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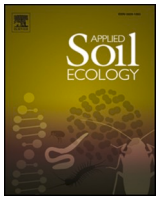

Research paper

Impact of cover cropping on root lesion nematodes (*Pratylenchus* spp.) and nematode communities in *Narcissus* fields

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ABSTRACT

Cover crops offer numerous benefits to the soil, including pest, pathogen suppression and enhanced fertility. Focussing on fields used for *Narcissus* production as a model, the potential of different cover crop treatments to suppress plant-parasitic nematodes while safeguarding beneficial nematode communities was evaluated. The root lesion nematode species, *Pratylenchus penetrans*, is known to significantly reduce *Narcissus* yields, a challenge further exacerbated by limited chemical control options and restricted land availability to deploy effective crop rotation. French marigold, oilseed radish, *Phacelia*, Japanese oats, alfalfa, and forage chicory were evaluated in two experiments under greenhouse conditions to assess their suitability as hosts for *P. penetrans* based on the nematode reproduction factor (Rf). *Phacelia* and Japanese oat were rated as maintenance hosts ($1 < Rf < 2$) while the remaining cover crops were identified as poor hosts ($0.15 < Rf < 1$). Thereafter, three field experiments assessed the effects of the same cover crop treatments, plus Indian mustard, on the abundance of *Pratylenchus*, *Aphelenchus, Aphelenchoides* spp., and bacterivore nematodes. Sampling occurred before sowing of the cover crop, three months after sowing and six weeks post-incorporation of the mature cover crop. Four of the tested cover crops (French marigold, oilseed radish, forage chicory and alfalfa) significantly reduced the abundance of *Pratylenchus* spp., by 53–75 % across all three experiments. *Phacelia* and Japanese oats had no effect, while Indian mustard increased the abundance of *Pratylenchus* spp., by 113–319 % across all experiments. Oilseed radish and Indian mustard increased the abundance of bacterivore nematodes, with oilseed radish showing the greatest increase of 335 %. Using 18S rRNA amplicon sequencing, cover crops showed no adverse effects on alpha and beta nematode diversity, while cover crop incorporation resulted in higher enrichment and lower structure indices. These findings strongly suggest that French marigold, oilseed radish, forage chicory, and alfalfa are potential options for managing *Pratylenchus* spp. without adverse effects on non-target beneficial soil nematode communities. Understanding cover crop–nematode interactions can expand their use beyond current production systems. This study offers a first step towards selecting cover crops that maintain/promote beneficial nematodes, support soil health restoration, and suppress *Pratylenchus* spp. in crops that form a typical UK arable rotation.

1. Introduction

Regenerative agriculture has garnered increasing attention as a farmer-led approach to preserving and restoring soil health through the adoption of a range of land management practices (Tittonell et al., 2022). The reduced or exclusion of synthetic pesticides, coupled with the adoption of integrated pest management (Hillocks, 2012), is regarded as an additional dimension of regenerative agriculture. However, a direct consequence of reducing or eliminating the use of pesticides is an increased vulnerability to pests and pathogens in specific cropping systems.

Cover cropping is integral to several regenerative principles (Wade et al., 2025), promoting plant diversity, soil cover, and year-round living root presence that confers multiple benefits, such as reducing soil erosion, enhancing nutrient cycling and soil fertility, and suppressing soilborne pathogens (Osipitan et al., 2019; Van Eerd et al., 2023). A recent national-scale survey on sustainable soil management practices in the UK reported that 67 % of 297 farmers and land managers were aware of cover cropping, while 44 % had adopted its use (Jaworski et al., 2024). In addition to their soil health benefits, cover crops also have the

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potential to suppress plant-parasitic nematodes through a range of mechanisms, including trap cropping, allelopathic interactions, biofumigation, and serving as non-host or poor-host species (Ntalli and Caboni, 2017).

The soil rhizosphere harbours a taxonomically and functionally diverse community of nematodes (van den Hoogen et al., 2019) whose composition and structure can serve as indicators of soil health (Gao et al., 2020; Du Preez et al., 2022). Although cover crops are increasingly promoted as an agronomic strategy for managing plant-parasitic nematodes, the evidence regarding their efficacy remains inconsistent, and their effects on beneficial nematode groups, which typically comprise the vast majority of soil nematode communities (van den Hoogen et al., 2019), are not fully understood. Some studies have demonstrated that cover crops can effectively suppress plant-parasitic nematodes without adversely affecting overall nematode community structure (Waisen et al., 2022). However, cover crop responses to nematodes often vary and are attributed to several factors, including cover crop cultivar traits, soil properties, climatic conditions, geographical variation, and the pathogenicity of specific nematode species or populations (Viaene et al., 2013; Rudolph et al., 2017). Additionally, experimental duration, initial nematode population density, and cover crop seeding rate influence nematode responses to cover cropping strategies (Taning et al., 2024).

Cover crops should ideally suppress plant-parasitic nematodes while maintaining or enhancing beneficial non-target nematode populations. However, quantifying the benefits of regenerative agriculture, such as cover cropping, is challenging because production systems, geographic location, and management interactions significantly influence outcomes (Wade et al., 2025).

The ornamental horticulture sector presents a valuable case study for exploring the efficacy of cover crop management in controlling plant-parasitic nematodes, particularly in the context of *Narcissus* production. The UK produces approximately 80 % of global *Narcissus*, valued at £100 million in cut flowers and £7.9 million in bulb exports (DEFRA, 2023). Plant-parasitic nematodes are significant pathogens of *Narcissus*, reducing bulb and flower quantity and quality. The most damaging plant-parasitic nematode species to *Narcissus* include the root-lesion nematode (*Pratylenchus penetrans*), stem and bulb nematode (*Ditylenchus dipsaci*) and *Aphelenchoides subtenuis* (Slootweg, 1956; Hanks, 2013). *Pratylenchus penetrans* is polyphagous, associated not only with *Narcissus* but also with major UK crops, which form a typical UK arable rotation including carrots, potatoes, peas, beans, cereals, and permanent pasture (Boag, 1980; Oliveira et al., 2017; Orlando et al., 2020). Additionally, *P. penetrans* forms disease complexes with the fungus *Cylindrocarpon destructans*, causing root rot in *Narcissus*, often referred to as "soil sickness," "decline," or "replant disease," particularly on the Isles of Scilly, England (Slootweg, 1956). Furthermore, economic losses occur when *Narcissus* bulbs are rejected for export due to contamination with quarantine nematodes such as the potato cyst nematode species *Globodera pallida* and *G. rostochiensis* (EPPO, 2017) in fields with potatoes as part of the crop rotation.

Since the withdrawal of nematicide use in 2020 across the *Narcissus* sector, growers have employed management strategies, such as hot-water treatments, which have achieved only partial control of plant-parasitic nematodes (Hanks, 2013). Current recommendations advise leaving *Narcissus* land fallow for at least five years, which is often impractical due to limited land availability for *Narcissus* production across the UK (Upcott et al., 2023) and contradicts one of the key principles of regenerative agriculture of minimising bare soil (Wade et al., 2025).

Therefore, to ensure the long-term sustainability of the UK *Narcissus* sector, it is crucial to identify cover crops that suppress plant-parasitic nematodes. Moreover, as the primary plant-parasitic nematode species affecting *Narcissus* also impact other significant UK crops, identifying suppressive cover crops could provide broader benefits to typical UK crop rotations. Equally, identifying cover crops that inadvertently promote the multiplication of economically important plant-parasitic nematodes is essential to prevent exacerbating nematode-driven production issues. The in-field lifting of *Narcissus* bulbs occurs in June, followed by replanting in September, which allows for a fallow period to establish short-season, nematode-suppressive cover crops. This timeframe presents an opportunity to evaluate various cover crops for their effectiveness in suppressing plant-parasitic nematodes and their compatibility with regenerative soil management objectives.

Preliminary soil sampling at all field sites confirmed that several *Pratylenchus* spp. were the dominant plant-parasitic nematodes present, with negligible or undetectable levels of *Ditylenchus dipsaci* and *Aphelenchoides subtenuis*. Consequently, the study focused exclusively on *Pratylenchus* spp. as the primary target for evaluating the nematode suppressiveness of cover crops. This study therefore employed a dual greenhouse and field-based approach to: 1) evaluate the host suitability of oilseed radish, French marigold, *Phacelia*, Japanese oats, forage chicory, and alfalfa for *P. penetrans* under controlled greenhouse conditions, 2) assess the impact of these cover crops on the abundance of *Pratylenchus*, *Aphelenchus, Aphelenchoides* spp., and bacterivore nematodes, in *Narcissus* fields using microscopy, 3) use real-time quantitative PCR (qPCR) to identify and quantify four common *Pratylenchus* species found in UK agricultural soils: *P. penetrans*, *P. crenatus*, *P. neglectus*, and *P. thornei*, and 4) evaluate the effects of the selected cover crops on overall soil nematode communities and food web indices across three field sites using 18S rRNA amplicon sequencing. It was hypothesised that cover crops significantly differ in their host suitability for *P. penetrans* and affect the overall composition of soil nematode communities.

2. Materials and methods

Cover crops used in this study were selected based on prior evidence of their nematode-suppressive potential (Neupane and Yan, 2023; Taning et al., 2024). All six cover crops are commonly used in UK agriculture, ensuring that the findings are relevant to a wide range of cropping systems.

Cover crop establishment was generally successful. Among the species evaluated, oilseed radish and Indian mustard consistently produced the highest biomass across both years (Supplementary Table S2). French marigold and forage chicory yielded between 4 and 8 t ha^{-1}, with no statistically significant differences observed between them.

2.1. Greenhouse experiments

2.1.1. Cover crop treatments, experiment design, and establishment

Two independent greenhouse studies were conducted to assess the host status of selected cover crops to *P. penetrans*. *Phacelia* (*Phacelia tanacetifolia*) was used as a positive control due to its known susceptibility to *P. penetrans* (Kimpinski et al., 2000), while fallow soil served as a negative control. Two oilseed radish (*Raphanus sativus*) cultivars (Contra and Angus) were included, as host susceptibility varies by cultivar (Viaene et al., 2013); the least susceptible (Contra) was later used in field trials. The remaining cover crops included French marigold (*Tagetes patula*), alfalfa (*Medicago sativa*), Japanese oats (*Avena sativa*) and forage chicory (*Cichorium intybus*). Sterilised loam soil (John Innes, UK) was mixed 1:1 with sand to mimic sandy loam conditions in which *P. penetrans* is most active (Florini et al., 1987) and used to fill 1-L pots. Soils were watered to field capacity before sowing seeds at the recommended rates, with thinning performed seven days after sowing. Treatments (Table 1) were arranged in a randomised complete block design with six replicates.

Mass culturing of *P. penetrans* was performed on carrot discs, followed by subculturing in monoxenic culture as described by Speijer and De Waele (1997). The nematodes used for the greenhouse experiments were extracted from the carrot discs using a modified Baermann funnel technique (Hooper, 1986). The purity of *P. penetrans* culture was

Table 1
Cover crop treatments used in both greenhouse experiments and all three field trials. Pi = sampling at planting, Pre = before incorporation of the cover crops and Post = after incorporation of cover crops to determine nematode abundance.

Greenhouse experiments			
Cover crop (variety)	Seed rate kg ha^{-1}	Source	Plants/pot
French marigold (MP04371)	8	Elsoms Seeds, UK	2
Forage chicory (334N)	6	Chiltern Seeds, UK	3
Japanese oat (Pratex)	100	P.H. Petersen Germany	4
Oilseed radish 1 (Angus)	30	P.H. Petersen Germany	2
Oilseed radish 2 (Contra)	30	P.H. Petersen Germany	2
Phacelia (Angelia)	10	Elsoms Seeds, UK	5
Alfalfa (Artemis)	25	Joordens, Netherlands	4
Fallow control	–	–	–

Field experiments	Seed rate kg ha^{-1}	Source	Site grown
French marigold (French marigold)	8	Joordens, Netherlands	All sites
Oilseed radish 2 (Contra)	30	P.H. Petersen Germany	All sites
Indian mustard (Caliente Rojo)	10	Tozer Seeds, UK	Site 1 and 2
Phacelia (Angelia)	10	Elsoms Seeds, UK	Site 1 and 2
Japanese oat (Pratex)	100	P.H. Petersen Germany	Site 1
Alfalfa (Artemis)	25	Joordens, Netherlands	Site 3
Forage chicory (Commander)	8	Barenbrug, UK	Site 3
Disturbed fallow	–	–	All sites
Undisturbed fallow	–	–	Site 1

Site characterisation		
Site 1, 2022	Site 2, 2022	Site 3, 2023
Montrose: 56.85672, 2.12874 pH: 5.4–5.6 Sand: 69 Silt: 21 Clay: 10	Isles of Scilly: 49.92706, 6.28622 pH: 5.3–6.0 Sand: 72 Silt: 24 Clay: 4	Perth: 56.62405, 3.17936 pH: 5.3–5.5 Sand: 73 Silt: 23 Clay: 4

Sampling intervals	Pi	Pre	Post
Site 1	6/6/2022	7/9/2022	2/11/2022
Site 2	8/7/2022	26/9/2022	4/2/2023
Site 3	29/6/2023	29/09/2023	–

Due to seed unavailability, different French marigold and forage chicory cultivars were used. Indian mustard (Brassica juncea) was included in field experiments because it is commonly grown in these regions, but its interactions with Pratylenchus spp. are unknown. A randomised complete block design was used, with four replicates in Montrose (12 × 3.66 m) and five replicates in the Isles of Scilly (3 × 1 m) and Perth (3 × 4 m).

confirmed by randomly selecting forty nematodes and extracting DNA from each nematode using a Purelink Genomic DNA kit according to the manufacturer's instructions. Extracted DNA was amplified using qPCR with species-specific primers and probe combinations (Table 2) with the following conditions: 95 °C for 3 min, 35 cycles for 10 s at 95 °C, and 69 °C for 60 s, as described previously (Orlando et al., 2024). Seven days after seedling thinning, approximately 1000 mixed-stage *P. penetrans* in aqueous suspension (1 ml) were pipetted into three holes (0.7 cm diameter, 4 cm deep) near the seedling roots. Experiments were maintained at 24 ± 2 °C day/16 °C night with an 18:6 light: dark cycle for eight weeks. Plants were watered every other day without fertilisation.

Table 2
Primers and probes used for diagnostic qPCR of *P. penetrans, P. crenatus*, *P. neglectus,* and *P. thornei.* Average DNA copy number of the D2-D3 region of the 28s rDNA per individual for the four target *Pratylenchus* species (Orlando et al., 2024).

Species	Primer/ probe	Sequence (5′ to 3′)	Mean DNA copy number ± SE
P. crenatus	Cren-AltF2	CCAAGTGGTGCATTTGCAGGT	7775 ± 199
	Cren-R	GAACATCACTCCTCCAGTCC	
	Cren-Probe	ATGAAGCCGCCCCAGGAGCC	
P. penetrans	Pen-F2	ATGGGTTCGAATTGGTGTGG	9555 ± 297
	Pen-AltF2b	ATGAGTTCGAGTTGGTGTGG	
	Pen-AltF2c	ATGGGTTCGCGTTGGTGTGG	
	Pen-R2	AGGACCGAATTGGCAGAAGG	
	Pen-Probe2	CACATGTTGCATGCAACTGCCACC	
P. neglectus	Neg-AltF2	AGCGTATCGGGCCAGCATTC	5292 ± 266
	Neg-R	CAAAAGCAGGTTCACACCG	
	Neg-Probe	ACAACCCCCACTCCGTCCCAATCT	
P. thornei	Th-AltF3	AGATTGGGACGGAGTTGGG	3624 ± 109
	Th-AltR3	CAACACCTCGAACAGCTCAG	
	Th-AltProbe3	ACCGCCCGTGGTGCATTTGCA	

2.1.2. Nematode extraction, enumeration, and staining

The glasshouse experiments ended eight weeks after nematode inoculation. Soil from each pot was mixed by hand, and a 200 cm^3 subsample was collected for nematode extraction. Plant roots were gently separated from the soil, washed, and weighed to determine their fresh weight. The roots were chopped into 1 cm-long pieces, and a 5 g subsample was macerated in tap water using a blender at maximum speed for 60 s to create exit points for nematodes. All collected roots were used for nematode extraction from pots that yielded <5 g root biomass.

Nematode extraction from soil and the root samples was done using a modified Baermann tray (Whitehead and Hemming, 1965). Nematodes were counted under a stereomicroscope at 40× magnification. Nematodes obtained from root subsamples were used to estimate the total number of nematodes in the root system. The mean final nematode population (Pf) was calculated as: Pf total number of nematodes extracted from the soil + total number of nematodes extracted from the whole root system. The nematode reproduction factor (Rf) was calculated as follows: Rf = Pf / Pi, where Pi is the initial population inoculated into the pots at the beginning of the experiment and Pf is the final population at the end of the experiment (Ferris et al., 1993). Based on Rf values, the host status of the cover crops was obtained by classifying the cover crops into five categories: excellent host (Rf > 4.0), good host (2.0 ≤ Rf ≤ 4.0), maintenance host (1.0 ≤ Rf ≤ 2.0), poor host (0.15 ≤ Rf < 1.0) and non-host (Rf < 0.15) (Ferris et al., 1993). Acid fuchsin staining of cover crop roots that yielded >5 g of root biomass was used to determine whether nematodes had successfully penetrated the roots. The roots were stained in boiling acid fuchsin stain according to a method described by Byrd Jr et al. (1983).

2.2. Field experiments

Three field experiments were conducted in Scotland and Cornwall, two of the UK's main regions for *Narcissus* production. Six fields with a history of nematode infestation were identified in each region; however, none of the sites tested positive for *D. dipsaci*; thus, sites with abundant *Pratylenchus* spp. were chosen. From the pool of six fields, two experimental sites were established in 2022 (Montrose and the Isles of Scilly) and one in 2023 (Perth). Site characteristics, location, treatments, and sampling dates are detailed in Table 1.

Before the field experiments commenced, *Narcissus* bulbs were lifted,

and the fields ploughed and harrowed in accordance with commercial practice. Cover crops were sown at the recommended rates detailed in Table 1. In Montrose, seeds were drilled using a small plot drill with Amazon Suffolk coulters and then rolled to achieve better soil-seed contact. Seeds were broadcast at the other two sites using an Earthway 2750 seeder due to the lack of available drilling equipment. Brassica treatments received 100 kg ha^{-1} nitrogen and 25 kg ha^{-1} sulphur as Sulfan (24 % N, 15 % SO_3) at planting to maximise glucosinolate production (Ngala et al., 2015). Above-ground dry biomass was assessed at peak flowering before incorporating the cover crops. Plant density was estimated from three 0.25 m^{-2} subplots per plot. Dry biomass was measured from ten representative plants by weighing the fresh material, then drying it at 60 °C for 72 h before re-weighing. Cover crop foliage was chopped and incorporated using a 4 m Standen Powavator rotavator, then rolled to seal the soil surface. Rainfall and temperature data recorded at each site throughout the duration of the experiments (Fig. 1) were obtained from Meteostat (https://meteostat.net/en/) for each site. Soil was sampled at planting, peak flowering, and after the incorporation of cover crops (Table 1). Twenty soil cores were taken from each plot at 10 cm depth using a grass plot sampler (2.3 cm diameter core) (Van Walt Ltd., UK). Most nematodes inhabit the 0–20 cm soil layer, and soil samples were taken from the 0–10 cm layer, which is the most biologically active part of the soil profile, thus, an appropriate depth for examining nematode community responses to cover cropping. The sampling pattern was W-shaped (Marshall et al., 1998) with equidistant points. Nematodes were extracted from a 200 g subsample for microscopy counts using a modified Baermann tray (Whitehead and Hemming, 1965) and identified to genus (Perry and Moens, 2006) or trophic group level (Yeates et al., 1993) under a compound microscope at 40× magnification.

For this experiment, *Aphelenchus* and *Aphelenchoides* were chosen as representatives of fungivores, while all the genera known to feed on bacteria were collectively categorised as bacterivores. *Aphelenchus* and *Aphelenchoides* are commonly recognised as obligate or predominant fungal feeders (Yeates et al., 1993). However, this approach excluded several other fungivorous taxa due to limitations in morphological identification skills. As such, the reliance on *Aphelenchus* and *Aphelenchoides* as proxies for fungivores should be interpreted with caution.

2.3. Effects of cover crops on soil nematode communities

Those cover crop treatments that reduced *Pratylenchus* spp. in field experiments described above were also used for soil nematode community analyses across all field sites. Thus, treatments used for amplicon sequencing of the total nematode community were French marigold, oilseed radish, forage chicory, alfalfa, and disturbed fallow control. Nematodes were extracted from a 200 g soil subsample (Wiesel et al., 2015) using a modified Baermann funnel technique (Brown and Boag, 1988). This extraction method produced a cleaner sample with less dirt than other Baermann methods, resulting in efficient DNA extraction (Donn et al., 2008).

2.3.1. Nematode DNA extraction, PCR amplification and clean-up

Nematode DNA was extracted and amplified as described by do Rêgo Barros et al. (2025). AMPure XP beads (Beckman Coulter, Indianapolis, USA) were used to purify the PCR products by removing primers and primer dimers, following the standard Illumina protocol. Cleaned PCR products were indexed using the Nextera XT Index Kit (Set D, MiSeq Illumina, San Diego, USA). PCR conditions and Index PCR Master-Mix are shown in Supplementary Table S1. PCR products were separated on a 1 % agarose gel and visualised under UV light. The DNA concentration of the final indexed amplicons was determined by Picogreen analysis.

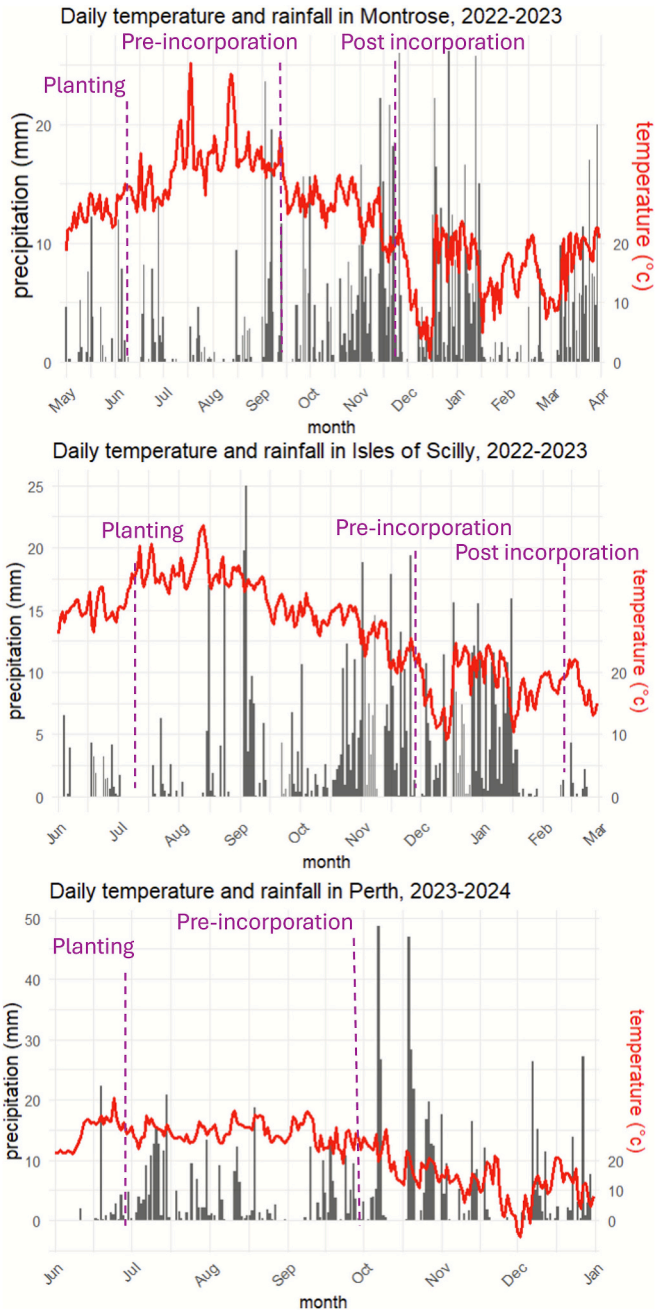


Fig. 1. Daily precipitation and average air temperatures for the three field sites recorded during the experiments. Dotted lines indicate when cover crops were planted and incorporated, and therefore when soil was collected.
(Data from Meteostat, Aberdeen (closest weather station for Montrose); Isles of Scilly; and Perth stations, https://meteostat.net/en/).

2.4. Molecular detection of Pratylenchus species using qPCR

Species-specific real-time quantitative PCR (qPCR) assays (Table 2) were used to detect *Pratylenchus crenatus*, *P. penetrans*, *P. neglectus*, and *P. thornei* in DNA extracted from each plot across all three field sites. qPCR reactions (20 µl total volume) included 10 µl TaqMan™ Fast Universal PCR Master Mix (2×) (ThermoFisher Scientific, UK), 0.6 µM primers, 0.25 µM probe, 2 µl template DNA, and PCR-grade water. The thermocycling conditions were: 95 °C for 3 min, followed by 35 cycles of 95 °C for 10 s and 69 °C for 60 s (Orlando et al., 2024). Species abundance was estimated by dividing the total DNA copy number per sample by the mean copy number for each species (Orlando et al., 2024).

2.5. Data analysis

2.5.1. Greenhouse and field experiments

An F-test was conducted to compare variances between the two greenhouse experiments and assess the suitability of a combined analysis. The variances were significantly different ($p \leq 0.05$); therefore, the experiments were analysed separately. After verifying the assumptions of the analysis of variance (ANOVA), mean final nematode abundance and reproduction factors for the different cover crop treatments were analysed using a one-way ANOVA. Pairwise comparisons of means were conducted following the ANOVA using Tukey HSD test ($p \leq 0.05$).

To analyse the impact of cover crop treatments on *Pratylenchus*, *Aphelenchus, Aphelenchoides* spp., and bacterivore nematodes, a generalised linear mixed-effects model (GLMM) was used. Cover crop treatment and sampling time were considered fixed effect predictors. A nested time: block was added to account for correlation in repeated measures within the same block. The 'lme4' package in R was used (Bates et al., 2015; R Core Team, 2022). The output of the model (*model <− lmer (abundance ~ Covercrop + Time: Covercrop + (1|Block) + (1|Time: Block), data = data*) showed the effects of cover crops and time on nematode abundance. Whenever there was significance, the 'emmeans multcomp' package in R (Hothorn et al., 2008) was used for pairwise comparison (Tukey HSD post hoc tests). Cover crop biomass was analysed using ANOVA, after log transformation, and Tukey HSD ($p \leq 0.05$) for post hoc analysis.

2.5.2. Effects of cover crops on soil food web indices and nematode communities

All sequences underwent quality checking using FastQC, (https://www.bioinformatics.babraham.ac.uk/projects/fastqc/), and Fastq-join (https://github.com/brwnj/fastq-join) was used to join the paired-end reads. Amplicon libraries were analysed using QIIME 2 (V. 2025.4) (Bolyen et al., 2019).

Sequences were demultiplexed and filtered using the QIIME2 demux plugin, yielding read counts ranging from 34,653 to 88,923 per sample. Primers were removed using cutadapt (Martin, 2011), and sequences were trimmed and denoised with the QIIME2 DADA2 plugin (Callahan et al., 2016), employing default settings and a 220-bp trimming length. Amplicon sequence variants (ASVs) were taxonomically assigned using the *classify-sklearn* method with a trained *Nemataxa_v1* classifier (Baker et al., 2023). All ASVs assigned to phyla other than Nematoda, or those that were unclassified or unknown, were removed. This accounted for 0.7 % of the total number of sequences, with 2038 individual ASVs retained for subsequent analysis. The ASVs, taxon tables, and sample metadata were merged into a phyloseq object (McMurdie and Holmes, 2013). A standard data frame was obtained for statistical analysis. Alpha diversity indices, Shannon Weaver (Shannon and Weaver, 1949) and Simpson (Simpson, 1949), were computed on rarefied samples in *phyloseq* using the *estimate_richness* function. A linear mixed-effects model was used to determine the effect of cover crop treatment and sampling time on nematode alpha diversity. If ANOVA assumptions were not met, data were log-transformed (log x + 1). Significant ANOVA results were followed by Tukey's HSD test ($p \leq 0.05$) for post hoc comparisons.

Beta diversity was evaluated using Euclidean distance matrices computed by the *vegan* package and *vegdist* functions (Oksanen et al., 2022). Principal coordinates analysis (PCoA) visualised differences in nematode communities. The *betadisper* function (Oksanen et al., 2022) assessed variability within factors through a dispersion test. A Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson, 2005) was employed to investigate the impact of cover crop treatments and sampling time on nematode communities, and post hoc analysis was conducted using the Adonis pairwise function in the *vegan* package. Where significant differences in nematode communities were observed, similarity percentage analysis (SIMPER) identified the taxa contributing to dissimilarity between treatments, using the *'metaMDS'* and *'SIMPER'* functions in *'vegan'*.

Nematode genera were classified into five trophic groups (Yeates et al., 1993) using NINJA (https://sieriebriennikov.shinyapps.io/ninja) (Sieriebriennikov et al., 2014), which also calculated enrichment (EI), structure (SI), channel indices (CI) (Ferris et al., 2001) and maturity (MI), (Bongers, 1990). The effects of cover crops on nematode trophic groups and food web indices were assessed using a linear mixed-effects model, with cover crop and sampling time as fixed factors and block as a random factor. Estimated marginal means and pairwise comparisons were performed using 'emmeans' (Lenth, 2022) and 'multcomp' (Hothorn et al., 2008) with Benjamini-Hochberg correction (Benjamini and Hochberg, 1995). All analyses were conducted in R (v4.1.3; R Core Team, 2022).

3. Results

3.1. Final nematode abundance, reproduction factor and cover crop host status

Pratylenchus penetrans abundance recovered from soil at the end of both glasshouse experiments significantly differed ($p < 0.001$) between cover crop treatments. Except for Japanese oat, mean *P. penetrans* abundance was significantly greater in the *Phacelia* positive control compared to the other cover crop treatments in both experiments (Table 3). In both experiments, final *P. penetrans* abundance in all cover

Table 3
Mean nematode abundance of *P. penetrans* ($n = 6$, ± standard errors) at the end of experiments, *p* value and CV%, reproduction factors, and host status of selected cover crop treatments eight weeks after inoculation with an initial population of approx. 1000 mixed-life stage nematodes. The mean final abundance is the total number of *P. penetrans* from 1 kg of soil, plus those in the root system. Different letters after the means indicate significant differences according to the Tukey HSD test ($p \leq 0.05$).

Cover crop	Mean final abundance (Soil+roots)		Reproduction factor		Host status	
	Exp 1	*Exp 2*	*Exp 1*	*Exp 2*	*Exp 1*	*Exp 2*
Phacelia	1152 ± 73 h	1305 ± 51 h	1.15 a	1.30 a	M	M
Japanese oat	1041 ± 43 gh	1157 ± 32 gh	1.04 ab	1.16 ab	M	M
Oilseed radish 1	525 ± 51 de	754 ± 36 de	0.53 ef	0.75 de	P	P
French marigold	498 ± 32 cd	584 ± 36 cd	0.50 ef	0.58 ef	P	P
Forage chicory	490 ± 21 cd	636 ± 43 cd	0.49 ef	0.63 ef	P	P
Oilseed radish 2	462 ± 16 cd	570 ± 25 cd	0.46 fg	0.57 ef	P	P
Alfalfa	277 ± 14 b	440 ± 80 b	0.27 gh	0.44 f	P	P
Fallow control	94 ± 15 a	110 ± 19 a	0.09 h	0.11 g	–	–
P value	<0.001	<0.001	<0.001	<0.001		

Cover crop	Nematodes in roots		Total fresh root weight (g)	
	Exp 2	Exp1	Exp 2	Exp 2
Phacelia	0 ± 0	1 ± 1	0.1	0.4
Japanese oat	23 ± 5	117 ± 48	2.9	3.7
Oilseed radish 1	1 ± 1	3 ± 2	3.8	4.2
French marigold	0 ± 0	0 ± 0	5	5.2
Forage chicory	5 ± 1	11 ± 5	7.3	9.1
Oilseed radish 2	1 ± 1	2 ± 1	3.1	3.6
Alfalfa	3 ± 1	11 ± 3	2.5	3.1
Fallow control	–	–	–	–

Host status was classified under five different categories: excellent host (E) ($Rf > 4.0$), good host (G) ($2.0 \leq Rf \leq 4.0$), maintenance host (M) ($1.0 \leq Rf \leq 2.0$), poor host (P) ($0.15 \leq Rf < 1.0$) and non-host ($Rf < 0.15$) ($R_f < 0.15$).

crop treatments was also significantly higher than the fallow control. Among the cover crop treatments, the lowest abundance of *P. penetrans* was observed with alfalfa in both experiments. Reproduction factors significantly differed between cover crop treatments in both experiments ($p < 0.001$), and except for Phacelia and Japanese oats, all other cover crops were categorised as poor hosts for *P. penetrans*. Differences among treatments were assessed using a one-way ANOVA, and pairwise comparisons were performed using Tukey's HSD test ($p < 0.05$).

3.2. Effects of cover crops on Pratylenchus, Aphelenchus, Aphelenchoides spp., and bacterivore nematodes

A generalised linear mixed-effects model (GLMM) was used to evaluate treatment differences in all three sites, and *p*-values were obtained from Tukey's HSD post hoc tests for pairwise comparisons.

3.2.1. Montrose – field site 1

A significant 58 % reduction in *Pratylenchus* spp. abundance was observed after growing and incorporating French marigold ($p = 0.01$) (Table 4). In contrast, Indian mustard significantly increased *Pratylenchus* spp. abundance by 319 % at the pre-incorporation stage ($p = 0.02$), suggesting that Indian mustard is a good host for *Pratylenchus* spp., during the growing season. Oilseed radish ($p = 0.65$), *Phacelia* ($p = 0.35$), and Japanese oats ($p = 0.65$) did not affect the abundance of *Pratylenchus* spp. Incorporating oilseed and Indian mustard cover crops significantly increased the abundance of bacterivore nematodes, with the greatest increase observed in oilseed radish (335 % increase). Japanese oats, *Phacelia* and oilseed radish significantly increased the abundance of *Aphelenchoides* spp. after incorporation ($p < 0.05$). Indian mustard significantly increased *Aphelenchus* spp. at the pre-incorporation stage ($p = 0.04$). Except for French marigold and Japanese oats, all cover crops, as well as the disturbed fallow, significantly increased the abundance of *Aphelenchus* spp. at the post-incorporation stage.

3.2.2. Isles of Scilly – field site 2

Significant reductions ($p < 0.05$) in *Pratylenchus* populations were observed after growing and incorporating oilseed radish (by 75 %) and French marigold (70 %) (Table 4). In contrast, Indian mustard significantly increased the abundance of *Pratylenchus* spp. by 113 % ($p = 0.01$). The abundance of *Pratylenchus* spp. was unaffected by disturbed fallow ($p = 0.90$) and *Phacelia* ($p = 0.86$) treatments at the pre-incorporation stage. After incorporation, all cover crops significantly increased abundance of bacterivores ($p < 0.05$). Oilseed radish and Indian mustard significantly increased *Aphelenchoides* spp. at the post-incorporation stage ($p \leq 0.05$). Except for the disturbed fallow control, all cover crops significantly increased the abundance of *Aphelenchus* spp. after incorporation ($p \leq 0.05$).

3.2.3. Perth – field site 3

Except for the disturbed fallow treatments, all cover crop treatments significantly reduced the abundance of *Pratylenchus* spp. ($p < 0.05$) (Table 4). Growing French marigold, oilseed radish, forage chicory, and alfalfa for three months without incorporation reduced *Pratylenchus* abundance by 60 %, 53 %, 54 %, and 67 %, respectively. However, at this site, none of the cover crops affected the abundance of bacterivores ($p = 0.06$), *Aphelenchus* ($p = 0.33$) and *Aphelenchoides* spp. ($p = 0.12$).

3.2.4. Detection of four Pratylenchus species at the field sites

qPCR was conducted to determine whether any of the four *Pratylenchus* species known to be prevalent in UK agricultural soils, namely, *P. penetrans, P. crenatus, P. neglectus*, and *P. thornei,* were present at all three sites. The Montrose site tested positive for *P. crenatus* and *P. thornei,* with *P. crenatus* being twice as dominant. The Isles of Scilly site tested positive for *P. penetrans* and *P. crenatus,* while the Perth site only tested positive for *P. crenatus*. *P. crenatus* was the most abundant in

Table 4
Mean abundance ± standard error of *Pratylenchus, Aphelenchus*, *Aphelenchoides* spp. and bacterivore nematodes per 200 g soil at planting (Pi), approx. Three months after planting (pre-incorporation, Pre) and six weeks post-incorporation (Pf) of oilseed radish (*Raphanus sativus*), Indian mustard (*Brassica juncea*), French marigold (*Tagetes patula*), Japanese oats (*Avena sativa*) and *Phacelia* (*Phacelia tanacetifolia*), forage chicory (*Cichorium intybus*), alfalfa (*Medicago sativa*) under field conditions at Montrose, Isles of Scilly and Perth. Significant changes in nematode abundance at different times of sampling for each treatment compared to the disturbed or undisturbed fallow control are indicated with asterisks after Tukey HSD post hoc test ($p \leq 0.05$).

Field Site 1, Montrose

Cover crop treatments	Pi	Pre	Pf	Pi	Pre	Pf
	Pratylenchus spp.			Bacterivores		
Undisturbed fallow	41 ± 4	44 ± 3	32 ± 3	546 ± 66	2014 ± 1016	2646 ± 1791
Disturbed fallow	22 ± 9	26 ± 15	29 ± 16	812 ± 227	1416 ± 401	2360 ± 748
French marigold	50 ± 7	31 ± 5	21 ± 7*	502 ± 47	1150 ± 424	2666 ± 953
Oilseed radish	61 ± 16	46 ± 12	48 ± 12	1376 ± 352	2781 ± 735	5990 ± 1233*
Indian mustard	26 ± 9	109 ± 38*	26 ± 13	873 ± 128	1895 ± 672	3558 ± 778*
Phacelia	59 ± 20	100 ± 35	41 ± 13	788 ± 149	2550 ± 1045	2742 ± 606
Japanese oats	40 ± 4	96 ± 45	38 ± 10	621 ± 141	1568 ± 395	1778 ± 315
	Aphelenchus spp.			*Aphelenchoides* spp.		
Undisturbed fallow	11 ± 5	23 ± 9	22 ± 9	5 ± 2	9 ± 4	7 ± 1
Disturbed fallow	7 ± 2	30 ± 13	78 ± 45*	4 ± 1	7 ± 3	35 ± 8
French marigold	8 ± 1	16 ± 2	35 ± 11	14 ± 6	19 ± 6	16 ± 3
Oilseed radish	7 ± 3	44 ± 28	146 ± 28*	7 ± 3	43 ± 20	222 ± 50*
Indian mustard	4 ± 1	54 ± 21*	72 ± 18*	2 ± 0	23 ± 5	34 ± 13
Phacelia	19 ± 5	50 ± 14	76 ± 28*	8 ± 2	16 ± 7	51 ± 15*
Japanese oats	11 ± 4	34 ± 10	51 ± 8	9 ± 4	11 ± 4	49 ± 24*

Field Site 2, Isles of Scilly

Cover crop treatments	Pi	Pre	Pf	Pi	Pre	Pf
	Pratylenchus spp.			Bacterivores		
Disturbed fallow	31 ± 5	30 ± 5	24 ± 5	581 ± 186	684 ± 192	1227 ± 154
French marigold	73 ± 10	14 ± 3*	22 ± 7*	710 ± 214	885 ± 242	1380 ± 107*
Oilseed radish	63 ± 14	15 ± 1*	16 ± 1*	504 ± 70	976 ± 231	1657 ± 259*
Indian mustard	77 ± 29	164 ± 40*	78 ± 22	655 ± 235	963 ± 216	1310 ± 64*
Phacelia	50 ± 4	51 ± 10	48 ± 3.0	356 ± 72	531 ± 242	1447 ± 233*
	Aphelenchus spp.			*Aphelenchoides* spp.		
Disturbed fallow	208 ± 30	258 ± 104	318 ± 104	2 ± 1	8 ± 3	35 ± 10
French marigold	108 ± 45	211 ± 91	462 ± 79*	1 ± 1	3 ± 3	40 ± 8
Oilseed radish	53 ± 13.7	143 ± 44	471 ± 90*	5 ± 2	8 ± 2	83 ± 58*
Indian mustard	67 ± 30	183 ± 50	441 ± 160*	3 ± 1	6 ± 2	70 ± 15*
Phacelia	79 ± 19	124 ± 38	358 ± 109*	4 ± 1	9 ± 2	24 ± 7

Field Site 3, Perth				
Cover crop treatments	Pi	Pre	Pi	Pre
	Pratylenchus spp.		Bacterivores	
Disturbed fallow	13 ± 1	10 ± 2	1038 ± 137	978 ± 229
French marigold	10 ± 1	4 ± 1*	558 ± 81	648 ± 95
Oilseed radish	15 ± 2	7 ± 1*	929 ± 171	815 ± 238
Forage chicory	13 ± 2	6 ± 1*	599 ± 106	710 ± 94
Alfalfa	15 ± 2	5 ± 1*	1007 ± 137	985 ± 135
	Aphelenchus spp.		*Aphelenchoides* spp.	
Disturbed fallow	45 ± 1	41 ± 4	9 ± 1	8 ± 1
French marigold	39 ± 2	39 ± 2	7 ± 1	5 ± 1
Oilseed radish	39 ± 3	41 ± 5	10 ± 1	9 ± 2
Forage chicory	41 ± 4	39 ± 2	8 ± 1	9 ± 1
Alfalfa	27 ± 5	23 ± 4	12 ± 5	10 ± 2

Montrose and Perth, whereas *P. penetrans* was more abundant than *P. crenatus* in the Isles of Scilly plots (Supplementary Table S3).

3.2.5. *Nematode community composition across the field sites*

From the three field sites, a total of 76 taxa were identified at the genus level (Supplementary Table S4), with most being bacterivores (28 genera), followed by plant-feeding (21 genera), predators (11 genera), fungivores (10 genera) and omnivores (6 genera). Sixty-five per cent of the recorded nematode genera were common to all three sites. In Montrose, *Rhabditis* (69 %), *Mesorhabditis* (3 %) and *Diphtherophora* (2 %) were the dominant genera; at the Isles of Scilly, the dominant genera were *Rhabditis* (25 %), *Pungentus* (11 %) and *Pristionchus* (9 %); and at the Perth site, *Rhabditis* (70 %), *Pristionchus* (9 %) and *Aphelenchoides* (2 %) were dominant.

3.3. *Effects of cover crops on nematode trophic groups and indices*

A linear mixed-effects model was used to analyse the treatment effects on nematode trophic groups and food web indices in all sites, and Tukey's HSD test was used for pairwise comparisons. Based on food web analysis, the Montrose site had highly nutrient-enriched soil, dominated by opportunistic bacterivore nematodes, and a well-structured, mature soil food web (Fig. 2A). The Isles of Scilly had a mature, N-enriched soil with bacterial-driven decomposition (Fig. 2B). The plots in Perth were predominantly maturing, with N-enriched bacterial decomposition food webs; however, a few plots had a disturbed, N-enriched, and conducive food web (Fig. 2C). There were no significant differences in the relative abundance of nematode trophic groups at Montrose ($p = 0.88$), Isles of Scilly ($p = 0.82$), and Perth ($p = 0.90$) (Fig. 3A–C) or nematode alpha diversity (Shannon and Simpson indices; Table 5) across all sites. Bacterivores dominated at all sites (Fig. 3A–C).

ANOVA revealed that cover crop treatments and sampling times had no significant effect on MI ($p = 0.21$), CI ($p = 0.48$), EI ($p = 0.27$), or SI ($p = 0.21$) in Montrose. However, there was a single marginal effect ($p = 0.06$) in the Simpson index for Montrose samples (Table 5). The channel index was unaffected by cover crop treatment in the Isles of Scilly. Significant differences in EI ($p = 0.01$), SI ($p = 0.04$), and MI ($p = 0.01$) were observed between cover crop treatments (Fig. 4B). The highest EI and SI occurred after incorporating oilseed radish and French marigold. In contrast, MI was significantly reduced by incorporating oilseed radish, French marigold, and a fallow plot (Fig. 4B). No effects of cover crop treatments were observed for any of the nematode indices in Perth.

3.4. *Effects of cover crops on nematode communities (beta-diversity)*

Non-metric Multidimensional Scaling (NMDS) plots were used to visualise the patterns of nematode community composition based on Euclidean distance matrices. For the Montrose site, the first and second NMDS axes explained 75.8 % and 15.4 % of the variation without clear clusters or groupings (Fig. 5A). PERMANOVA showed a marginal significant effect of cover crop treatment ($p = 0.06$) and no effect of sampling time ($p = 0.08$) on nematode beta diversity. For the Isles of Scilly, the first and second NMDS axes explained 59.9 % and 20.1 % of the variation, respectively, with no clear patterns (Fig. 5B). Nematode beta diversity was not significantly affected by either cover crop treatment (p

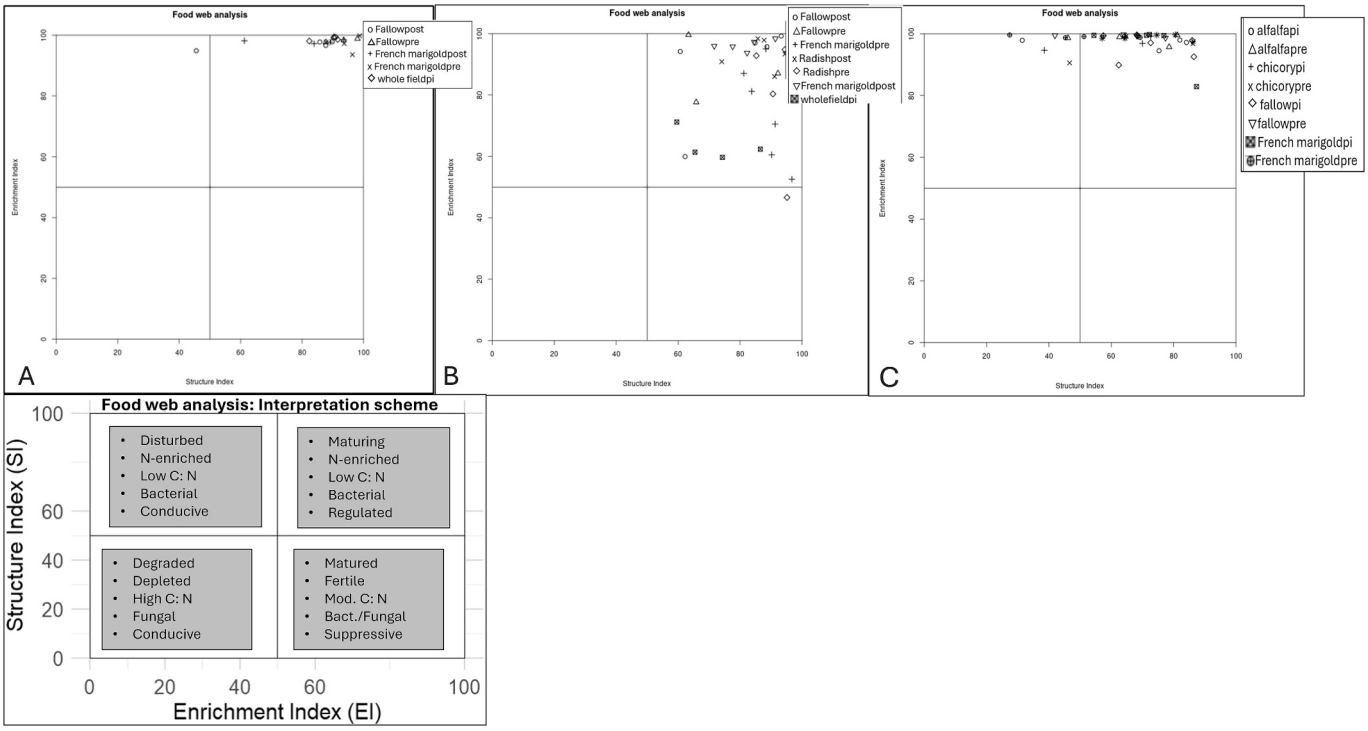
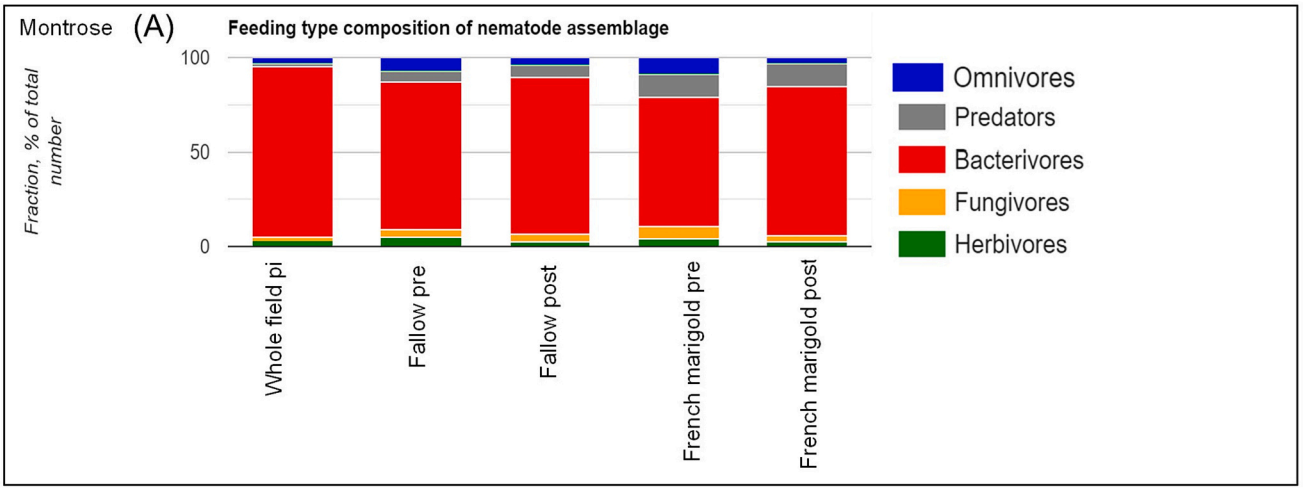
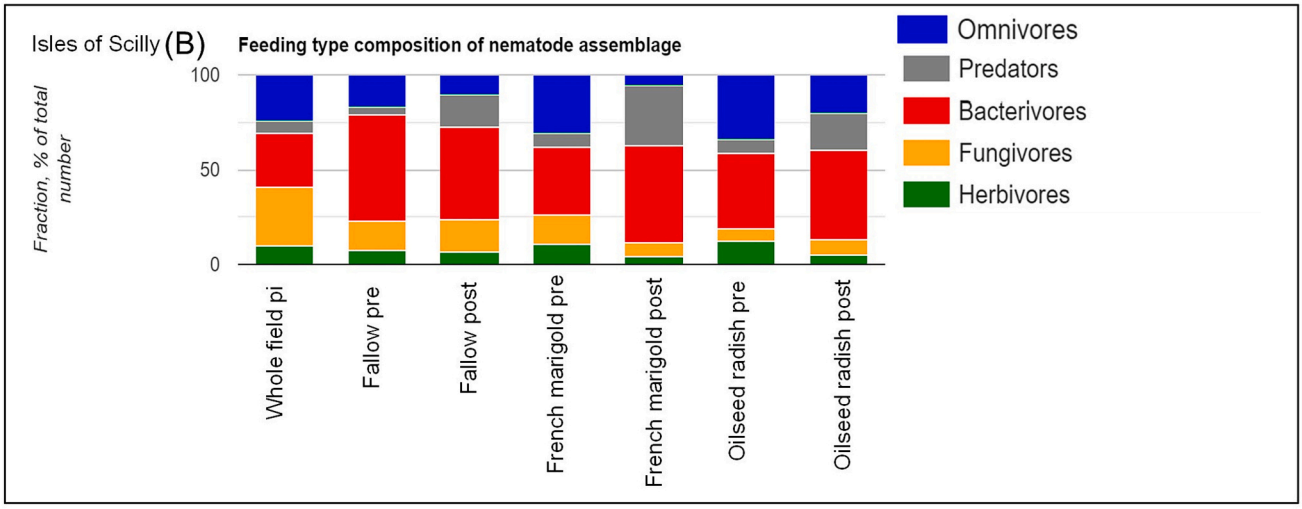


Fig. 2. Illustration of the enrichment and maturity of the soil food web in Montrose (a), Isles of Scilly (b) and Perth (c). Each graph is divided into four quadrants that represent the level of nitrogen enrichment and system disturbance, according to Ferris et al. (2001). Quadrant food web interpretation (D) represents the following food webs: 1) disturbed and N-enriched, 2) maturing and N-enriched, 3) degraded and N-depleted, and 4) mature and fertile.





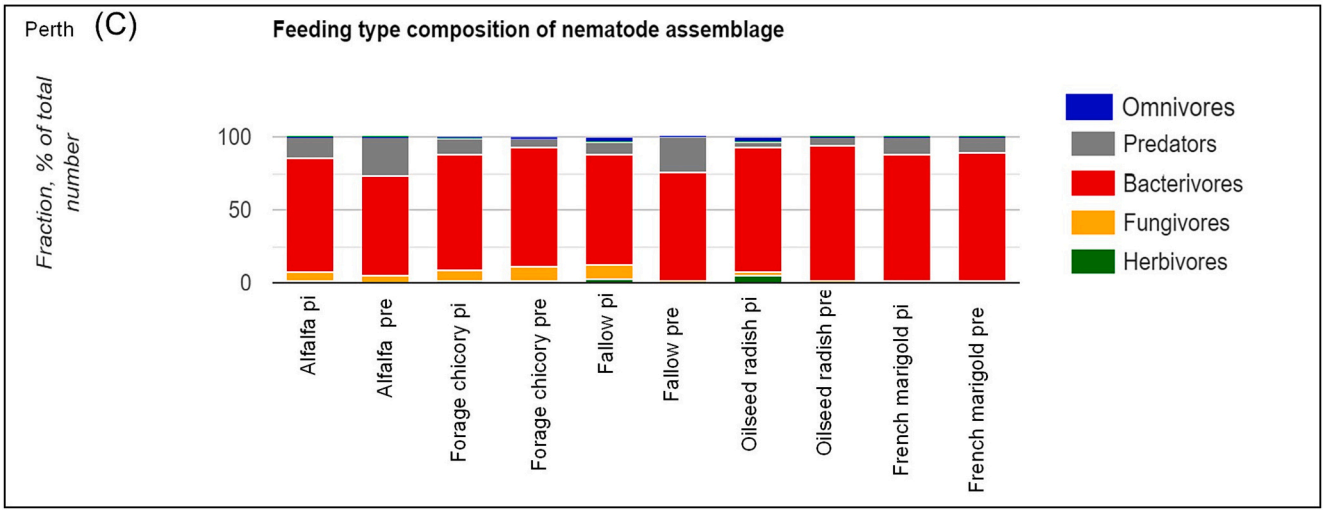


Fig. 3. Abundance of nematode trophic groups across cover crop treatments and time of sampling at Montrose (A), Isles of Scilly (B) and Perth (C). pi = At planting, pre = pre-incorporation stage, post = post-incorporation. There were no significant differences in nematode abundances between the individual plots at the time of planting, as determined by microscopic counts. Therefore, the treatments were compared to the whole field at planting to reduce costs in Montrose and the Isles of Scilly. Due to the missed post-incorporation stage, individual plots at planting and pre-incorporation (3 months after planting) were compared in Perth.

= 0.5) or sampling time ($p = 0.3$).

For Perth, NMDS axis 1 explained 36.6 % of the variation in the community, while axis 2 explained 13.9 % (Fig. 5C). PERMANOVA revealed that nematode beta diversity was significantly affected by sampling time ($p = 0.02$) but not by cover crop treatment ($p = 0.19$). Pairwise comparisons revealed that nematode communities differed significantly at the planting, pre-incorporation, and post-incorporation stages. SIMPER analysis showed that eight genera (*Rhabditis, Mesorhabditis, Diphtherophora, Neopsilenchus, Prodorylaimus, Plectus, Oxydirus* and *Pungentus)* contributed the most to dissimilarities between post- and

Table 5
Average Shannon and Simpson indices ± standard error for cover crop treatments at planting and pre-incorporation and 6 weeks post incorporation stage at Montrose, Isles of Scilly and Perth. There were no significant differences between treatments, Tukey HSD test at $p \geq 0.05$.

Cover crop treatment	Time	Shannon	Simpson	Channel index
Montrose				
Whole field	pi	1.45 ± 0.2	0.46 ± 0.1	0.31
Fallow	pre	1.89 ± 0.3	0.63 ± 0.1	0.47
	post	2.27 ± 0.1	0.78 ± 0.0	1.05
French marigold	pre	2.15 ± 0.4	0.68 ± 0.1	1.70
	post	2.13 ± 0.1	0.73 ± 0.1	0.55
	p-value	0.46	0.06	0.48
Isles of Scilly				
Whole field	pi	2.72 ± 0.1	0.87 ± 0.1	39.93
Fallow	pre	2.33 ± 0.4	0.83 ± 0.1	9.48
	post	2.25 ± 0.1	0.78 ± 0.0	16.18
French marigold	pre	2.46 ± 0.1	0.83 ± 0.0	24.36
	post	2.26 ± 0.1	0.80 ± 0.0	3.8
Oilseed radish	pre	2.48 ± 0.2	0.84 ± 0.0	13.84
	post	2.26 ± 0.1	0.80 ± 0.0	5.10
	p-value	0.10	0.80	0.11
Perth				
Fallow	pi	2.22 ± 0.2	0.75 ± 0.1	3.75
	pre	1.22 ± 0.0	0.50 ± 0.0	0.30
Oilseed radish	pi	1.48 ± 0.4	0.8 ± 0.1	1.57
	pre	1.37 ± 0.2	0.8 ± 0.1	0.3
French marigold	pi	1.26 ± 0.1	0.52 ± 0.1	0.14
	pre	1.18 ± 0.1	0.48 ± 0.1	0.14
Forage chicory	pi	1.83 ± 0.1	0.66 ± 0.0	2.29
	pre	1.90 ± 0.3	0.69 ± 0.1	3.53
Alfalfa	pi	1.85 ± 0.3	0.65 ± 0.1	2.51
	pre	1.73 ± 0.0	0.73 ± 0.0	1.80
	p-value	0.27	0.31	0.12

pre-incorporation stages (71.5 % dissimilarity), with *Rhabditis* contributing the most (19 %). In contrast, *Pungentus* contributed the least (5.0 %) (Fig. 5D). Nine genera (*Rhabditis, Mesorhabditis, Aporcella, Diphtherophora, Prodorylaimus, Neopsilenchus, Plectus, Acrobeloides* and *Mylonchulus*) were most influential in dissimilarity between planting and post-incorporation stages (72 % dissimilarity). *Rhabditis* contributed the most (20 %), while *Mylonchulus* contributed the least (3.9 %) (Fig. 5D). Nine genera (*Rhabditis, Aporcella, Oxydirus, Diphtherophora, Pungentus, Mylonchulus, Plectus*, *Acrobeloides and Mesorhabditis*) were the main drivers in dissimilarity between pre-incorporation and planting stages (70 % dissimilarity).

4. Discussion

Under controlled glasshouse conditions, this study assessed the host status of several cover crops for the root lesion nematode, *P. penetrans*. Based on reproduction factors (Ferris et al., 1993), only *Phacelia* and Japanese oat were classified as maintenance hosts; the remaining studied cover crops were rated as poor hosts. These observations align with previous greenhouse studies, in which *Phacelia* and Japanese oats were identified as maintenance hosts, while French marigold and alfalfa were classified as poor hosts (Evenhuis et al., 2004; Neupane and Yan, 2023; Taning et al., 2024). Subsequent results from three field sites naturally infested with *Pratylenchus* spp. including *P. penetrans* supported the hypothesis that several cover crops (oilseed radish, French marigold, forage chicory, and alfalfa) reduced *Pratylenchus* spp., abundance without adversely affecting non-target communities. In contrast, Indian mustard significantly increased *P. penetrans*, consistent with previous field studies (Rudolph et al., 2017). Field assessment of cover crop incorporation was associated with increased EI and reduced MI and SI, reflecting disturbance and enrichment of soils. These findings align with previous research conducted under European conditions, which has shown that cover crops can reduce plant-parasitic nematodes while supporting beneficial nematodes (Valdes et al., 2012; Van Himbeeck et al., 2024). Although a recent meta-analysis reported that cover cropping increases the abundance of both plant-parasitic and bacterivore nematodes (Puissant et al., 2021), our findings only partially align with this: we observed an increase in bacterivore nematodes following the incorporation of cover crops. However, in contrast to the meta-analysis, we did not detect an increase in the relative abundance of total plant-parasitic nematodes. Overall, these results support the hypothesis that cover cropping reduces some plant-parasitic nematode species and enhances soil food web enrichment without negatively impacting the wider nematode community structure.

Pratylenchus crenatus was the most abundant species at the two Scottish field sites, aligning with its reported prevalence in Scottish potato fields (Orlando et al., 2020). Both sites had been in *Narcissus* monoculture for over ten years, although the pathogenicity of *P. crenatus* on *Narcissus* remains unreported. In the Isles of Scilly, *P. penetrans* was detected, previously reported to be associated with 'soil sickness' caused by *P. penetrans* and *Cylindrocarpon destructans* (Lane, 1984). The occurrence of *P. penetrans* depends on host availability. Due to limited land availability on the Isles of Scilly, extensive *Narcissus* monoculture is practiced, promoting its survival. The sandy soils found in the locality are preferred by *P. penetrans* (Castillo and Vovlas, 2007) and further support its establishment and reproduction.

French marigold reduced *Pratylenchus* spp., consistent with the findings of Kimpinski et al. (2000) and Evenhuis et al. (2004), who rated French marigold as a poor host for *P. penetrans*. French marigold produces α-terthienyl, a compound that generates biocidal reactive oxygen species upon UV activation (Gommers and Bakker, 1988). While used in the Netherlands to control *P. penetrans* in *Narcissus*, adoption in the UK could be encouraged as it is mainly cultivated for aesthetic purposes. A prior study using French marigold in the Isles of Scilly was inconclusive due to the absence of *Pratylenchus* in control plots (Tompsett, 2004). Oilseed radish reduced *Pratylenchus* spp. at two trial sites in this study, supporting recent findings (Taning et al., 2024; van Himbeeck et al., 2024). Oilseed radish reduced *Pratylenchus* spp., before cover crop incorporation, which may indicate that it is a poor host or a partial biofumigant, continually releasing low levels of GSLS from its roots during growth (Ngala et al., 2015). Brassica ITCs produced by oilseed radish, including 2-Phenylethyl, are toxic to *P. penetrans* in vitro (Chekanai et al., 2024). However, contrasting results have been reported; Grabau et al. (2017) observed an increase in *P. penetrans* after growing oilseed radish under field conditions, which could be attributed to differences in cultivars.

Growing alfalfa reduced *P. crenatus* abundance, aligning with earlier findings that *P. crenatus* does not reproduce on alfalfa under field conditions (Willis et al., 1982). Alfalfa is also considered a poor host for *P. penetrans* (Neupane and Yan, 2023; Taning et al., 2024). While the suppressive mechanism remains unclear, some studies suggest tannin accumulation in root cells may play a role (Vieira et al., 2019). Japanese oats and *Phacelia* neither reduced nor increased *Pratylenchus* spp., post-incorporation, supporting their previous classification as maintenance hosts for *P. penetrans* (Knoetze et al., 2023; Taning et al., 2024; van Himbeeck et al., 2024). Forage chicory was rated as a poor host to *P. penetrans* under greenhouse conditions, consistent with field data in this study, which resulted in a significant decline in *Pratylenchus* spp. Forage chicory (*Cichorium intybus*) is widely used as a feed additive in livestock production, and its secondary metabolites have been extensively studied for their anthelmintic effects against gastrointestinal nematodes in both ruminant and monogastric animals (Komáromyová et al., 2025; Rambaud et al., 2025). However, interactions between forage chicory and plant-parasitic nematodes remain largely unexplored. To our knowledge, this is the first study to investigate the effects of forage chicory on *Pratylenchus* spp.

Brassica cover crops are known for their biofumigation properties against plant-parasitic nematodes (Ngala et al., 2015), where

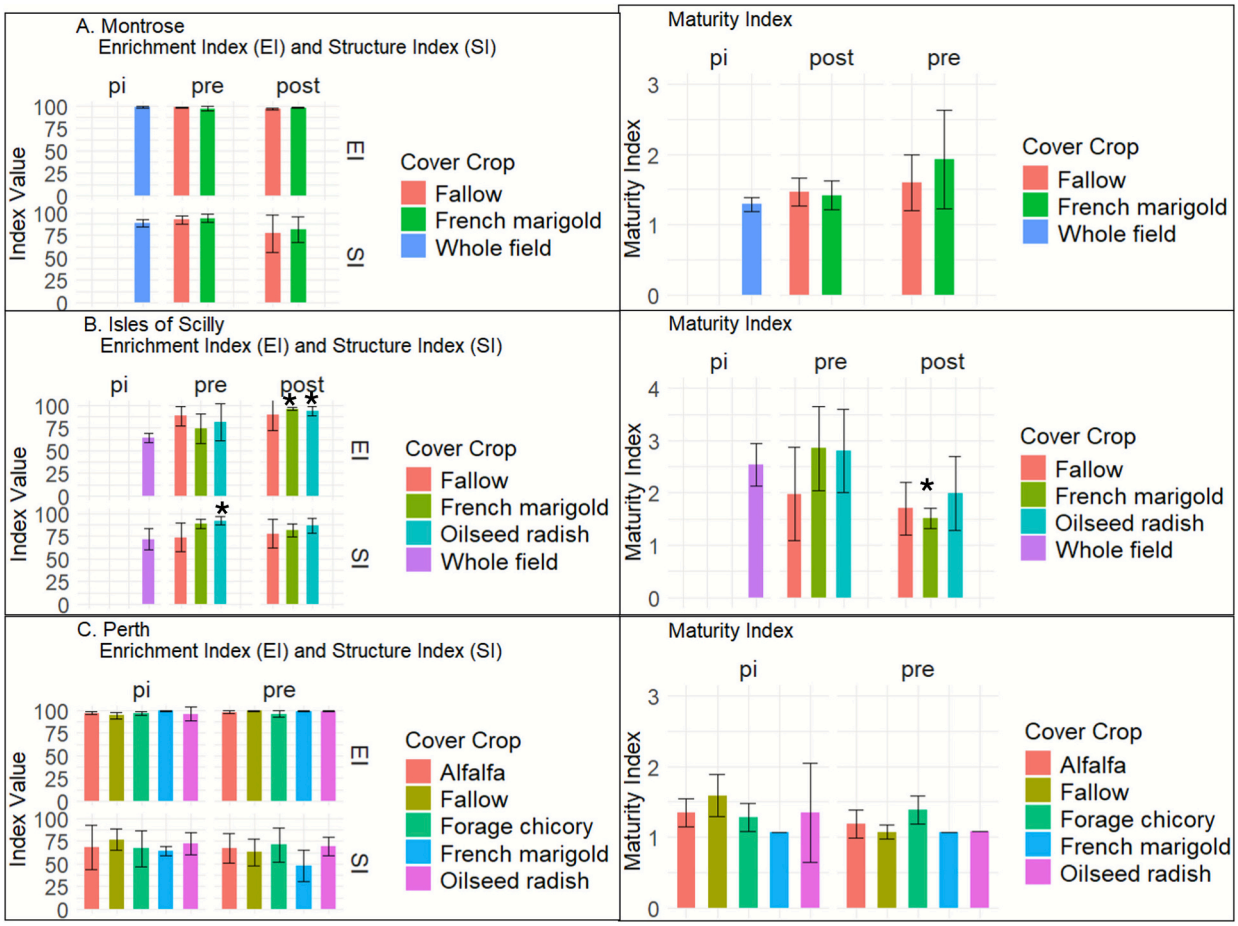


Fig. 4. Average Enrichment (EI), Structure (SI) and Maturity (MI) values ± standard error for the cover crop treatments at planting, three months after planting (pre-incorporation) and post-incorporation at Montrose (A), Isles of Scilly (B) and Perth (C). Asterisk * represents a significant difference after Tukey HSD test ($p \leq 0.05$) between treatment and whole field control at planting.

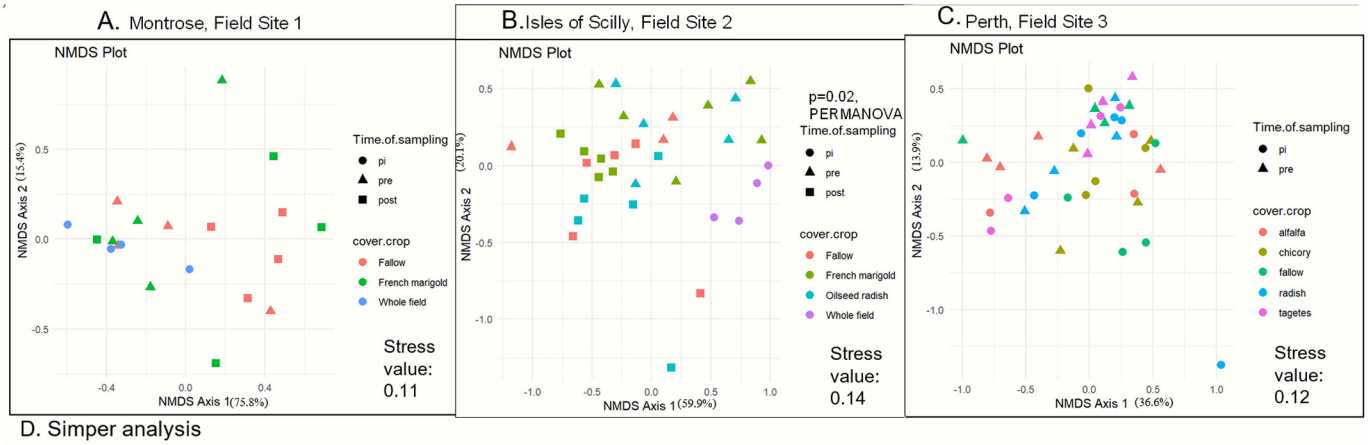
glucosinolates are converted to nematicidal isothiocyanates upon incorporation. *Pratylenchus* spp., abundance under field conditions increased after three months with Indian mustard, confirming it as a suitable host, consistent with previous studies (Rudolph et al., 2017; LaMondia, 2021; Neupane and Yan, 2023). No biofumigation effect was observed with Indian mustard, likely because it supports nematode reproduction, thereby masking any biofumigation effects (Vervoort et al., 2014). Given the widespread use of Indian mustard by *Narcissus* growers, these findings strongly suggest considering alternative cover crops to prevent an increase in the abundance of *Pratylenchus* spp.

In contrast to current findings, a field study in Dundee, Scotland, found no effect of oilseed radish, Indian mustard, or cover crop mixes with *Phacelia* and Japanese oats on *Pratylenchus* spp. (Holland et al., 2021), perhaps because they were grown as winter cover crops and sampled only once. Oilseed radish performance varied by site in this study, consistent with earlier findings of site-dependent effects (Grabau et al., 2017). Such variability underscores the influence of site conditions and initial nematode densities (LaMondia, 2021), highlighting the need for caution in generalising host responses. Cover crop responses to plant-parasitic nematodes vary with cultivar genetics, local conditions, and planting time (Viaene et al., 2013; Rudolph et al., 2017).

Soil food web indices can reveal shifts in nematode communities not evident from trophic group data alone. The Maturity Index (MI) reflects nematode sensitivity to disturbance (Freckman and Ettema, 1993). In this study, MI was unaffected by cover crops or sampling time at Montrose and Perth but declined, along with the Structure Index (SI), after incorporating French marigold and oilseed radish in the Isles of Scilly. Low MI and SI values indicate a less structured nematode community, characterised by fewer persistent nematodes with higher c-*p* values. Cover crop incorporation disturbs the soil, impacting sensitive persister nematodes (Ferris et al., 2001). Low MI values after incorporation reflect this disturbance, while higher MI values at planting and before incorporation suggest low disturbance and a greater presence of persisters (Yeates and Bongers, 1999). Before the incorporation of cover crops, the SI was higher than the fallow treatment, suggesting that growing cover crops stabilises the soil and maintains a structured food web with more linkages. The Channel Index (CI) remained unaffected by cover crop treatment or sampling time. The observed CI values below 50 % across all sites suggest a dominance of bacterial over fungal-driven decomposition (Ferris et al., 2001).

All three sites were predominantly N-enriched, with low C:N ratios, maturing bacterial decomposition channels, and regulatory characteristics. Incorporation of oilseed radish and French marigold increased bacterivore and fungivore nematodes Enrichment Index (EI), indicating sufficient organic input to stimulate bacterial pathways. EI reflects the activity of opportunistic bacterivores and overall soil fertility (Forge et al., 2003). Cover crop incorporation enhances bacterial activity, favouring colonisers with low c-p values (Freckman and Ettema, 1993). Oilseed radish, for example, stimulates bacterial families such as Pseudomonaceae and Erwiniaceae (Cazzaniga et al., 2023). Nematode abundance remained stable at the Perth site, where incorporation did not occur.

These results support previous findings (DuPont et al., 2009; Puissant et al., 2021; van Himbeeck et al., 2024) that cover crops promote bacterivore nematodes. Bacterivores were the most abundant group across sites, consistent with findings in global arable soils (van den Hoogen



D. Simper analysis

Results of SIMPER analysis of the genera that contributed most to the dissimilarity of soil nematode communities at different sampling times in the Isles of Scilly.

Post vs pre-incorporation (71.5% dissimilarity)

Genus	%contribution to difference	% relative abundance	
		post	pre
Rhabditis	19.3	36.3	42.9
Mesorhabditis	13.3	13.1	1.7
Diphtherophora	9.9	5.7	4.7
Prodorylaimus	6.1	5.7	0.4
Neopsilenchus	6.6	6.2	0.4
Plectus	5.9	3.3	2.6
Oxydirus	5.5	3.1	6.8
Pungentus	5.0	2.4	4.2

Post-incorporation vs planting (72% dissimilarity)

Genus	%contribution to difference	% relative abundance	
		post	pi
Rhabditis	19.9	36.3	19.8
Mesorhabditis	12.2	13.1	2.3
Aporcella	7.8	2.7	9.9
Diphtherophora	6.6	5.7	1.8
Neopsilenchus	6.0	6.2	1.3
Prodorylaimus	6.0	5.7	0.1
Acrobeloides	5.5	2.0	6.0
Plectus	5.1	3.3	2.5
Mylonchulus	3.9	0.1	3.8

Pre-incorporation vs planting (70% dissimilarity)

Genus	%contribution to difference	% relative abundance	
		pre	pi
Rhabditis	28.2	42.9	19.8
Aporcella	8.4	2.9	9.9
Oxydirus	6.2	6.8	2.7
Diphtherophora	6.1	4.7	1.8
Pungentus	4.7	4.2	0.6
Mylonchulus	4.5	0.4	3.8
Plectus	4.3	2.6	2.5
Acrobeloides	4.2	2.9	6.0
Mesorhabditis	3.5	1.7	2.3

Fig. 5. Euclidean distance-based Non-metric Multidimensional Scaling plots for different times of sampling and cover crop treatments at Montrose, Perth, and the Isles of Scilly. After PERMANOVA, only the time of sampling at the Isles of Scilly was significant ($p = 0.02$). Therefore, a SIMPER analysis was done to identify the genera that contributed most to the dissimilarity of soil nematode communities at different sampling times.

et al., 2019). Community shifts post cover crop incorporation involved increases in the abundance of opportunistic bacterivores (*Rhabditis, Mesorhabditis, Plectus, Oxydirus*), the fungivore *Diphtherophora*, and predators such as *Prodorylaimus* and *Pungentus.* The increased abundance of *Aphelenchus* spp. after growing Indian mustard may be attributed to fungal stimulation by root exudates. Plants release carbon-rich compounds through mucilage, exudates, and root cell turnover (Wu and Yu, 2019), and some cover crops, such as sorghum-sudan grass, are known to promote fungal activity via such exudates (Paudel et al., 2021).

Regenerative agriculture is often promoted to improve soil health and reduce reliance on synthetic inputs. However, despite such claims, the scientific evidence supporting these benefits remains limited, which creates hesitation regarding its widespread adoption. A recent review aimed to identify the advantages and mechanisms of regenerative agriculture, based on available scientific data. For example, cover cropping has been shown to enhance soil health under specific climatic and soil conditions (Khangura et al., 2023). Yet, these benefits are not universal and may vary considerably across different agroecosystems. Furthermore, many reported gains are based on theoretical assumptions that often overlook the practical challenges of implementing cover crops in diverse cropping systems (Zimmer et al., 2025). Therefore, there is a clear need for robust, system-specific trials to better understand the mechanisms and outcomes of regenerative practices. This case study contributes to that effort by demonstrating that cover cropping can suppress plant-parasitic nematodes without negatively affecting the broader soil nematode community, thereby supporting the ecological benefits of regenerative agriculture. These findings provide a firmer evidence base for growers and policymakers contemplating the integration of cover crops into sustainable farming systems.

5. Conclusions

This study examined the interactions between cover crops and soil nematodes under both glasshouse and field conditions. Of the seven cover crops tested, three (Indian mustard, Japanese oats, and *Phacelia*) had no effect or increased *Pratylenchus* spp., while four exhibited a suppressive effect. This suggests that certain cover crops can reduce *Pratylenchus* spp., without negatively impacting soil nematode communities. Cover crops shift in-field soil nematode communities towards nitrogen-enriched bacterial-dominated decomposition. Based on this research, *Narcissus* growers could potentially use French marigold, oilseed radish, chicory, and alfalfa as summer cover crops (grown for at least three months) to manage *Pratylenchus* spp. These findings align with standard practices, easing adoption by growers and adding to the evidence that cover cropping in regenerative agriculture benefits soil

ecosystems.

CRediT authorship contribution statement

Vongai Chekanai: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Roy Neilson:** Writing – review & editing, Validation, Supervision, Funding acquisition, Conceptualization. **David Roberts:** Writing – review & editing, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Simon G. Edwards:** Writing – review & editing, Validation, Supervision. **Matthew A. Back:** Writing – review & editing, Validation, Supervision, Project administration, Funding acquisition, Conceptualization.

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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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2025.106779.

Data availability

The datasets will be made available upon request. Sequence data associated with this article are available at the National Centre for Biotechnology Information (NCBI) under accession numbers PX099275 - PX101312.

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