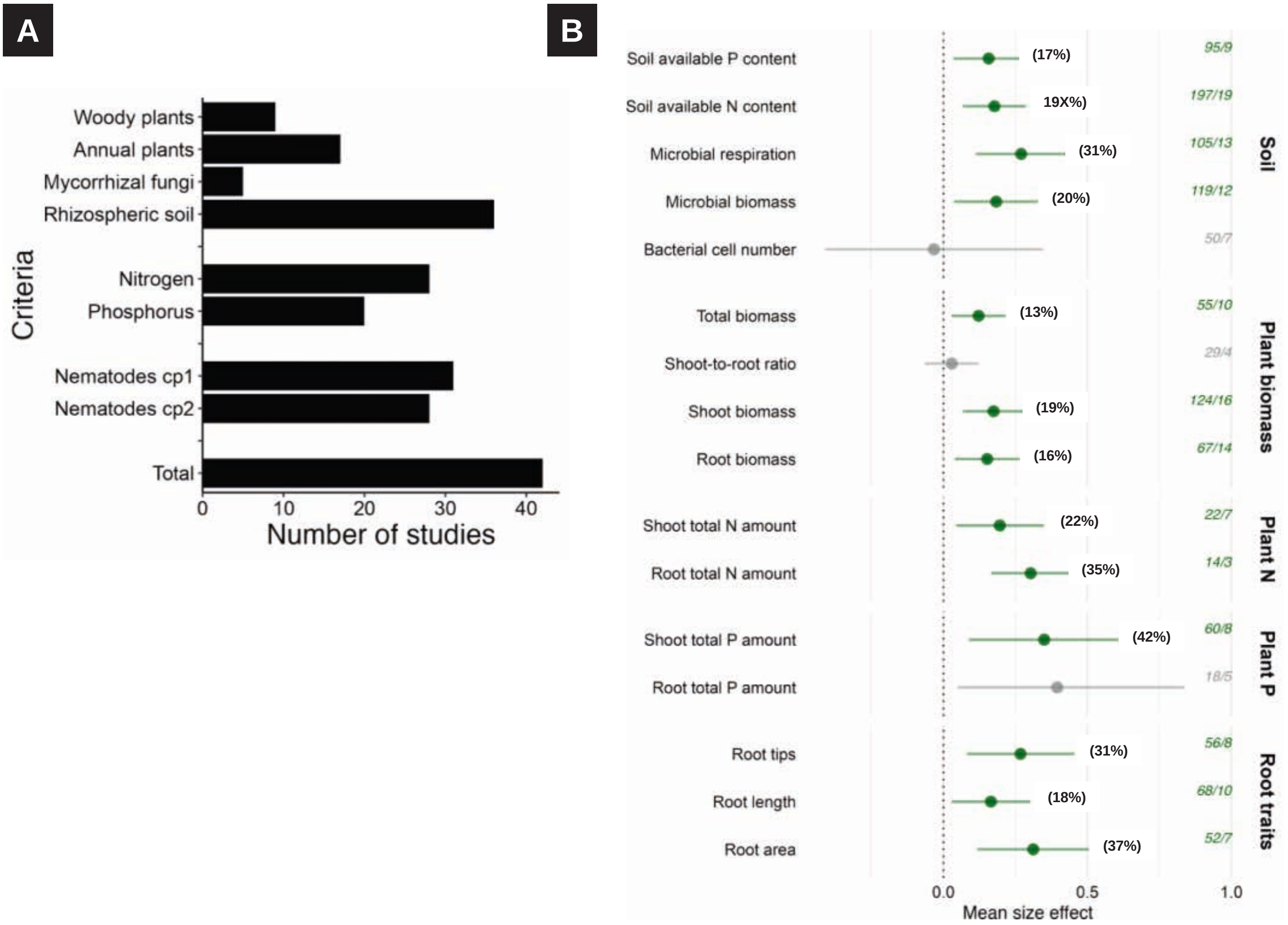

Fig. 1. A. Number of studies included in the *meta*-analysis (total and per criteria). B. Mean effect size of bacterivorous nematodes on soil and plant functions (percentage). The total number of observations and studies for one summary effect size are indicated on the left and right side of the slash symbol, respectively. Values are the mean ± 95 % confidence intervals. Green rounds indicate significant positive effects at the 5 % threshold. Grey circles are not significantly different from zero. Soil available N content refers to ammonium and nitrate.

functions of BN. CICES offers a structured framework for evaluating ecosystem services, distinguishing among provisioning, regulation and maintenance, and cultural services. Our focus was primarily on the Regulation & Maintenance section, specifically subcategories such as *the regulation of soil quality* (2.3.4.2), *reduction of waste and toxic substances* (2.1.1), and *pest and disease control* (2.3.3). Additionally, relevant functions under Provisioning services, such as *biomass of cultivated terrestrial plants* (1.1.1), were also considered. This classification allowed us to link specific BN-mediated processes to recognized ecosystem service categories, providing a standardized and policy-relevant interpretation of their ecological contributions. The full CICES v5.1 framework is available at https://cices.eu. For each function, we first highlighted the general role of BN in the relevant CICES category, followed by a discussion of sources of variation and proposed mechanisms.

2.2. *Literature search*

The *meta*-analysis followed the PRISMA guidelines and recommendations proposed by Vetter et al. (2013) and Gurevitch et al. (2018). Data were gathered from studies that examined the sole effect of soil BN on numerous soil and plant functions. On the basis of the work conducted by Trap et al. (2016), Mezeli et al. (2020), Lang et al. (2023), we focused on specific soil functions for which we believe the available data will allow us to conduct a robust analysis, namely soil N and P mineralization, microbial biomass and bacterial abundance, microbial respiration and plant nutrition and growth. The Common International Classification of Ecosystem Services (CICES) version 5.1 was used to systematically categorize the ecological functions of BN.

A literature search was conducted in the Web of Science – All Databases option for peer-reviewed articles published prior to February 14, 2024, using the following search string: soil AND (bacter* AND (nemato* OR *Caenorhabditis* OR *Pristionchus* OR *Acrobeloides* OR Cephalo* OR Rhabdi*)) AND (mineralize* OR phosph* OR nitrogen OR nitrate OR ammonium OR “cell number” OR respiration OR microbial OR biomass OR plant OR growth OR nutrition OR root). This search strategy, which focused on article titles and abstract, resulted in the identification of a total of 3619 articles (Fig. S1). The literature search was completed by considering additional six relevant publications identified through other sources (Anderson et al., 1981; Baath et al., 1981; Elliott et al., 1979; Ingham et al., 1985; Irshad et al., 2013; Trofymow et al., 1983) (Fig. S1).

2.3. *Inclusion criteria and data collection*

The literature search yielded 3625 articles, which were initially screened based on their title and abstract. Meta-analysis and review papers, along with articles unrelated to soil systems (e.g., those pertaining to freshwater) or to entomopathogenic and plant-parasitic nematodes, were discarded. During this step, all relevant publications for the review have been selected for inclusion. After this initial selection step, 74 articles were further assessed according to specific inclusion criteria:

(1) Data should be available in the article, either presented in tables or graphical formats. If the data were not directly available in the text, the GetData Graph Digitizer (version 2.26) software was used to extract the data from graphical representations.
(2) Studies had to report at least one of the targeted variables, which included bacterial cell number, microbial biomass, microbial carbon (C) respiration, soil available N content, soil available P content, shoot and/or root biomass, total plant biomass, shoot-to-root ratio, total N and/or P amount in shoots and/or roots and root traits (length, number of tips and area).
(3) Studies should also include a distinct control group and a treatment group. The control group was defined as the absence of nematodes, while the treatment group consisted of modalities with clearly identified bacterial-feeding nematodes. Studies using soil-native nematode communities as treatment group were thus excluded. Moreover, when protists were also studied along with nematodes, the treatment “protist + nematodes” was compared to the treatment “+ protists,” defined as the control group.
(4) The selected studies had to include means (X), standard deviations (SD), or standard errors (SE), as well as sample size (n, number of true replications) in both control and treatment groups. Missing data points resulted in the exclusion of articles, as they are required to compute the effect size (Gurevitch et al., 2018; Vetter et al., 2013).

A total of 42 articles met the inclusion criteria and were included in the *meta*-analysis (Fig. S1; Fig. 1A). The list of these articles is in Table S1. Furthermore, the database encompassed additional moderator variables collected from each paper, including the duration of incubation, nematode species used in each study, initial absolute nematode density at inoculation and density at sampling time. It also comprised soil qualitative description provided in the article (i.e., textural class), along with soil physico-chemical characteristics (i.e., pH, total C content, total and available N content, available P content, C:N ratio), and fertilization conditions used in the experiment (e.g., chitin, cellulose, glucose, ammonium or phosphate fertilization). When bacteria were inoculated prior to the incubation, or if plants or mycorrhizal fungi were present in an experiment, the database recorded both the species name of the organism and their initial density. The collected data were double-checked to prevent any errors from manual entry, and outliers were identified by ranking all “effect sizes” to spot potential data entry mistakes. Any instances of the same study data being published in multiple sources were also checked for, and it was confirmed that there were no duplicate data. Due to different units and ways of reporting data between articles, data were converted and homogenized into the same units. If only the standard error (SE) was reported, the standard deviation (SD) was calculated as follows: $SD = SE.\sqrt{n}$ (Altman and Bland, 2005).

2.4. *Statistical analyses*

To assess the impact of BN on soil and plant functions, the effect size was calculated using the natural log response ratio lnRR (Hedges et al., 1999; Lajeunesse, 2011; Puissant et al., 2021). This ratio quantifies the proportional change in the means of a treatment group compared to a control group by taking the natural logarithm (Hedges et al., 1999). The effect size (equation (1)) and its corresponding variance (equation (2)) were computed using the ‘escalc’ function of the metafor package (Viechtbauer, 2010), implemented in R (Team, 2016), as follows:

$$\ln RR = \ln(\frac{\overline{X}_t}{\overline{X}_c} \qquad (1)$$

$$var(RR) = \frac{(SD_t)^2}{n_t\overline{X}_t} + \frac{(SD_c)^2}{n_c\overline{X}_c} \qquad (2)$$

where X, SD and n represent the mean, standard deviation and sample size, respectively, of the control (c) or the treatment group (t).

To express the effect sizes as a percentage, the following equation (3) was used:

$$\ln RR\ (\text{expressed in}\%) = (e^{\ln RR} - 1)*100 \qquad (3)$$

A total of 1131 effect size were computed (Table S2). We calculated the combined effect size and its corresponding variance using a multilevel *meta*-analysis model (mixed model) with the “rma.mv” function from the Metafor package (Viechtbauer, 2010). The model was fed the calculated effect sizes and sampling variances as described above, and then fitted via restricted maximum-likelihood estimation. To account for the dependencies among estimates from the same study, a mixed model

Table 1
Significant drivers of BN effect on ecological functions.

Variables	Moderators (unit)$	Estimate	% of BN effect
Microbial biomass	Duration (days)	−0.001***	−0.5
C-respiration	C:N	−1.568**	−581
	cp class (1–2)	−0.012***	−4.4
	Duration (days)	0.001***	0.5
Soil available N content	C:N	0.004*	2.7
	cp class (1–2)	−0.198*	−117
	Duration (days)	0.001*	0.5
Soil available P content	cp class (1–2)	−0.023*	−16
	Duration (days)	0.002*	1.3
	Initial soil available P content (mg-P kg)	0.023*	15
Shoot biomass	C:N	−0.022*	−13
	cp class (1–2)	−0.015*	−9.1
	Duration (days)	−0.001*	−0.5
Root total N amount	cp class (1–2)	−0.082*	−27
	Duration (days)	−0.013*	−4.3
Shoot total P amount	Duration (days)	0.010*	3.0
Root length	Duration (days)	−0.003*	−2.1
Root tips	cp class (1–2)	−0.019*	−7.3
	Duration (days)	−0.003*	−1.3
Root area	cp class (1–2)	−0.037***	−12
	Duration (days)	0.002***	0.6
	Initial soil available P content (mg-P kg)	0.109*	35
	pH	−0.505*	−163

$Moderators correspond to any variables extracted from the original articles that could explain differences in the response to BN presence.
Percentage of BN effect corresponding to the estimate of the moderator divided by the mean effect size times 100.
* *P*-value $<$ 0.05; ***P*-value $<$ 0.01; *** *P*-value $<$ 0.001.

with "study identification" (study ID) as a random factor was used, given that multiple effect size values were obtained per study (e.g., several sampling dates). We initially conducted a random-effect model to estimate the overall impact of BN on soil and plant variables. The average response ratios were assessed for heterogeneity in effect sizes using the QE statistic (Hedges et al., 1999; Viechtbauer, 2010). When the QE was significant (p-value $<$ 0.05), the collected metadata (moderators) were added to the models to explain this heterogeneity (Table 1). These moderators correspond to all potentially relevant variables extracted from the original articles that could explain differences in the response to BN presence, such as experimental duration, soil nutrient status, or the presence of plants. We used a mixed model with moderator variables as a fixed factor and 'study ID' as a random factor. This second mixed-model was run separately for each moderator variable under study. Levels of significance for *meta*-regressions were adjusted and corrected with the truncated product method for combining P-values (Zaykin et al., 2002). When evaluating publication bias, we visually inspected the funnel plot (Fig. S1). The x-axis represented observed effect sizes while the y-axis represented standard error to identify any asymmetrical distributions and heterogeneity. We tested for asymmetry of effect sizes by using the variance of effect size "VI" as a moderator in the *meta*-analysis model with the "rma.mv" function (Egger's test; (Jennions et al., 2013)). Rosenberg's fail-safe number was utilized for this method, determining the quantity of studies with no effect size required to potentially reverse the outcome. On average, the Rosenberg's fail-safe number for each model was 34,250 times the number of observations, indicating the robustness of our results. However, we found two models that exhibited asymmetry in the distribution of effect sizes and a Rosenberg's fail-safe number that is less than three times the number of observations collected in this *meta*-analysis (root biomass model, shoot-to-root ratio model). The effect sizes of these models were thus not interpreted (Puissant et al., 2021).

3. Functional roles of soil bacterivorous nematodes

3.1. Regulation of soil quality – Direct effects on decomposition (CICES 2.3.4.2)

3.1.1. Bacterivorous nematodes as reservoirs of carbon and nutrients

BN are known to be highly abundant in the top 15 cm soi layer, with an estimated number of 1.92 ± 0.20 x 10^{20} nematodes inhabiting global surface soils (Van Den Hoogen et al., 2019). This corresponds to a biomass of 7.13 Mt carbon (C). With an average mass C:N ratio of 6 (Ferris et al., 1998; Venette and Ferris, 1998) and a C:P of 47 (Borkott, 1989), the global stocks of N and P in BN biomass are estimated at approximately 1.18 Mt N and 0.15 Mt P. Thus, BN represent a significant biological reservoir of carbon, N and P in soils. As BN serve as prey for a wide range of soil organisms, e.g., collembolan (Chamberlain et al., 2006), mites (Heidemann et al., 2011), predatory nematodes (Bilgrami and Gaugler, 2004), nematophagous fungi (Dijksterhuis et al., 1994) and even protists (Bjornlund and Rønn, 2008; Geisen et al., 2015), they play a key role in channeling the flow of C, N, and P to higher trophic levels in the soil food web. This transfer of nutrients up the food chain is crucial for maintaining the productivity and functioning of soil ecosystems.

Sources of variation – The amount of carbon, N and P flowing through the soil food web specifically via BN has poorly been quantified (Kudrin et al., 2015; Vestergård et al., 2019). This represents a promising frontier in soil ecological research. The transfer of plant-derived C through components of the soil food web has been done at the whole nematode community level (Paterson et al., 2011) or for plant-parasitic nematodes (Neilson & Brown, 1999). Consequently, identifying the sources of variation remains challenging. However, the abundance and biomass of BN communities are influenced by factors such as climate (Nielsen et al., 2014), soil type (Nisa et al., 2021), vegetation cover (Viketoft and Sohlenius, 2011), the prey and its nutrient status (Ferris et al., 1997), and other key drivers of nematode community structure that likely contribute to variation in carbon and nutrient stocks within this biological compartment.

Putative mechanisms – The role of BN as nutrient reservoirs is primarily governed by their feeding activity on bacterial biomass and their rapid turnover. Their fast population dynamics contribute to accumulation of substantial carbon and nutrient pools. The stoichiometric imbalance between bacterial prey and BN drives the excretion of excess nutrients, influencing both the nutrient flux and the final C and nutrient content of BN biomass.

3.1.2. Bacterivorous nematodes as promoters of nutrient cycling

The effects of BN on nutrient cycling have been extensively studied (Ferris et al., 1998; Gebremikael et al., 2014; Irshad et al., 2013; Jiang et al., 2023a; Xiao et al., 2010; Zheng et al., 2022), with early research dating back to the late 1970s, often alongside investigations of their impact on microbial growth and activity (Cole et al., 1978; Coleman et al., 1978). These studies have primarily focused on examining the effects of BN on net N and P mineralization in the absence of plants (typically inferred using soil chemical-extractable N and P contents), while their influence on denitrification has received comparatively less attention (Djigal et al., 2010; Hu et al., 2024; Zhu et al., 2018). Our *meta*-analysis included more studies assessing the effect of BN on soil available N content (n = 19, 197 observations) than on soil available P content (n = 9, 95 observations) (Fig. 1A).

The presence of BN in soil can either stimulate (Anderson et al., 1981; Baath et al., 1981; Gilarte et al., 2024; Griffiths, 1986; Luo et al., 2008) or have no effect on available N and P contents (Bardgett and Chan, 1999; Cole et al., 1978; Djigal et al., 2004b; Irshad and Yergeau, 2018). BN can have varying effects on net nitrification. Some studies reported stimulation of nitrifying bacteria, leading to increased soil nitrate (NO_3^-) contents (Bouwman and Zwart, 1994; Griffiths, 1986; Jiang et al., 2012; Xiao et al., 2010; Xu et al., 2015), while others found no effect (Holajjer et al., 2016; Jiang et al., 2020) or even a reduction in soil NO_3^- contents (Alphei et al., 1996; Holajjer et al., 2016; Jiang et al., 2020). In our *meta*-analysis, the presence of BN led to a significant 19 % increase in soil available N content and a 17 % increase in soil available P content compared to the control group, regardless of plant presence and its N uptake (Fig. 1B).

Sources of variation – The initial nutrient status of the soil significantly influenced the effect of BN on available N and P content (Table 1). The effect of BN on soil available N content increased with higher soil C:N ratio values, averaging a 2.7 % increase per unit rise in the C:N ratio (Table 1). This result contradict the hypothesis of Ferris et al. (1998) who suggested that low C:N ratio limited bacterial growth and microbial N immobilization, resulting in higher nematode contribution in net C and N mineralization in comparison to high C:N ratio. However, Ferris et al. (1998) showed that the relationship between BN contribution to N mineralization and substrate C:N ratio is neither clear-cut nor linear. For example, the amount of N mineralized in the Acrobeloides buetschlii experiment was marginally greatest at the highest C-to-N ratios, and highly variable for the other species. Similarly, Postma-Blaauw et al. (2005) observed that *Plectus parvus* significantly increased soil mineral N concentrations in both low (C:N = 13) and high (C:N = 25) organic matter treatments compared to controls, whereas *B. monhystera* and *A. nanus* significantly enhanced N mineralization only under low C:N conditions. The authors also showed that the effects of BN on N mineralization became clear at the end of the experiment in the low C:N ratio treatment, whereas in the high C:N ratio, the effects were clear throughout the experiment. It is therefore highly likely that the effect of soil C:N ratio on nematode contribution to available soil N content is not generic but strongly dependent on the experimental conditions and the nematode species considered.

Although our analysis revealed a positive relationship between soil C:N ratio and the BN-induced increase in available N content, the mechanisms underlying this trend remain uncertain. One possible explanation is that soils with higher C:N ratios may promote more intense bacterial turnover and predator–prey interactions, leading to enhanced N mineralization from microbial biomass despite overall N limitation. Importantly, the way the C:N ratio is modified may strongly influence the outcome: an increase in C:N due to higher C inputs (e.g., addition of labile or recalcitrant carbon) may stimulate microbial growth and nematode grazing differently than an increase or decrease in soil mineral N. Similarly, changes in the quality of the added carbon source, more labile vs. more recalcitrant, could alter the microbial community structure and the efficiency of nutrient recycling by BN. Additionally, associated soil properties such as pH, clay content, or total organic carbon could modulate this relationship by influencing microbial activity, N sorption, or ammonium retention. Clarifying these mechanisms will require targeted experiments that disentangle whether the C:N ratio effect arises from changes in C quality, N content, or both, ideally across a gradient of substrate qualities and nematode species.

Besides C:N ratio, high initial soil available P content amplified the positive effect of BN on final soil available P contents (Table 1), suggesting that soil microorganisms use BN-induced excess P to support their growth and metabolism. This, in turn, could enhance microbial biomass and promote greater mineralization of organic P. Our analysis also showed that BN species identity matters. *Bursilla labiata* (renamed as *Mesorhabditis*) and *Mesodiplogaster lheritieri* displayed the highest positive effects on nutrient mineralization. In contrast, *Acrobeloides* had a broad range of effects, negatively affecting soil available P but positively affecting available N. Additionally, *Mesorhabditis* and *Cephalobus* had the greatest positive effect sizes for soil available P content. Species-specific effects of BN on net N and P mineralization have also been reported in the literature (Cheng et al., 2011; Fu et al., 2005). However, cp classes may provide a more comprehensive explanatory framework than species identity alone (Brondani et al., 2022; Postma-Blaauw et al., 2005). Our *meta*-analysis supports this hypothesis (Table 1), showing that cp1 nematodes had the strongest positive effects on both soil available N and available P contents compared to cp2 nematodes. In particular, compared to the cp1 nematodes, cp2 nematodes reduced BN-effects on soil available N and P contents by 117 % and 16 %, respectively (Table 1). We also observed a positive relationship between experimental duration and the effect of BN on both soil available N and P (Table 1). Effect sizes increased with experimental duration, approximately 0.5 % per day for available N and 1.3 % per day for available P (Table 1). However, the beneficial effects of BN on nutrient availability do not follow a strictly linear pattern over time. Fluctuations are likely driven by changes in population dynamic patterns. In natural ecosystems, the coexistence of cp1 and cp2 nematodes may enable functional complementarity (Ferris, 2010), where their distinct life history strategies jointly enhancing N and P mineralization over time. Another important source of variation is the presence or absence of plants in the experimental setup. As plants rapidly absorb excreted nutrients, BN presence did not always lead to increased soil N and P content in the soil solution. For example, Djigal et al. (2004b) reported no change in soil ammonium content after 51 days under a corn crop, despite the presence of BN. Conversely, BN treatments exhibited higher soil NH_4^+ contents than controls where plants were absent.

Putative mechanisms – The main mechanism proposed to explain the effect of BN on soil available N and P content refers to a direct pathway based on the “consumer-driven nutrient recycling theory” (Elser and Urabe, 1999), which also underpins the soil microbial loop hypothesis (Bonkowski and Clarholm, 2012; Clarholm, 1985). BN contribute to the re-mineralization of N and P by excreting excess nutrients into the soil solution. BN have a low assimilation efficiency, i.e., they utilize only 30–40 % of ingested C for biomass production, while most of it is respired (Trap et al., 2016). To compensate for C losses due to respiration and to maintain their internal C:nutrient stoichiometry, BN excrete a substantial portion of ingested N and P as available forms (NH_4^+ and PO_4^{3-} for N and P, respectively), as well as in organic compounds (Anderson et al., 1983; Ferris et al., 1998). The bacterial C:N:P ratio directly influences the quantity of N excreted by BN. According to Ferris et al. (1998), BN can excrete between 1.2 and 5.8 ng of N per day and per individual, depending on the species. Trap et al. (2016) estimated the theoretical nutrient percentages excreted by BN using stoichiometric ratios (C:N = 5.6; C:P = 9.4; N:P = 1.9) and production efficiency (69.4 %), as defined in the literature (Borkott, 1989; Ferris et al., 1998). Their calculations showed that N assimilation values vary from 9 % to 20 %, while P assimilation values range from 66 % to 76 %. However, these theoretical estimates do not account for several biotic factors, such as nutrient immobilization in microbial biomass, plant uptake, and soil stoichiometry, or abiotic processes like phosphorus adsorption, which occur after nutrient excretion into the soil solution. A second, indirect mechanism, involves stimulation of the microbial community through the predatory activity of BN (Trap et al., 2016). Precisely, BN grazing can alter microbial community composition as discussed below, thereby enhancing biogeochemical processes. By promoting the growth of more metabolically active bacteria, this indirect pathway can ultimately increase the availability of N and P in the soil ecosystem. Among indirect mechanism, BN also act as prey for higher trophic levels, thereby indirectly contributing to nutrient flows through the effect of their predators on nutrient mineralization (Franco et al., 2019; Neilson et al., 2020).

3.1.3. Bacterivorous nematodes as regulators of carbon sequestration

Multiple observations highlight the importance of soil BN in the C cycle, particularly in C sequestration (Kou et al., 2023; Shi et al., 2023; Zhang et al., 2013). For instance, Martin and Sprunger (2021) found that the abundance of BN was associated with SOC stabilization, but only in mid-sized soil aggregates, in a *meta*-analysis including 98 observations from 11 papers. Kou et al. (2023), using a ^{13}C-labeled straw amendment in an 11-year no-tillage experiment in Jilin Province, northeastern China, demonstrated that soil microbial grazers act as temporary storage reservoirs and indirectly promote microbial necromass accumulation, playing a crucial role in mediating soil C sequestration. Microbial turnover driven by these grazers may enhance the stability of soil organic C. Although BN stimulate short-term C loss through microbial respiration and priming effect, i.e., the increase in soil organic matter decomposition rate after fresh organic matter input to soil (Fontaine et al., 2003), BN can contribute to long-term C stabilization by transferring C into persistent and protected soil organic matter through necromass entombment (Camenzind et al., 2023; Kou et al., 2023). Necromass entombment refers to the process by which microbial residues are physically or chemically protected within soil aggregates or bound to mineral surfaces, thereby contributing to the long-term stabilization of organic carbon (Camenzind et al., 2023). Consequently, incorporating microbial grazers into ecosystem models significantly improves model accuracy (Chertov et al., 2022). Such models would further benefit from: (i) accounting for nutrient release to plants, which enhances C inputs via increased root growth and rhizodeposition, and (ii) including the return of organic C to soil organic matter through faunal excreta and necromass, which partially offsets respiration-induced C losses.

Sources of variation – At present, insufficient data prevent the identification of key factors influencing BN effects on C sequestration. These effects may vary depending on species identity, soil type, organic matter quality, and microbial community composition.

Putative mechanisms – First, BN strongly enhance microbial respiration, especially microbial metabolic quotient (qCO_2) and microbial C use efficiency (Shi et al., 2023; Trap et al., 2016). Second, BN significantly increase C inputs into the soil by (i) stimulating rhizodeposition (Sundin et al., 1990) and (ii) creating positive feedback through the soil microbial loop (Clarholm, 1985), thereby enhancing net assimilation of plant derived C into the soil microbial biomass (Mielke et al., 2022). Since soil organic matter formation and C sequestration are driven by the microbial pump and microbial necromass (Kästner et al., 2021; Zhu et al., 2020), BN likely exert a positive influence on both soil organic matter formation and C sequestration, despite the associate increase in microbial respiration. Nevertheless, experimental data remain limited, and further studies are needed to quantity the impact of BN on C sequestration and to clarify the underlying mechanisms.

3.2. *Regulation of soil quality – Top-down microbial stimulation (CICES 2.3.4.2)*

3.2.1. *Bacterivorous nematodes as promoters of microbial biomass and abundance*

The effect of BN on soil microbial biomass or abundance has been investigated since the late 1970s (Anderson et al., 1978; Cole et al., 1978; Coleman et al., 1978). Specifically, soil microbial biomass was estimated by fumigation-extraction (Baath et al., 1981; Djigal et al., 2004a; Ingham et al., 1985; Postma-Blaauw et al., 2005), while bacterial abundance was estimated using cultivable microbial cell numbers from nutrient agar plates (Baath et al., 1981; Djigal et al., 2004a; Irshad et al., 2012). As the fumigation-extraction technique accounts for non-cultivable cells, microbial biomass has been more frequently investigated than bacterial abundance. In our *meta*-analyzed, 12 studies focused on microbial biomass (119 observations), compared to only 7 studies examining bacterial cell numbers (50 observations) (Fig. 1A).

The literature reports positive (Holajjer et al., 2016; Ingham et al., 1985; Jiang et al., 2023b), neutral (Bardgett and Chan, 1999; Maboreke et al., 2018; Postma-Blaauw et al., 2005) or negative (Anderson et al., 1981; Djigal et al., 2004a) effects of BN on microbial biomass. Similar variability is observed for microbial abundance, which was either stimulated (Elliott et al., 1980; Hai-Feng et al., 2014; Holajjer et al., 2016; Irshad et al., 2012) or hampered (Baath et al., 1981; García-Sánchez et al., 2021; Jiang et al., 2020; Postma-Blaauw et al., 2005) by BN. Moreover, microbial biomass and abundance do not always respond in parallel to the presence of BN. For instance, Djigal et al. (2004a) found no difference in microbial biomass between control and BN treatments, but observed a significant reduction in bacterial cell numbers in the maize rhizosphere following BN addition. This divergence between biomass and abundance responses was also evident in our *meta*-analysis. Overall, BN presence increased soil microbial biomass by 20 %, but had no significant effect on bacterial cell numbers, which were highly variable (Fig. 1B).

Sources of variation – The contrasting responses described above may stem from several influencing factors. However, experiment duration was the sole significant factor (Table 1). The positive effect of BN on microbial biomass decreased by approximately 0.5 % per day of experimental duration. BN influence on microbial biomass may decrease over time as microbial communities adapt to grazing pressure from BN. Although not significant in our *meta*-analysis, other factors may explain the variability in BN-effect on microbial biomass. For instance, each 1 mg/kg increase in soil available P enhanced the effect of BN on microbial biomass by 8 % (data not shown). This pattern likely reflects the high P demand of rapidly growing microbes under grazing pressure. Indeed, P is essential for bacterial growth, as it is a key component of DNA, RNA, and cell membranes (Dill et al., 2011; Karpinets et al., 2006). Also, soil texture can play an important role. Elliott et al. (1980) found that soil texture significantly influence the response of bacterial abundance to the addition of *Mesodiplogaster lheritieri*. The number of bacterial cells in fine- and coarse-textured soils was twice and four times higher, respectively, when BN were present compared to the control after 4 days of incubation. Other chemical parameters, such as the availability of labile C or N in soil can also influence the effect of BN on microbial biomass (Anderson et al., 1981; Baath et al., 1981; Elliott et al., 1980).

Putative mechanisms – The main mechanism mentioned in the literature to explain the positive effects of BN on prey biomass is their role in maintaining a metabolically active microbial community (Trap et al., 2016). By consuming senescent or dormant bacterial cells, BN promote microbial turnover and support the proliferation of younger, more metabolically active bacterial populations (Bonkowski, 2004). As bacteria pass through the digestive tract of BN, undigested particles, labile C, and essential nutrients are released (Griffiths, 1994; Pussard et al., 1994). These excreted compounds serve as substrates that further stimulate surrounding microbial growth. Since most bacteria ingested by BN are not fully digested (Chantanao and Jensen, 1969), nematodes can excrete viable bacteria for over 24 h post ingestion (Griffiths, 1994; Sohlenius, 1980). Undigested bacteria reintroduced into the soil may benefit from more favorable conditions, leading to renewed proliferation (Chantanao and Jensen, 1969; Jatala et al., 1974). An increase in microbial biomass without a corresponding rise in bacterial abundance suggests either a shift in microbial community composition, potentially due to greater fungal dominance. Indeed, BN exhibit feeding preferences (see Box 1 for details) (Abada et al., 2009; Liu et al., 2017), often targeting small, gram-negative bacteria (Avery and Shtonda, 2003; Djigal et al., 2004a; García-Sánchez et al., 2021; Salinas et al., 2007; Shtonda and Avery, 2006). Larger or thick-walled bacteria (Gram-positives, filamentous forms) may therefore be less affected by grazing pressure, potentially altering community composition (Tamang et al., 2024). It is also possible that some bacterial cells were overlooked, for instance taxa that cannot be cultured on media or that form biofilms, which may complicate their detection and quantification. This effect may be especially pronounced in cp2 nematodes, which possess a narrow, funnel-shaped buccal cavity that restricts them to smaller prey compared to cp1 nematodes. This morphological difference may help explain the contrasting effects of cp1 and cp2 nematodes on microbial biomass responses to grazing (Table 1). However, to our knowledge, no study has directly demonstrated that this selective feeding results in an overall increase in the average bacterial cell size within communities.

3.2.2. *Bacterivorous nematodes as stimulators of microbial activity*

Research on the effects of BN on soil microbial activity began in the late 1970s, alongside studies of bacterial abundance and microbial

Table 2
Bacterivorous nematodes effects on enzymatic activities.

Enzymatic activities	Authors	Year	Modalities	Effect
Phosphatase	Djigal *et al.*	2004a		+
	Djigal *et al.*	2004b		+
	Jiang *et al.*	2017		+
	Irshad & Yergeau	2018		+
	Rehman *et al.*	2018		+
Denitrification	Djigal *et al.*	2010		−
FDA hydrolysis	Mingming *et al.*	2017	+ pyrene	+
	Zhou *et al.*	2012	+ prometryne	+
	Zhou *et al.*	2013	+ prometryne	+
	Zhou *et al.*	2018	+ oil	+
Catalase	*Sun et al.*	2017	+ pyrene	+
	Zhou *et al.*	2012	+ prometryne	+
	Zhou *et al.*	2013	+ prometryne	+
	Zhou *et al.*	2019	+ oil	+
Dehydrogenase	Gebremikael *et al.*	2015		n.s.
	Sun *et al.*	2017	+ pyrene	+
	Zhou *et al.*	2018	+ oil	+
Betaglucosidase	Gebremikael *et al.*	2015		n.s.
Urease	Zhou *et al.*	2019	+ oil	+

« + » indicates a significant positive effect.
« - » indicates a significant negative effect.
« n.s. » indicates no significant effect.

biomass. This early research primarily focused on microbial respiration (Anderson et al., 1978; Coleman et al., 1978; Elliott et al., 1979). More recently, assessments of microbial activity have expanded to include additional processes such as enzyme activities, although these studies remain relatively limited (Djigal et al., 2004a; Djigal et al., 2004b; Irshad and Yergeau, 2018; Jiang et al., 2017; Sun et al., 2017; Zhou et al., 2018; Zhou et al., 2013; Zhou et al., 2012). Our *meta*-analysis included 13 studies on BN effects on microbial respiration, totaling 105 observations. We also reviewed studies assessing the impact of BN on soil enzyme activity (Table 2), but the data were insufficient to support a *meta*-analysis.

Most studies reported a positive effect of BN on microbial respiration (Cheng et al., 2011; Hai-Feng et al., 2014; Jiang et al., 2020; Jiang et al., 2012; Zhou et al., 2012), although one study found no significant effect (Baath et al., 1981). Our *meta*-analysis revealed a significant overall increase of 31 % in microbial respiration when BN were present, compared to controls (Fig. 1B). Beyond respiration, enzyme activity responses to BN varied depending on the specific enzyme assessed, although the overall trend was positive (Table 2). Notably, BN presence significantly increases soil phosphatase activity, which likely contribute to the observed positive effect of BN on soil available P (Djigal et al., 2004a; Djigal et al., 2004b; Irshad and Yergeau, 2018; Jiang et al., 2017). Conversely, BN presence reduced the activity of enzymes involved in denitrification (DEA), likely due to a decrease in denitrifier biomass rather than direct enzyme inhibition (Djigal et al., 2010). Other studies have shown that BN can enhance enzymatic activity involved in contaminant degradation, such as increasing fluorescein diacetate (FDA) hydrolysis, catalase, and urease activity in contaminated soils (Sun et al., 2017; Zhou et al., 2018; Zhou et al., 2013; Zhou et al., 2012; Zhou et al., 2011) (Table 2).

Sources of variation – The effects of BN on microbial respiration showed limited variation. However, the soil C:N ratio significantly influences the size of the positive effect of BN on microbial respiration. As the C:N ratio increases, the stimulatory effect of BN decreases (Table 1). In contrast to soil available N content as discussed above, microbial respiration thus appears to be much more dependent on the soil C:N ratio. We also found that BN-induced stimulation of microbial respiration depended on experimental conditions, particularly the duration of the incubation period (Table 1). Indeed, the positive effect of BN on microbial respiration increased by approximately 0.5 % for each additional day of incubation (Table 1). As trophic interactions between BN and soil microbes become more established over time, the influence of BN on microbial activity intensifies, coinciding with increased microbial growth. Finally, nematode species identity and life-history traits also influenced the degree of microbial respiration stimulation (Table 1). In our *meta*-analysis, Cephalobus persegnis, Pelodera, and P. filiformis exhibited the highest effect sizes on microbial respiration, while Acrobeloides nanus showed the lowest. Furthermore, the stimulatory effect of BN on microbial respiration was greater for cp1 nematodes than for cp2 nematodes by 4.4 %.

Putative mechanisms – The stimulatory effect of BN on microbial respiration supports the same mechanisms proposed earlier for microbial biomass. Similar mechanisms are involved: BN maintain an active

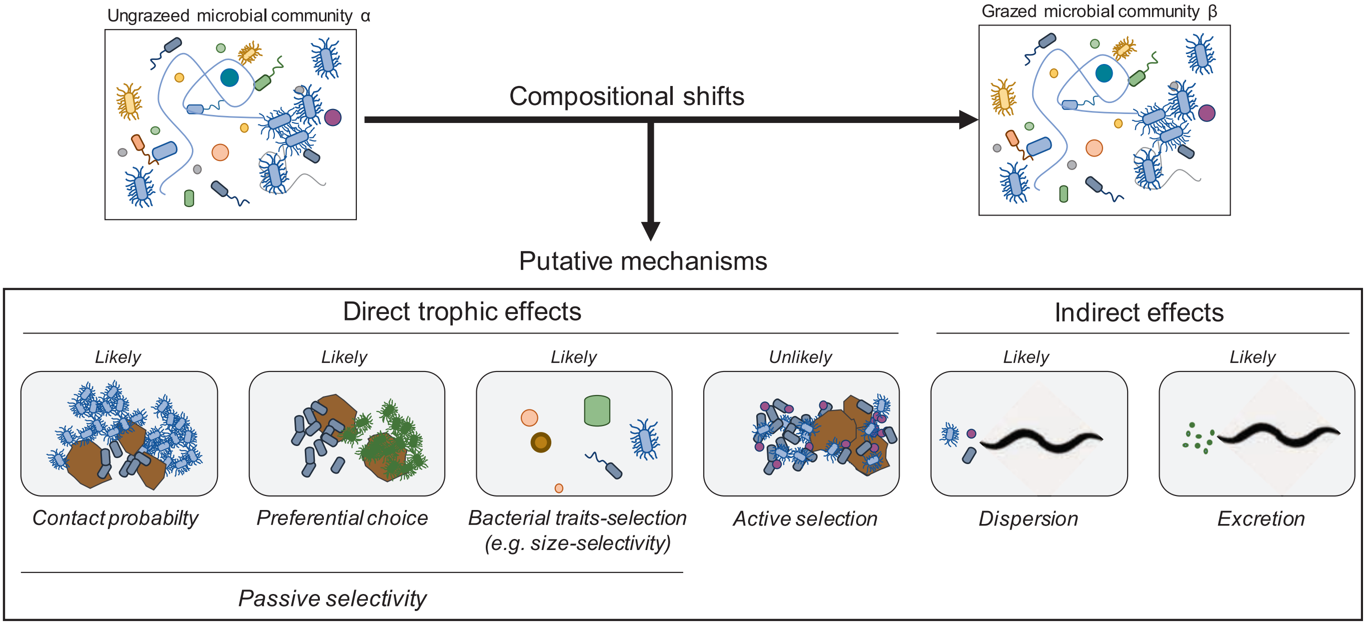

Fig. 2. Mechanisms involved in microbial compositional shift under BN grazing. Direct trophic effects included passive selection such as contact probability, preferential choice or bacterial traits-selection (size-selectivity). Active selection is a potential mechanism but appears unlikely at our current knowledge. Indirect effects correspond to (i) dispersion of bacterial cells by BN through defecation or by phoretic transport and (ii) through excretion of nutrients and defecation of labile carbon.

microbial community and promote microbial turnover by releasing nutrients, removing senescent cells, and transporting microbial cells throughout the soil.

3.2.3. Bacterivorous nematodes as regulators of bacterial community composition

Since the 2000 s, traditional assessments of microbial growth, based on microbial biomass and bacterial cell abundance, have been increasingly replaced by analyses of bacterial community composition, enabled by advances in molecular technique (Blanc et al., 2006). This shift enabled researchers to characterize how BN influence bacterial community composition (Blanc et al., 2006; Brondani et al., 2022; De Mesel et al., 2003; Djigal et al., 2004a; Djigal et al., 2004b; Griffiths et al., 1999; Hai-Feng et al., 2014; Jiang et al., 2017; Jiang et al., 2023b; Postma-Blaauw et al., 2005). BN presence has been linked to increased bacterial diversity, reflected by a higher number of DNA bands using DGGE, and to shifts in the relative abundance of dominant bacterial taxa (Djigal et al., 2004a; Postma-Blaauw et al., 2005). Moreover, BN alter microbial taxa associated to specific functions (Djigal et al., 2010; Jiang et al., 2023b; Sun et al., 2017; Xiao et al., 2010), such as nitrification (Djigal et al., 2010) or P mineralization (Djigal et al., 2004a) by enriching P-cycling associated bacteria (Jiang et al., 2023b). Xiao et al. (2010a) also found that BN presence shifted the composition of ammonia-oxidizing bacteria (AOB), with a greater abundance of Nitrosomonas spp. compared to Nitrosospira spp. in controls, based on DGGE targeting the amoA gene. A recent work showed that BN *Acrobeloides buetschlii* caused a succession of microbial groups, likely driven by feeding behavior of the BN, different microbial resource use efficiencies and substrate specialization in a soil amended with maize litter (Tamang et al., 2024).

Source of variation – The impact of BN on bacterial community structure is highly species-specific (Brondani et al., 2022; Djigal et al., 2004a). Djigal et al. (2004a) showed that three different BN species modified the DGGE banding patterns of the microbial community, with Acrobeloides nanus inducing greatest changes compared to control soils. Life-history traits of BN also significantly influence their effect on bacterial community composition. Brondani et al. (2022) found that cp2 nematodes caused greater shifts in bacterial composition than cp1 taxa in the rhizosphere of Pinus pinaster. Morpho-anatomical traits of BN, such as mouth width, procorpus width, and the ability to form dauer larvae, explained a significant portion of the variation in bacterial community composition.

Putative mechanisms – Several mechanisms likely underlie the influence of BN on bacterial community composition (Fig. 2). One set of mechanisms involves direct trophic effects. As discussed in Box 1, BN exhibit selective feeding behavior (Abada et al., 2009; Liu et al., 2017; Shtonda and Avery, 2006; Weber and Traunspurger, 2013). Such feeding preferences can alter the relative abundance of bacterial taxa, thereby reshaping overall community composition. BN may also engage in passive selection, preferentially feeding on more abundant bacteria due to higher encounter rates or specific traits such as cell size. A second set of mechanisms involves indirect effects, such as dispersal and excretion. BN facilitate bacterial dispersal to new soil niches by transporting microbes externally on their cuticle (phoresy) and internally via their digestive tract (Chantanao and Jensen, 1969; Horiuchi et al., 2005; Jatala et al., 1974; Nykyri et al., 2014). Internal dissemination is linked to the high ingestion capacity of BN, which can consume up to 20 bacterial cells per pumping cycle (Ferris et al., 1997; Ferris et al., 1998). Most bacteria ingested by BN are not digested, allowing for continuous excretion of viable bacteria for more than 24 h after ingestion (Chantanao and Jensen, 1969; Griffiths, 1994; Smerda et al., 1971; Sohlenius, 1980). This bacterial dissemination facilitates colonization of new soil microhabitats and enhances substrate decomposition. BN can also act as vectors for bacteriophages, transporting viruses between spatially distinct bacterial populations (Dennehy et al., 2006; van Sluijs et al., 2025). This suggests that nematodes may play a key role in initiating viral cycles in soil ecosystems (Kuzyakov and Mason-Jones, 2018). However, Ackermann et al. (2016) tested bacterial transport by *Acrobeloides buetschlii* in modular soil microcosms using PLFA biomarkers to trace bacterial biomass. Despite strong grazing effects (e.g., a 50 % decline in *Pseudomonas putida* biomass), the authors found no evidence for nematode-mediated transport of bacteria across soil compartments. These results suggest that this transport mechanism may strongly depend on specific controlling factors such as soil type, bacterial strain, or nematode species. Finally, both direct and indirect BN effects may shift competitive dynamics within the bacterial community, significantly affecting its composition. For example, BN grazing on dominant bacterial taxa can reduce their abundance, creating ecological space for less competitive or subdominant species.

3.3. Reduction and mediation of wastes or toxic substances (CICES 2.1.1)

3.3.1. Bacterivorous nematodes as degrading agents of soil contaminants

An important yet under-studied and poorly quantified role of BN is their contribution to the degradation of soil contaminants. Several studies have shown that BN can accelerate the breakdown of organic contaminants by stimulating microbial activity (Zhou et al., 2018; Zhou et al., 2012). For instance, BN can enhance the degradation of herbicides like prometryne (Zhou et al., 2012; Zhou et al., 2013) and insecticides such as chlorpyrifos (Thakar et al., 2024). Additionally, these nematodes have been used in the remediation of hydrocarbon-contaminated soils, facilitating the degradation of compounds like pyrene (Sun et al., 2017) and BN have proven effective in the bioremediation of oil-contaminated soils (Zhou et al., 2019; Zhou et al., 2018). Although the effectiveness of BN across diverse remediation contexts requires further investigation, existing studies highlight their potential as valuable tools for improving soil health and mitigating contaminant impacts.

Sources of variation – Due to the limited number of studies, it is currently not possible to identify consistent factors that explain variability in BN effects on contaminant degradation.

Putative mechanisms – Several plausible mechanisms may explain how BN contribute to contaminant degradation in soil. Through bacterial grazing, BN stimulate microbial turnover and metabolic activity, leading to enhanced enzymatic degradation of organic pollutants. This stimulation may increase the expression of specific catabolic enzymes involved in contaminant breakdown (Zhou et al., 2012). Second, it is also possible, although highly speculative, that pollutant-degrading microorganisms become dominant members of the community in polluted soils, thereby increasing their potential encounter with BN. In such a scenario, nematode grazing and stimulation of microbial activity could potentially have a disproportionately effect on these taxa, which might in turn contribute to enhanced pollutant degradation. This remains a hypothesis that needed to be experimentally tested. Third, BN movement through soil micropores may enhance microbial dispersal and improve contact between microbes and contaminants (Knox et al., 2003). Finally, BN may indirectly enhance degradation through nutrient mineralization, increasing N and P availability to support microbial growth under the nutrient-limited conditions typical of contaminated soils (Trap et al., 2016). Although these mechanisms remain largely hypothetical and require empirical validation, they offer plausible explanations for the observed enhancement of contaminant degradation in BN-inoculated soils.

3.4. Pest and disease control (CICES 2.3.3)

3.4.1. Bacterivorous nematodes as regulators of pathogens

Another important function of healthy soil is its capacity to suppress pests and pathogens (Li et al., 2024). Soil suppressiveness refers to the ability of soil to limit or reduce populations of harmful organisms, thereby preventing the development of plant diseases even when pathogens are present. This suppressive function is largely mediated by the activities of beneficial soil organisms, such as BN, which play a key role in regulating the soil community (Xu et al., 2024). For instance, Xu et al. (2024) demonstrated that bio–organic fertilizer application increased the abundance of BN (*Protorhabditis* spp.), and that these nematodes preferentially preyed upon non–pathogen–antagonistic bacteria, thereby favoring the proliferation of pathogen–antagonistic *Bacillus* spp., which subsequently suppressed *Ralstonia solanacearum* and reduced tomato bacterial wilt incidence. Also, through the apparent competition (Ferris et al., 2012), BN inoculation enhances the population growth of predatory mites, which in turn increases predation pressure on a wide range of agricultural pests (Azevedo et al., 2019; Azevedo et al., 2020; Beretta et al., 2022; Rueda-Ramirez et al., 2022). Sustainable soil management practices that support BN communities can enhance the conservation and effectiveness of predator populations, leading to improved biological control and pest suppression in agroecosystems. Recent work by Rueda-Ramírez et al. (2025) showed that the nutritional quality of BN as prey strongly influences the growth and reproduction of the predatory mite Parasitus sp.; diets based on ω3-rich species such as *Acrobeloides bodenheimeri* and *Panagrolaimus* sp. supported better development and oviposition, whereas ω3-poor species such as *Meloidogyne incognita* and *Oscheius tipulae* proved less suitable.

Sources of variation – The limited number of studies constrains our ability to identify consistent sources of variation. Moreover, the existing studies are highly heterogeneous, as they target different types of pathogens, including bacteria, fungi, and nematodes, which makes it difficult to draw general conclusions or compare results across systems.

Putative mechanisms – The mechanisms through which BN influence pathogen dynamics likely vary depending on the pathogen type. For microbial pathogens, BN may indirectly suppress disease by consuming target cells or by promoting microbial communities that outcompete pathogenic taxa. In contrast, for plant-parasitic nematodes, suppression may occur through apparent competition, where BN and parasitic nematodes share predators or are affected by similar microbial antagonists, resulting in indirect control. These diverse, pathogen-specific interactions underscore the complexity of BN-mediated disease suppression and highlight the need for targeted research to elucidate the underlying mechanisms.

3.5. Biomass of cultivated terrestrial plants (CICES 1.1.1)

3.5.1. Bacterivorous nematodes as promoters of plant nutrition

Since the late 1990 s, researchers have explored whether changes induced by BN produce positive feedback effects on plant nutrition. Our *meta*-analysis included 26 publications investigating the effects of soil BN on plant performance (Fig. 1A). Seventeen of these studies examined effects on annual plant species, while nine focused on woody taxa. Additionally, five studies included plant species forming symbiotic associations with mycorrhizal fungi. Commonly studied species included maritime pine (*Pinus pinaster*, n = 5), rice (*Oryza sativa*, n = 4), thale cress (*Arabidopsis thaliana*, n = 3), Scots pine (*Pinus sylvestris*, n = 2), maize (*Zea mays*, n = 2), and wheat (*Triticum aestivum*, n = 2).

This literature showed that BN had positive effects on plant N and P nutrition (Bjornlund et al., 2012; Brondani et al., 2022; Djigal et al., 2004a; Djigal et al., 2004b; Irshad et al., 2011; Ranoarisoa et al., 2018; Xu et al., 2015). However, some studies reported no significant effect of BN on plant N or P uptake, even when there is an increase in plant biomass (Bardgett and Chan, 1999; Irshad et al., 2013; Setala et al., 1999). Our *meta*-analysis revealed a significant increase in total N amount in both shoots and roots in the presence of BN (Fig. 1B). The N amount increased by 22 % in the shoot and 35 % in the root compared to the control group. The amount of P in plant shoot increased by 42 %. The amount of P in root showed no significant change (*P*-value 0.081) despite a numerical increase (+48 %) (Fig. 1B).

Sources of variation – Soil fertilization significantly modulated plant nutritional responses to BN presence. For instance, Rehman et al. (2018) reported that the presence of BN in phosphate-amended soil increased P content in *Pinus roxburghii* by 25 % in shoots and 120 % in roots, but no significant differences were observed when the soil was unamended. Nematode species identity also played a major role. *Panagrellus redivivus* had a negative effect on shoot and root N amount but exhibited the highest effect sizes for shoot and root P amount. In contrast, *Panagrolaimus* and *Brevibucca* had the greatest impact on shoot N amount, while *Brevibucca* and *Oscheius akosreti* had the highest effect size for root N amount. Regarding shoot P amount, *Acrobeloides*, *Mesorhabditis*, and *Rhabditis* exhibited substantial variation in their effects. We also found a significant influence of nematode cp class on root N amount, i.e., cp1 nematodes had higher effect (9.1 % more) than cp2 species (Table 1). These results are in agreement with the study of Brondani et al. (2022) who reported that the total amount of N and P in plants varied significantly among the eight BN species included in their study, with a stronger influence of cp1 nematodes compared to cp2 nematodes. Experimental duration was another significant factor, for both root total N amount and shoot total P amount in response to BN-inoculation (Table 1). However, the direction of this temporal effect was not consistent: Bn effects on root total N amount tended to fade over time (−4.3 % per day), whereas theirs effects on shoot total P amount increased (+3% per day). Without further evidence, we can assume that this opposite time pattern may reflect changing plant nutrient demands over time. It may also reflect the higher mobility of N compared to P: BN effects on N are likely more immediate, whereas P, being less mobile, shows a slower and more progressive response over time.

Putative mechanisms – The primary pathway underlying BN-induced improvement in plant N and P nutrition is the microbial loop, whereby grazing releases nutrients sequestered in bacterial biomass (Trap et al., 2016). BN grazing also stimulates microbial growth and activity across the broader soil community, including bacteria, fungi, and other microbes, resulting in higher gross nutrient mineralization (Ranoarisoa et al., 2018). A second pathway involves non-nutritional pathways, such as hormonal signaling effects, as discussed further below.

3.5.2. Bacterivorous nematodes as promoters of plant growth

Our *meta*-analysis encompassed 16 studies that examined the impact of BN on shoot biomass, as well as an additional 14 studies that investigated the effects on both shoot biomass and 10 studies on total plant biomass (Fig. 1B). Numerous studies have linked BN to the enhanced growth of both woody (Brondani et al., 2022; Gilarte et al., 2024; Irshad et al., 2012; Irshad et al., 2011; Setala et al., 1999) and herbaceous plants (Alphei et al., 1996; Bjornlund et al., 2012; Bonkowski et al., 2000; Cheng et al., 2011; Djigal et al., 2004a; Djigal et al., 2004b; Jiang et al., 2020; Matus-Acuña et al., 2018; Ranoarisoa et al., 2018; Xu et al., 2015). However, some papers reported no effect of BN on plant growth, either on woody (Baath et al., 1981; Irshad et al., 2013) or herbaceous plants (Bardgett and Chan, 1999; Bonkowski et al., 2000; Gilarte et al., 2020). In our *meta*-analysis, we found a significant positive effect of the presence of BN on plant growth, with a 19 % increase in shoot biomass (124 observations) and a 13 % increase in total plant biomass (55 observations; Fig. 1A).

Sources of variation – The disparities may come from similar factors already discussed. First, higher C:N ratio reduced the effect of BN on shoot biomass; the BN effect on shoot biomass decreasing by 13 % for each unit increase in the C:N ratio (Table 1). Second, nematode species identity is a critical determinant even though all nematode species generally had a positive effect on shoot biomass, with the notable exception of *Mesorhabditis* which exhibited a negative effect size for one observation. *Acrobeloides* displayed the highest and most variable effect size on plant biomass. Again, the life-history traits of BN significantly impact their influence on shoot biomass (Table 1). Precisely, the cp1 nematodes had the greatest positive impact on shoot biomass, approximately 13 % higher than the impact of cp2 nematodes. Finally, we found that the duration of the experiment had a negative effect on the impact of BN on shoot biomass, with a 0.5 % decrease per day of

Table 3
Effects of bacterivorous nematodes on plant root traits. Significant positive effects between control and treatment groups are indicated by "+", while significant negative effects are indicated by "–" and "n.s." represents non-significant effects.

Authors	Year	Plant	Duration	Nematode	Root trait						
					Length	SRL$	Area	Tips	Forks	Cross	Branching
Mao *et al.*	2006	*L. esculentum*		Soil native community	+	+	+	+	+	+	+
Mao *et al.*	2007	*L. esculentum*	5 days	Soil native community	n.s.		n.s.	+	n.s.		
			5 days		n.s.		n.s.	+	n.s.		
			10 days		+		+	–	n.s.		
			10 days		+		n.s.	–	n.s.		
Cheng *et al.*	2011	*O. sativa*	14 days	*Cephalobus*	+			+			
			20 days		+			+			
			14 days	*C. elegans*	+			+			
			20 days		n.s.			n.s.			
Irshad *et al.*	2011	*P. pinaster*	35 days	*Rhabditis*				+	+	–	
Irshad *et al.*	2012	*P. pinaster*	60 days	*Acrobeloides*	+		n.s.	+	+		
					n.s.		n.s.	+	n.s.		
				Rhabditis	+		+	n.s.	+		
					n.s.		n.s.	n.s.	n.s.		
Jiang *et al.*	2012	*A. thaliana*	10 days	*Cephalobus*							
			20 days								
Irshad *et al.*	2013	*P. pinaster*	35 days	*Rhabditis*	n.s.		n.s.	n.s.	n.s.		
Li *et al.*	2015	*A. hypogea*	14 days	*Cephalobus*	+		+	+			
			28 days	*Mesorhabditis*	+		+	+			
			42 days		+		+	+			
Cheng *et al.*	2016	*O. sativa*	20 days	*Cephalobus* *C. elegans*							
Maboreke *et al.*	2018	*Q. robur*	28 days	*A. buetschlii*	n.s.						
			56 days		n.s.						
Matus-Acuna *et al.*	2018	*Z. maysA. thaliana*	28 days	*C. elegans*	–						+
Ranoarisoa *et al.*	2018	*O. sativa*	28 days	*Acrobeloides*	+	n.s.	+	+			–
Jiang *et al.*	2020	*A. thaliana*	10 days	*CephalobusMesorhabditis*	+		+	+			
			20 days		+		+	+			
			30 days		+		+	n.s.			
Ranoarisoa *et al.*	2020	*P. pinaster*	100 days	*Rhabditis*	n.s.		n.s.	n.s.	n.s.	n.s.	
Jiang *et al.*	2023	*A. thaliana*	10 days	*Rhabditis*	n.s.		n.s.	n.s.			
			20 days	*Protorhabditis*	+		n.s.	+			
			30 days	*Cephalobus* *Eucephalobus* *Chiloplacus*	n.s.		+	+			

$SRL: Specific Root Length.

incubation (Table 1).

Putative mechanisms – The presence of BN has a beneficial effect on plant growth by regulating the mineralization of nutrients, which enhances nutrient availability for plants. This increased nutrient availability supports optimal plant nutrition, essential for key physiological processes like photosynthesis. The tight synchronization between plant nutrient demand and microbial nutrient supply is achieved through the microbial loop (Bonkowski and Clarholm, 2012; Clarholm, 1985). Mineralization of nutrients is driven by the plant provision of C compounds through root exudates and decaying organic matter, enabling a balanced exchange between plant demand and microbial supply, and thereby optimizing plant biomass production and growth (Kuzyakov, 2002; Kuzyakov and Mason-Jones, 2018; Kuzyakov and Xu, 2013). This close coupling between plant carbon inputs and microbial nutrient mineralization is crucial for efficient nutrient cycling, ensuring that the nutrients released by microbes and BN are readily absorbed by plants, ultimately supporting optimal plant growth and productivity. Moreover, we cannot exclude non nutritional hormonal mechanisms as discussed by Trap et al. (2016) and below in the following section.

3.5.3. *Bacterivorous nematodes as regulators of root traits*

In addition to plant biomass and nutrition, BN can significantly influence root traits (Cheng et al., 2011; Irshad et al., 2012; Jiang et al., 2023b; Jiang et al., 2020; Jiang et al., 2012; Mao et al., 2007). Inoculating BN can rapidly increase rhizodeposition, up to 2.6 times higher compared to the control, and change rhizodeposition biochemical composition (Sundin et al., 1990). This increased C input induced by BN stimulates the microbial community, representing the starting point of the soil microbial loop. In addition, some studies have shown that the presence of BN can promote the growth of plant roots (Cheng et al., 2011; Irshad et al., 2012). Irshad et al. (2012) observed that the presence of *Acrobeloides* led to a 46 % increase in the number of tips and a 36 % increase in the number of forks in *P. pinaster* compared to the control group after 60 days. It was also found that *O. sativa* plants developed longer and more branched roots when *Cephalobus* and *C. elegans* were present in soil (Cheng et al., 2011). In our *meta*-analysis, the presence of BN increased root length, tip number and area by 18 %, 31 % and 37 %, respectively (Fig. 1B). Other root traits have been analyzed in the literature, but the number of available data points was insufficient to perform a *meta*-analysis. Nevertheless, we compiled the available information in Table 3.

Sources of variation – Two factors appear to be important in modulating the effect of BN on root traits: the duration of the experiment and the cp-class (Table 1). Both factors influence root length and the number of tips. Regarding root surface area, initial soil available P content plays a critical role, the more available the P, the stronger the nematode effect. Soil pH also seems to significantly influence the effect of BN on root traits. Nevertheless, whether these moderators act as actual controlling factors remains to be experimentally verified, and additional studies are required to establish their causal role.

Putative mechanisms – These positive effects of BN on plant roots led to an interest in the hormonal hypothesis (Chen et al., 2007; Jiang et al., 2023b; Jiang et al., 2020; Jiang et al., 2012; Mao et al., 2007) proposed for protists (Bonkowski, 2004; Bonkowski and Clarholm, 2012). This hypothesis formulated by Bonkowski (2004) is based on non-nutritional mechanisms where protists increase lateral root branching by altering microbe-root communication, with strong consequences on plant internal auxin metabolism (Bonkowski and Brandt, 2002; Jentschke et al., 1995; Kreuzer et al., 2006; Krome et al., 2009a; Krome et al., 2009b; Rosenberg et al., 2009). The growth of lateral roots allows the plant to explore a greater volume of soil thereby increasing the uptake of nutrients. Regarding BN, promising results have been obtained by Jiang et al. (2020) who showed an increase in the concentration of IAA (indoleacetic acid) in the soil when *Cephalobus* and *Mesorhabditis* nematodes were co-inoculated with an auxin-producing bacterium (*B. amyloliquefaciens*). Furthermore, the expression of two genes, IAA3 and IAA13 from the Aux/IAA family, increased in the roots when exposed to IAA-producing bacteria, particularly in the presence of BN. However, the effects of these two BN on plant growth and nutrition, as well as on root traits, were not influenced by the presence or absence of IAA-producing bacterial strains. Using the Rhizobox technique, Ranoarisoa et al. (2018) demonstrated that the presence of *Acrobeloides*, although it had beneficial effects on rice nutrition and root growth, had no effect on roots branching. Using the data from Jiang et al. (2012), the calculation of root branching (number of root caps per unit of root length) revealed similar values between the treatments (presence or absence of BN). These results indicate that increased plant and root growth is attributed to higher nutrient mineralization caused by BN, but there are no corresponding changes in root branching due to hormonal influences. Thus, we still lack of evidence that BN induce positive effect on plant growth in unlimited nutrient conditions.

3.5.4. Bacterivorous nematodes as promoters of plant mutualistic symbioses

Some studies have investigated the interactions among BN and plant mutualistic symbioses, such as mycorrhizal fungi (Irshad et al., 2012; Irshad et al., 2013; Ranoarisoa et al., 2020; Setala et al., 1999; Trap et al., 2021) or N-fixing plants (Gilarte et al., 2024; Horiuchi et al., 2005). Using a set of six microcosm experiments conducted in contrasting P situations, Trap et al. (2021) found a high and significant correlation ($R^2 = 0.70$) between the increasing addition of soil mutualist organisms (BN, ectomycorrhizal fungi and phytase-producing bacteria) and *P. pinaster* P-acquisition. Horiuchi et al. (2005) found that *Caenorhabditis elegans* positively mediates the interaction between roots and rhizobia by facilitating nodulation. Conversely, other studies have shown that BN such as Acrobeloides buetschlii can exert deleterious effects on rhizobial symbiosis by invading nodules and strongly reducing N_2 fixation, although without affecting nodule number or short-term plant growth (Westcott and Barker, 1976).

Sources of variation – Due to the limited number of available studies, *meta*-regressions could not be performed. Numerous factors are likely to modulate the effects of BN on mutualistic symbiotic associations. For instance, in Trap et al. (2021), this relationship was observed only in a high P-sorbing soil amended with an organic P source. Thus, soil P status strongly influences the functional interaction between BN and ectomycorrhizal fungi. Regarding BN-rhizobia interactions, the work of Gilarte et al. (2024) suggests that the interaction between BN and N-fixing plants is highly variable and context-dependent. Using *Acrobeloides*, the authors examined how BN affect the interactions between N-fixing Acacia and non-fixing Banksia tree seedlings at different stages of forest succession. The effect of BN on interspecific plant interactions depends upon successional stage of origin in tree seedlings, i.e., in the early successional stage scenario, BN reduced total plant biomass, nodulation and nitrogenase activity in *Acacia leiocalyx*, indicating that BN could hinder the symbiotic relationship between Acacia and rhizobia in the early successional stages. However, in later successional stages, BN had a more positive effect, i.e., BN promoted biomass growth and N content in the shoots of both *Acacia flavescens* and *Banksia*. *A. flavescens* showed improved nodulation and nitrogenase activity when BN were present in mixed cultures with *Banksia aemula*. This suggests that BN acted as vectors for rhizobia, facilitating the establishment of N-fixing bacteria in Acacia roots and thereby promoting N fixation.

Putative mechanisms – The underlying mechanisms likely vary depending on the type of mutualistic symbiont involved. In the case of mycorrhizal associations, it is likely that nematodes enhance nutrient availability for fungal hyphae or transport spores on the nematode cuticle. In the case of rhizobia, BN can disperse the rhizobial species *Sinorhizobium meliloti* to the roots of the legume *Medicago truncatula* in response to plant-released volatiles that attract the nematode (Horiuchi et al., 2005). A similar mechanism has recently been observed in plant-parasitic nematodes. Virus-induced changes in root volatile emissions have been shown to attract soil nematode vectors to infected plants, thereby promoting virus transmission (van Griethuysen et al., 2024). Further research is needed to clarify these interactions and determine the generality of such mechanisms across different mutualistic organisms.

3.6. Potential deleterious implications of BN on soil and agroecosystem health

While much of the literature emphasizes positive roles of BN, few works highlighted that under certain conditions, BN may also have deleterious effects on soil and agroecosystem health. For instance, as mentioned earlier, Westcott & Barker (1976) demonstrated that *Acrobeloides buetschlii* can invade legume root nodules and significantly inhibit nitrogen fixation, by up to 80 %, even though the total number of nodules formed and short-term plant growth remained unaffected. More recently, Chan et al. (2023) reported that BN can act as vectors for the spread of antibiotic-resistant bacteria and antibiotic-adsorbed nanoplastics. Such dissemination by BN may inadvertently enhance the environmental persistence and dispersion of pollutants and resistant microbial strains, with potentially serious repercussions for soil health and agricultural sustainability. BN can also influence the dispersal and survival of soil pathogens (Anderson et al., 2003; Chantanao and Jensen, 1969; Kroupitski et al., 2015; Nykyri et al., 2014; Yulia et al., 2015). BN can transport bacteria externally on their cuticle or internally through their gut, effectively dispersing microbial cells, including potential plant pathogens, across soil aggregates and between different soil compartments (Trap et al., 2016). A key challenge is thus to develop integrative approaches that capture the multiple functions of BN, in order to objectively assess the balance between their beneficial contributions and potential deleterious effects in soils and agroecosystems, although current evidence suggests that positive effects largely predominate.

4. Conclusion and perspectives

BN are key actors in terrestrial ecosystem functioning. They contribute to multiple essential soil functions, including C and nutrient storage in the soil food web, stimulation of microbial growth and activity, regulation of microbial community composition, degradation of soil contaminants, suppression of soil pathogens, enhancement of nutrient mineralization, promotion of plant nutrition and growth, and C sequestration. Through *meta*-analysis, we quantified the overall positive impacts of BN on these functions and identified key sources of variation across studies. However, it is important to highlight that our findings are derived from controlled experiments that may not fully capture the complexity of field environments. Also, while BN should ideally be considered within the broader context of soil food webs to fully capture their interactions with other trophic groups (Bjornlund et al., 2006), in this study we deliberately restricted our search terms to this functional group. Network-based studies typically address entire communities, making it difficult to disentangle the specific causal effects of BN. Lastly, several aspects of BN functions remain underexplored. Notably, limited research exists on BN interactions with plant symbiotic mutualists, their role in pollutant degradation, and their influence on root traits. Although BN have been implicated in pathogen suppression and plant health, the available evidence is still scarce and critical knowledge gaps remain, particularly regarding the mechanisms underlying these interactions and their consistency under field conditions (Li et al., 2024; Topalović and Geisen, 2023). Addressing these gaps will be essential to assess the potential of BN as allies in sustainable disease management.

To better capture the functional roles of BN in ecosystems, we propose that future research prioritizes the following areas:

1. ***Timeframe of interactions***. The duration of coexistence appears to be a crucial factor in determining the functional outcomes of co-inoculation experiments. Fewer than 20 % of studies in our *meta*-analysis exceeded 60 days of incubation, suggesting that the long-term dynamics of nematode populations remain poorly understood. Conducting longer co-inoculation experiments appears crucial for gaining deeper insights into the effects of BN on plant and soil functions.
2. *Spatial context and small-scale heterogeneity*. BN should be considered within the spatial structure of soil environments, as ecosystem functions mediated by these organisms are likely influenced by spatial heterogeneity. For instance, small-scale environmental heterogeneity significantly enhances species richness of soil nematodes, suggesting that spatial complexity plays a key role in belowground community assembly and function (Martin and Sprunger, 2021; Nielsen et al., 2010). Investigating spatial heterogeneity, such as patchiness in resource availability, soil structure, moisture gradients, or root distribution is necessary to better capture the functional roles of BN in ecosystems.
3. ***Species and life-history traits.*** Species-specific effects and life-history strategies of BN significantly moderated several soil and plant functions. Our understanding of how nematode population dynamics modulate soil and plant responses to the presence of BN is strongly limited (Zelenev et al., 2004; Zelenev et al., 2006). We encourage the community to give greater consideration to the life history traits of nematodes, especially when they are introduced in assemblages. In addition, given the frequent and significant influence of species identity observed in our analysis, it is essential to ensure accurate identification of nematode species used in experiments. Misidentification may occur and this uncertainty should be acknowledged when interpreting species-level effects (De Santiago et al., 2025).
4. ***Interspecific interactions.*** Most studies examining BN effects focus on a single species, highlighting the need to investigate the effects of multiple coexisting BN species. In the field, nematode communities are typically composed of 5–12 coexisting genera. As most field taxonomic surveys identify nematodes at the genus level, the actual species richness is likely higher; assuming several species per genus, total richness can reasonably be estimated at around 10–20 species. Lower richness is usually observed in highly disturbed environments, whereas higher values are expected in less disturbed, organic-rich soils. How interspecific competition and functional complementarity, linked to different feeding preferences or life strategies, drive the effects of nematodes in assemblages remains largely understudied.
5. ***Soil nutrient status.*** A deeper understanding of soil nutrient status, particularly P availability, is also essential (Trap et al., 2021). There is a lack of studies exploring how soil nutrient status and fertilization gradients modulate the impact of BN on soil and plant function, which is especially important for interpreting the results of field studies.
6. ***Soil C sequestration***. Future research should aim to clarify the contribution of BN to soil C sequestration through dedicated experiments. While current evidence suggests that BN can simultaneously stimulate short-term C losses and promote long-term stabilization via microbial necromass formation, the mechanisms remain insufficiently quantified. Addressing this will probably require long-term experiments, ideally using stable isotope tracing approaches to follow C fluxes across biological and soil pools. In addition, modeling BN-driven microbial turnover, nutrient release, and necromass recycling would greatly improve our ability to predict BN contributions to soil C storage. Such efforts will be essential to establish the causal role of BN in regulating soil C sequestration across different ecosystems and management contexts.
7. ***Microbial-Viral loop complementarity***. The potential complementarity between the microbial loop and the viral loop remains unexplored (Kuzyakov and Mason-Jones, 2018). Considering viruses and nematodes in the functioning of the micro-trophic network

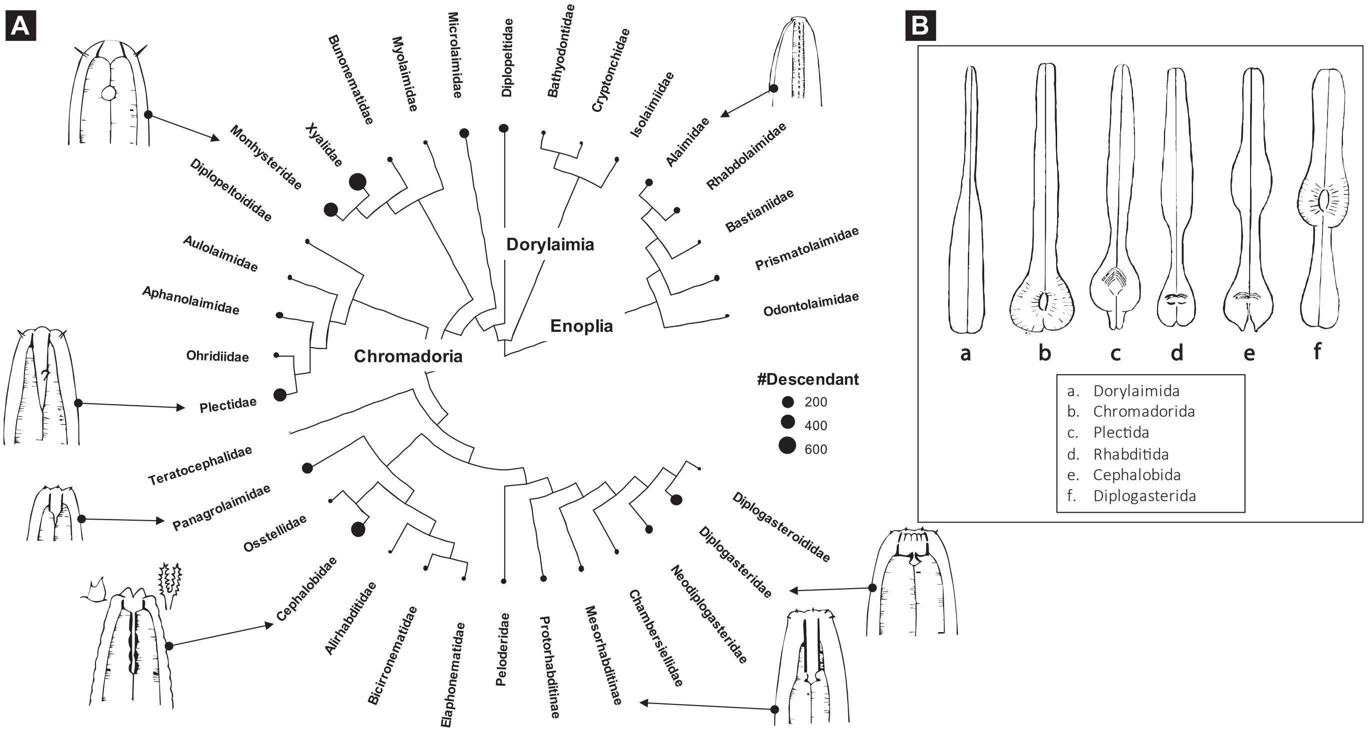

Fig. 3. A. Phylogenetic tree of bacterivorous nematodes (source Open Tree of Life) with example of mouth shapes. B. Different pharynx types found in bacterivorous nematode taxa.

represents an interesting research avenue, likely allowing us to better understand the effects of nematodes.

8. ***Diet and microbiome***. As discussed in Box 1, the diet of BN remains largely unknown, especially under conditions of species assemblages. Recent molecular tools and analyses of the nematode microbiome could certainly help us better understand niche segregation strategies in these species and their functional complementarities (Baquiran et al., 2013; Dahan et al., 2020; Dirksen et al., 2016; Haçariz et al., 2021; Herman et al., 2022; Zhang et al., 2017). In this context, research on nematode-associated microbiomes has markedly intensified in recent years, further highlighting the potential of this approach for disentangling BN functional roles (Herman et al., 2022; Martini et al., 2024; Singh and Luallen, 2024; Zimmermann et al., 2024).

Addressing these gaps through interdisciplinary research, longer-term studies, and molecular tools will greatly enhance our understanding of BN within soil food webs. Together, these research directions will offer a more comprehensive understanding of BN ecological roles and support the development of more sustainable soil management strategies.

CRediT authorship contribution statement

Jean Trap: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Margot Brondani:** Writing – original draft, Visualization, Formal analysis, Data curation. **Claude Plassard:** Writing – review & editing. **Mickaël Hedde:** Writing – review & editing. **Jeremy Puissant:** Writing – review & editing, Visualization, Methodology, Formal analysis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Box 1. What are bacterivorous nematodes?

Defining a bacterivorous nematode (BN) might initially appear to be a relatively straightforward task: it refers to nematodes whose diet primarily consists of bacteria. However, the task becomes more complex when considering the limited information available on the actual feeding habits of BN. Currently, the classification of soil nematodes into trophic groups is largely based on the seminal work of Yeates et al. (1993). Even at the time, Yeates et al. (1993) discussed the degree of food flexibility among BN species, noting that it was possible to cultivate Cephalobidae or Rhabditidae on fungi such as *Phoma* sp. and *Pythium middletonii*. Similarly, it is well known that BN can be cultured under axenic conditions by absorbing organic molecules (Loulou et al., 2023). Thus, Yeates et al. (1993) considered bacteria to be the primary energy source for these nematodes, with growth being significantly reduced in axenic media. Consequently, Group (3), "Bacterial feeding," was defined as comprising nematodes that primarily consume prokaryotes but can also absorb nutrients from other sources. They further noted that species with larger mouths may ingest other types of food as well. Finally, species belonging to Group 6, "Unicellular eukaryote feeding," which consume diatoms, algae, fungal spores, and yeast cells, such as *Chromadoria*, *Desmodora*, *Diplogaster*, *Fictor*, *Glauxinema*, or *Prochromadora*, are usually classified as bacterivorous by most authors. Nematodes defined as bacterivorous therefore have a diet that is far from being composed solely of bacteria, and the proportion of bacteria as a source of carbon remains difficult to quantify. It should also be acknowledged that trophic plasticity is not restricted to nematodes classified as bacterivorous. Taxa assigned to other trophic groups may opportunistically exploit bacterial resources as well. The term "bacterivorous" therefore reflects a functional grouping based on the predominant feeding strategy, rather than an absolute exclusion of other trophic interactions.

When focusing only on bacteria, there is increasing evidence that BN exhibit preferences for specific bacterial taxa (Newsham et al., 2004; Salinas et al., 2007), mostly based on traits such as size, morphology, cell-wall or metabolite production (Abada et al., 2009; Bjornlund et al., 2006; Liu et al., 2017; Shtonda and Avery, 2006; Weber and Traunspurger, 2013). BN prefer small-sized gram-negative bacteria over gram-positive bacteria, likely due to the thinner cell wall (Abada et al., 2009; Rønn et al., 2012; Shtonda and Avery, 2006; Yu et al., 2015), but avoid bacteria producing nematicidal metabolites and toxicants (Khan et al., 2018). Key bacterial traits such as water content or C:N ratio were also identified as selective criteria by BN (Hemmerling et al., 2023; Liu et al., 2017). While it has been suggested that BN are also capable of active selection (Liu et al., 2017; Weber and Traunspurger, 2013), their active selective capacity is likely less developed than that of protists when bacterial cells are in mixture (Jousset et al., 2009). These observations suggest that BN may not exhibit strict dietary preferences or actively select their prey but can instead consume a broader range of bacterial types.

Consequently, the group of BN is highly diverse, taxonomically, phylogenetically (Fig. 3), and functionally (Hodda, 2022a; Hodda, 2022c). Functionally, BN are the only trophic group to span the entire "cp" scale, 41 % are cp1, 25 % are cp2, 28 % are cp3, 5 % are cp4 and 1 % are cp5 at the genus level (Bongers, 1990; Bongers and Bongers, 1998). Additionally, this group exhibits substantial morphological and anatomical diversity, particularly in the buccal cavity and esophageal shape, which enables them to exploit the large panel of resources quoted earlier (Fig. 3A). For instance, the shape of the labial probolae and the development of cephalic probolae at the nematode head in the Cephalobidae allow passive food specialization, thereby optimizing niche partitioning among co-occurring BN species (De Ley, 1992). Some BN taxa possess a tubular stoma and a grinder-like structure within their terminal bulb, a muscular component located at the posterior end of the pharynx (Chiang et al., 2006; Fürst von Lieven, 2003; Munn and Munn, 2002). This physical adaptation allows these nematodes to take up bacterial cells from the environment through a pumping action of the muscular pharynx and to physically crush and consume bacteria with thick cell walls that are largely hardly digestible for other BN. Pharyngeal morphology varies widely among BN taxa, with two-, three-, or four-part structures that differ in musculature (Fig. 3B). In conclusion, BN comprise a highly diverse group of nematode species, both phylogenetically, ecologically and functionally, and their exact diet in natural environments over space and time remains largely unknown.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2025.117575.

Data availability

Data will be made available on request.

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