BRILL

Nematology 27 (2025) 813-838

Nematology
brill.com/nemy

Comparison of grassland nematode communities in the European and middle eastern Mediterranean under different forage plants

Martin EWALD [1,*], Randy INGELMANN [1], M.-Teresa SEBASTIÀ [2,3], Simon WEHBE [3,9], Angela RIBAS [4,5], Stefania MATTANA [6], Juliette BLOOR [7], Katja KLUMPP [7], Branko LUKAČ [8], Tomaž ŽNIDARŠIČ [8], Rodrigue ELBALAA [9], Abdoul RJOUB [10] and Liliane RUESS [1]

[1] *Institute of Biology, Humboldt-Universität Berlin, Philippstraße 13, 10115 Berlin, Germany*
[2] *Forest Science and Technology Centre of Catalonia (CTFC), Crta. de St. Llorenç de Morunys, 25280 Solsona, Spain*
[3] *Department DCEFA, University of Lleida, 25198 Lleida, Spain*
[4] *CREAF, Cerdanyola del Valles 08193, Catalonia, Spain*
[5] *BABVE, Edifici C, Universitat Autònoma de Barcelona, 08193 Bellaterra, Spain*
[6] *Department of Agri-Food Engineering and Biotechnology Universitat Politècnica de Catalunya, Campus Baix Llobregat, Castelldefels, Spain*
[7] *Université Clermont Auvergne, INRAE, VetAgro Sup, 63000 Clermont-Ferrand, France*
[8] *Agricultural Institute of Slovenia (KIS), Hacquetova ulica 17, SI-1000 Ljubljana, Slovenia*
[9] *Agricultural Value Chain Development Center, University of Balamand, 9Q7J+WX Balamand, Lebanon*
[10] *Computer Engineering Dep., JUST, 22110 Irbid, Jordan*
ORCID iDs: Ewald: 0009-0005-2681-0145; Sebastià: 0000-0002-9017-3575; Wehbe: 0000-0001-6185-2897; Ribas: 0000-0002-5938-2408; Mattana: 0000-0001-8427-8816; Bloor: 0000-0002-8668-1323; Klumpp: 0000-0002-4799-5231; Lukač: 0000-0002-0494-344X; Žnidaršič: 0000-0001-7554-0683; Rjoub: 0000-0001-8948-8070; Ruess: 0000-0001-8061-6208

Received: 23 April 2025; revised: 2 July 2025
Accepted for publication: 7 July 2025; published online: 18 August 2025

Summary – Grassland ecosystems are key biodiversity reservoirs, especially for the soil fauna. Among them, nematodes have been widely used as bioindicators to assess soil conditions and health in grasslands. However, their interactions with plant functional types, particularly in hot and dry climates like the Mediterranean region, remain poorly understood. The development of management strategies to optimise the resilience and productivity of grassland requires a better understanding of these biotic relationships. To address this, nematode communities were examined in grassland monocultures of three plant functional groups (grasses, legumes, forbs) in the Mediterranean. In France, Slovenia, Spain, Jordan and Lebanon, grasslands differing in soil properties and climate were investigated in autumn and spring in consecutive seasons. The genus composition of nematode assemblages was assessed, and their ecological indices and metabolic footprints were related to site characteristics and plant functional type. The Renkonen and Sörensen Index revealed that nematode communities differed greatly among regions. The western Mediterranean grasslands were dominated by bacterial feeders like *Rhabditis* and *Eucephalobus*, resulting in a low Channel Index and high Enrichment Index. The eastern Mediterranean sites showed higher proportions of fungal and plant feeders like *Aphelenchus* and *Geocenamus* and a higher Channel Index but lower Enrichment Index. Due to prolonged drought, the Spanish soils were infested by plant feeders such as *Scutylenchus* and *Pratylenchus*. The forage plant had only a minor impact, with legumes enhancing certain bacterial-feeding genera and grasses fostering some plant-parasitic nematodes. Overall, regional factors shape the nematode community more than forage plant cover. The dry conditions in the eastern Mediterranean, as well as the drought in Spain, increased herbivores and decreased top-down control, which is relevant in the light of future climate change.

Keywords – bioindicator, climate, climate change, drought, free-living nematodes, monoculture, plant type, soil micro-fauna.

* Corresponding author, e-mail: martin.ewald@hu-berlin.de

Grasslands are important global reservoirs for biodiversity and also provide a wide range of goods for humans (O'Mara, 2012; Bardgett *et al*., 2021). However, modern agricultural practice leads to a reduction in biodiversity as well as soil quality and health (Gardi *et al*., 2002; Askari & Holden, 2014). According to the EAA Report (August 2022), in Europe this is an increasing pressure under grasslands (Baritz *et al*., 2023). In the Mediterranean area, grassland monocultures are widely used as pasture-based livestock systems due to their high performance (Porqueddu *et al*., 2016; Paudel *et al*., 2021).

One way to assign soil conditions, for example, to determine sustainable soil management strategies, is to analyse soil nematode communities (Khanum *et al*., 2021; Melakeberhan *et al*., 2021). Nematodes are among the most frequently used bioindicators in soil ecosystems due to their high density, species and trophic diversity, as well as their sensitivity to disturbance (Wilson & Kakouli-Duarte, 2009). Key points are: *i*) nematodes reflect changes in abiotic (physicochemical properties) and biotic (food source) soil conditions; *ii*) the ratio of bacterial to fungal feeders indicates the nature of decomposition pathways; and *iii*) omnivores and predators respond to pollutants or disturbance of soil ecosystems (Bongers, 1990; Ferris *et al*., 2001). These multiple functions resulted in the development of a suite of ecological indices based on nematode community structure (Lu *et al*., 2020; Du Preez *et al*., 2022).

Among the factors shaping the nematode community, particular emphasis lies on the provision of the food source (Yeates *et al*., 1993). In grasslands, plants are the main resource for nutrients, fostering plant-feeding nematodes *via* living root tissue as well as bacterial- and fungal-feeding taxa *via* plant litter (Crotty *et al*., 2014; Ruess, 2024). Furthermore, plants modify the composition and density of the rhizosphere microbial community by excreting exudates, including readily available substrates such as sugars, amino acids and organic acids (Huang *et al*., 2014). The composition of these rhizodeposits depends mainly on plant type, with their nature and amount affecting below-ground interactions (Ehlers *et al*., 2020). For example, legumes are known to enhance the bacterial channel and thus bacterial-feeding nematodes (Zhao *et al*., 2014; Wang *et al*., 2024), especially strong *r*-strategists such as *Rhabditis* and *Panagrolaimus* (Viketoft *et al*., 2005). On the other hand, the fungal channel is positively influenced by the presence of forbs, which is mirrored by fungal-feeding nematodes (Viketoft *et al*., 2005, 2009; Steinauer *et al*., 2020). Grasses with their complex and large root systems are associated with plant-feeding nematodes (Neher, 2010), particularly of the genera *Paratylenchus* and *Tylenchus* (Fleming *et al*., 2016). While plant identity is the primary factor determining plant exudates, also the plant growth stage, the season and the local environment (*e.g.*, soil type, climate, nutrition) are shaping the exudation pattern (Herz *et al*., 2018; Dietz *et al*., 2020).

Within the classification 'Mediterranean climate' (Cs-climate, Köppen-Geiger; Köppen, 1936), precipitation and temperature can vary considerably between Mediterranean regions (Peel *et al*., 2007). The northern and western parts of the Mediterranean area present a marine west coast climate with equable conditions and only few extremes of temperature and precipitation. The southern and eastern regions are considered as hot-summer Mediterranean climate, with high temperatures and low precipitation as well as summer droughts (Lionello *et al*., 2006; Peel *et al*., 2007). Especially the hotter regions of the Mediterranean area pose significant challenges to soil nematodes. While temperature influences the nematode life cycle directly (Ruess *et al*., 1999), soil water content affects the activity and function of the entire community (Neher, 2010) since nematodes live, hunt and reproduce in the water film between soil particles. This is especially true for bacterial-feeding nematodes as well as omnivores and predators, since they are more dependent on water film for movement, while plant and fungal feeders live near or even in their food source (Neher, 2010). Furthermore, fungi can grow in air-filled pores, while bacteria need the water-filled pores as habitat (de Vries *et al*., 2018; Guan *et al*., 2021).

Due to this, the physical structure of the soil is a determinant for trophic interactions, *e.g.*, pore geometry, connectivity and hydration (Erktan *et al*., 2020). Therefore, differences in soil types and climate across Mediterranean regions can act as drivers for abundance and diversity of local nematode assemblages.

Nematode community structure as a tool to evaluate the performance of grasslands as well as soil quality and health is well studied in Europe (*e.g.*, Viketoft *et al*., 2005; Fleming *et al*., 2016; Haugwitz *et al*., 2016; Franco *et al*., 2019), but has rarely been applied in the Mediterranean area. Especially in the Middle East regions, mainly plant parasites such as *Meloidogyne* have been studied (Abu-Gharbieh *et al*., 2005; Ibrahim *et al*., 2017), while free-living nematodes have been generally neglected. To the best of our knowledge, this work represents the first investigation of grassland nematode

communities in Jordan and Lebanon. However, such data are needed as, according to the IPCC sixth Assessment Report, the Mediterranean region is expected to face a 20% higher rate of warming compared to the global average (Ali *et al*., 2022). The related increase in heat waves, with droughts and decreased precipitation, will pose a significant thread to grassland systems (Tuel & Eltahir, 2020).

Knowledge about the influence of different plant functional types on belowground biota is essential to adapt management practices, *e.g.*, to mitigate climate change, while optimising the resilience and productivity of grasslands. Combining nematode ecological indices for soil conditions and health with the benefits of different forage monocultures provides a first step to develop such sustainable management. This study compares the influence of functional groups of forage plants (grasses, legumes, non-legume forbs) on the nematode communities in five locations across the Mediterranean. Sites sown with monocultures of these forage plants were established in Spain, France, Slovenia, Lebanon and Jordan, representing common climate conditions ranging from hot and wet to hot and dry regions. We hypothesise that: *i*) regional differences between western and eastern Mediterranean areas (*e.g.*, climate, soil type) shape nematode communities; *ii*) the dry, hot summer Mediterranean climate results in a lower food web stability and higher contribution of the fungal decomposition pathway; and *iii*) legumes and forbs foster the presence of microbial grazers, while grasses favour plant feeders.

Materials and methods

Study sites

The study was performed at experimental farms in five countries in the Mediterranean area. Field sites were established in central France in the region of Puy-de-Dôme near Clermont-Ferrand (45°42′N, 3°00′E; 800 m AMSL), south-western Slovenia near Povir in the region of Obalno-kraška (45°41′N, 13°57′E; 400 m AMSL), north-eastern Spain close to the city of Solsona in Catalonia (41°58′N, 1°33′E; 700 m AMSL), western Lebanon in the area Bekaa near Terbol (33°48′N, 35°59E; 900 m AMSL), and north-eastern Jordan (32°30′N, 35°54′E; 600 m AMSL). These sites represent a range of typical climate conditions, *i.e.*, from the typical hot and dry to warm and wet (Porqueddu *et al*., 2016). In the western Mediterranean, the average annual temperatures during the experiment ranged between 10.1°C, 12.5°C and 14.1°C for the experimental fields in France, Slovenia and Spain, respectively. The eastern Mediterranean showed higher temperatures, with 18.9°C in Jordan and 19.1°C at the site in Lebanon. The annual rainfall separates the locations into three groups: the experimental field in Slovenia is with 1178 mm the wettest, followed by France with 975 mm. The warmest regions were at the same time the driest, with an annual precipitation of 602 mm in Lebanon and 417 mm in Jordan. The Spanish site was with 530 mm unusually dry (series annual mean of 854 mm) during the experiment. The prevalent soil type differed with Cambisol, Luvisol, Leptosol, Vertisol and Entisol in the fields in France, Slovenia, Spain, Jordan and Lebanon, respectively. Furthermore, the soils in Slovenia comprised the highest amount of C_{org}, organic matter, and nitrogen, while the soils in France showed the highest phosphorus content (Olsen). For further details on soil properties, see Supplementary Table S1.

To address the influence of climate (*e.g.*, temperature and precipitation) on the nematode community, long term means as well as the daily weather from the experimental fields were calculated. A detailed pattern of temperature and precipitation at the different sites is given in Supplementary Figure S1. For France, Slovenia and Spain, weather stations on site recorded these data. For Jordan and Lebanon, climate values were taken from the weather stations at the nearest city – Irbid for Jordan and Terbol for Lebanon.

The field trials were established in Spain, Slovenia, Jordan and Lebanon in autumn 2021, and in France in spring 2022. At each site, a total of 40 plots (3 × 10 m) were set up in two rows (20 plots per row). The plots consisted of different mixtures of one, three, four or six plant species used as forage. Between plots, buffer zones were installed as corridors (0.5 m) with the same plant species grown as in the adjacent plots. Before the experiment, the soil was ploughed to incorporate residues. Then, mixtures of one, three, four or six different plant species were sown in the respective plots, representing different forage plant types and diversities. Also, the soil in Slovenia was fertilised with 300 kg ha^{-1} mineral fertiliser (NPK) at the beginning of each growing season based on local practice. Regarding site history, the fields in France, Spain, Jordan and Lebanon were used as arable land, while the site in Slovenia was maintained as meadow.

The present study investigates monocultures within the framework of these diversity experiments. We exam-

ined three functional plant types – grasses, legumes, and non-legume forbs (henceforward termed forbs). Grasses used were *Lolium perenne* (L.) and *Dactylis glomerata* (L.); legumes comprised *Medicago sativa* (L.) and *Onobrychis viciifolia* (Scop.), the latter substituted by *Trifolium repens* (L.) in France; and forbs were *Cichorium intybus* (L.) and *Plantago lanceolata* (L.). Due to local climate, some species had to be changed in the eastern Mediterranean. For grasses, *Lolium rigidum* (Gaud.) and *Hordeum vulgare* (L.), and for legumes, *Medicago sativa* (L.) and *Trifolium incarnatum* (L.) were sown in Jordan and Lebanon. The forb species were not modified across countries.

The amount of seeds varied based on the species and local management practices: the densities for Slovenia and Spain were 35, 30, 40, 110, 15 and 20 kg ha^{-1} for *L. perenne*, *D. glomerata*, *M. sativa*, *O. viciifolia*, *C. intybus* and *P. lanceolata*, respectively. The densities for France were 38, 23, 25, 10, 10 and 10 kg ha^{-1} for *L. perenne*, *D. glomerata*, *M. sativa*, *T. repens*, *C. intybus* and *P. lanceolata*, respectively. In Jordan and Lebanon, 30, 100, 35, 15, 5 and 20 kg ha^{-1} of *L. rigidum*, *H. vulgare*, *M. sativa*, *T. incarnatum*, *C. intybus* and *P. lanceolata* were sown, respectively. This was performed by hand in Slovenia, Jordan, and Lebanon, and by sowing machine in Spain and France.

Soil sampling

The first soil sampling campaign was carried out in 2022 in autumn, after the last harvest on October 3 (France) and October 10 (Slovenia), November 4 (Spain), December 10 (Jordan) and December 12 (Lebanon). The second sampling campaign took place in 2023 in spring, after the first harvest at May 31, 23 and 30 and June 19 and 6 for France, Slovenia, Spain, Jordan and Lebanon, respectively. For each plant functional type, two species (see Nematode analysis section below for taxa in the respective country) were sown in monocultures at each site. Two plots for each plant species were established at a site, resulting in four replicates per plant functional group. At the western experimental fields, soil samples were collected with a soil core (3 cm diam.). Due to local adaptations in Jordan and Lebanon, soil samples were taken with a spade. To obtain a composite sample, 3-8 single samples were taken randomly, bulked and mixed by hand. Soil samples were sent overnight at 4°C and processed directly after arrival. Overall, there were 12 samples per site and date, resulting in a total of 120 soil samples for the nematode analysis. To determine the soil moisture, 20 g of wet soil from each plot was weighed, dried for 3 days at 60°C, re-weighed, and the water content calculated.

Nematode analyses

About 40-60 g of soil were used to extract nematodes following a modified Baermann method described by Ruess (1995). Before the extraction, samples were placed on a milk filter (Calvatis), supported by a wire screen in a funnel. The funnel was connected to a glass vial (50 ml) and filled with tap water and transferred to a Kempson extractor. First, the samples stayed at room temperature for 24 h, followed by a heating regime from 20-45°C with a stepwise increase of 5°C for 6 h using infrared lamps. After the extraction, the nematodes were fixed in a 4% cold formaldehyde solution. The samples were analysed by counting the total number of nematodes for each sample and determining 10% of the individuals (but not less than 100 specimens) to genus level, following Bongers (1987). The trophic groups were classified according to Yeates *et al.* (1993) as plant feeders, bacterial feeders, fungal feeders, omnivores and predators.

Afterwards, nematode ecological indices were calculated. For the Maturity Index (MI), nematodes were assigned to a c-p value ranging from coloniser (1) to persister (5), according to Bongers (1990). The index is calculated as $MI = \sum_{i=1}^{n} v(i) * f(i)$, where $v(i)$ and $f(i)$ are the c-p value of the taxon i and the frequency of that taxon in the nematode population, respectively. Low numbers point to a disturbed environment, while higher values indicate more stable conditions. For plant-parasitic nematodes, the plant parasite index (PPI) was calculated using the same formula for plant-feeding nematodes.

To calculate the Channel Index (CI), nematode trophic groups are combined with their life history (c-p value). The CI is calculated by $CI = 100 * (0.8 * Fu_2)/(3.2 * Ba_1 + 0.8 * Fu_2)$, where Ba_1 represents the bacterial feeder with a c-p value of 1, and Fu_2 the fungal feeder with a c-p value of 2 (Ferris *et al.*, 2001). The CI provides information on the soil decomposition pathways, with high values indicating a fungal-dominated and low values a bacterial-dominated process. The food web conditions were examined using the enrichment (EI) and structure (SI) index. These were assigned as $EI = 100 * e/e + b$, $SI = 100 * s/s + b$, where b is the basal, s the structure and e the enrichment component (Ferris *et al.*, 2001). The impact of nutrient enrichment or pulses is attributed to the EI, while the SI gives information on the stability

of the food web. Furthermore, the basal index (BI) was calculated as BI $= 100 * b/(e + b + s)$, where values correspond with soil perturbation.

To further survey the differences among regions, the Sörensen Index and the Renkonen Index were calculated. The Sörensen Index is a community similarity coefficient representing the proportion of taxa in common at the different sites. It was calculated as: $S\ (\%) = (2{*}G/(S_\mathrm{A} + S_\mathrm{B})) * 100$, where G is the number of genera present in both sites, and S_A and S_B the number of species in sites A and B, respectively. The result can take percentage values between 0 and 100%, whereby higher numbers indicate a higher similarity in taxa composition. The Renkonen Index determines the alignment in dominance structure between two different sites and was calculated as the sum of the smallest dominance value of the genus present in both locations: Re $(\%) = \sum \min \mathrm{D_{A,B}}$, with $D = n_\mathrm{A}/N_\mathrm{A}$ or $n_\mathrm{B}/N_\mathrm{B}$, where D is the dominance value, $n_\mathrm{A,B}$ the number of individuals in location A or B, respectively, and $N_\mathrm{A,B}$ the total number of individuals in site A or B. The results can take percentage values between 0 and 100%, whereby higher numbers indicate a higher similarity in dominant taxa.

Ferris (2010) developed the metabolic footprint, which gives a more detailed view on the metabolic activity of nematode groups, and the magnitudes of carbon (C) and energy flow in food webs. It is calculated as: $F = \sum(N_t\left(0.1\,(W_t/m_t) + 0.237(W_t^{0.75})\right))$, where N_t, W_t and m_t are the number of individuals, the body weight, and the c-p value of the taxon t, respectively. The 0.1 in the formula mirrors the amount of C of body fresh weight and the 0.237 the molecular weights of C and O_2 or 12/44 (Ferris, 2010). The metabolic footprint can be adjusted to gain different information: nematodes of a single trophic group can be combined in the respective footprint, which indicates C and energy fluxes in this explicit food chain. The susceptibility to resource pulses is given by the enrichment footprint (F_e) calculated as the sum of taxa indicating enrichment. The structure footprint (F_s) shows the impact on higher trophic levels and is calculated as the sum of taxa indicating a structured environment.

Statistical analysis

Statistics were performed with Statistica 10 for Windows (StatSoft). The analyses were conducted at the level of plant functional groups. For this, the samples belonging to the same plant functional group were pooled at each location. Based on the Kolmogorov-Smirnov-Lilliefors-test, data were not normally distributed. Therefore, the effects of location on the nematode community were analysed with the non-parametric Kruskal-Wallis one-way ANOVA (analysis of variance). Differences between means were assigned using the Dunn *Post-hoc* test, while seasonal effects (*i.e.*, sampling date) were analysed by the non-parametric Mann-Whitney U-test. To analyse the impact of plant functional group and plant identity, R (R Development Core Team 2012 - version 4.3.2), was used to create linear mixed models (lme4 and lmtest). Location was used as a random factor, while plant functional group and plant identity were used as fixed factors.

Using CANOCO 5 (ter Braak & Šmilauer, 2012) a redundancy analysis (RDA) was performed, to investigate the impact of location, plant functional group, and season on nematode community structure. Significance of terms were analysed by unrestricted Monte Carlo permutation test (number of permutations = 10 000).

Results

Nematode community structure

A total of 69 different nematode genera were detected at the five Mediterranean grassland sites (Suppl. Tables S2-S6). In autumn, 37, 42, 34, 44 and 47 genera were identified in the soils of France, Slovenia, Spain, Jordan and Lebanon, respectively. Moreover, several genera showed sporadic dispersal, occurring in one or two samples only, especially at the site in Lebanon (Suppl. Table S5). In spring, the number of genera was higher in soils of France and Slovenia with 45 and 48, respectively, but lower in Spain, Jordan and Lebanese soils with 38, 38 and 40, respectively.

Each region showed a unique nematode assemblage, with some genera restricted to a single site. The grasslands in Western and Eastern Mediterranean showed the following general differences. In autumn, the plant-feeding *Geocenamus* and *Psilenchus*; the bacterial-feeding *Cibronema*, *Drilocephalobus* and *Kirjanovia* as well as the omnivorous *Aporcelaimellus* were only detected in the eastern Mediterranean (Suppl. Tables S5, S6). The plant-feeding *Merlinius* as well as the bacterial-feeding *Metateratocephalobus* were restricted to the western Mediterranean. In spring, many genera only appeared in the western areas: *Merlinius*, *Nagelus*, *Pratylenchoides*, *Scutylenchus*, *Panagrellus*, *Anaplectus*, *Prismatolaimus*, *Bursila*, *Pellioditis*, *Rhabditis*, *Metateratocephalobus*, *Mesodorylaimus*, *Epidorylaimus*, *Dorydorella* and *Allodorylaimus*. In the eastern regions, *Geocenamus*,

Paratrophurus, *Tylenchus*, *Aprutides*, *Alaimus*, *Cibronema*, *Kirjarovia* and *Ecumenicus* were exclusive.

Redundancy analysis (RDA) was applied to analyse further the influence of site and plant functional groups (Fig. 1). The variable 'region' accounted for 37.8% of the separation of data, with the first and second axes explaining 18 and 13%, respectively ($P < 0.01$). By contrast, the contribution of 'plant functional group' to data discrimination was negligible (5.3%). The nematode communities at the sites in France and Slovenia and those in Jordan and Lebanon grouped together, while the nematode assemblages in Spain were strongly separated from all other regions. The communities in France and Slovenia were both distinguished by bacterial feeders, especially colonisers (c-p 1) like *Pellioditis*, *Rhabditis*, *Mesorhabditis* and *Panagrellus* as well as opportunists (c-p 2) like *Monhystera*, *Heterocephalobus* and *Eucephalobus* (Fig. 1). Both eastern Mediterranean soils were distinguished mainly by *Geocenamus*, *Paratrophurus*, *Chiloplacus* and *Cervidelus* exclusive to these areas. *Acrobeloides*, *Eumonhystera* and *Ditylenchus* were also associated with Jordan and Lebanon, but are present in the other regions as well. The Spanish site was populated by a wide array of plant-parasitic nematodes; the RDA revealed that especially *Bitylenchus*, *Scutylencus Dolichorhynchus*, *Amplimerlinius* and *Pratylenchus* are correlated to this site, while omnivores were rare and predators were not found at all (Suppl. Table S4).

Corresponding to the RDA, the Sörensen index assigned the highest similarity of genera for the soils in Jordan and Lebanon (90%) as well as in France and Slovenia (73%) in spring (Table 1). In autumn, the pattern was less clear, with a similarity of 73% between Jordan and Lebanon and of 66% between France and Slovenia. At both sampling dates, the genera pattern at the site in Spain was most separated from the other regions, with values around 50% (Table 1). The dominance identity assigned by the Renkonen index also showed the highest comparability for the nematode communities at the sites in Jordan and Lebanon, with 85 and 72% for autumn and spring, respectively (Table 1). The lowest similarities were observed between the Spanish and French soils at both sampling dates.

The nematode ecological indices varied across sites, with differences mainly related to region, but only minor effects of season (Table 2). The MI was lowest (<1.6), *i.e.*, the disturbance was highest (Bongers, 1990), for the nematode communities in France, while at the Slovenian, Spanish, Lebanese and Jordan sites, the MI ranged above 2 ($P < 0.001$). The pattern of the PPI across regions differed considerably (Table 2): the nematode communities at the Spanish site displayed the highest PPI (2.7-2.8), Jordan and Lebanon the lowest (2.0-2.1), and France and Slovenia intermediate (2.3-2.6) values ($P < 0.001$). The BI was also lowest in the French soils with 14 and 15 for autumn and spring, respectively, while the Spanish, Jordan and Lebanese soils, with a BI above 50, showed the highest values across seasons ($P < 0.01$; Table 2).

According to the Shannon Index (H'), nematode diversity was at 3.2 highest in the soils at the Lebanese site in autumn ($P < 0.001$) compared to all other regions. In spring the pattern differed; now the diversity of the nematode communities at the site in Slovenia had a higher diversity with an H' of 3.1 compared to Jordan (2.4) and Lebanon (2.3) ($P < 0.001$), with the communities in Spain (2.7) and France (2.5) in between (Table 2).

Food web conditions

The EI and SI are indicators for the N-enrichment and the structure of the soil micro-food web (Table 2). At both sampling dates, an EI of 84 indicated a high enrichment for the food webs in the soils at the French site compared to Spain, Jordan and Lebanon, which were in a depleted stage ($P < 0.05$). The latter three sites can be regarded as degraded environments with a high C:N ratio and a fungal-mediated decomposition (Ferris *et al*., 2001). The Slovenian site kept an intermediate position and, moreover, showed a seasonal change with the EI increasing from 51 to 62 between autumn and spring ($P < 0.05$), which was also shown by the linear mixed models (Suppl. Table S7). By contrast, there were no changes in the N-enrichment of the soil micro-food web in the other regions. The indications of the EI on the dominant decomposition processes was supported by the CI, which was highest in the Spanish, Lebanese, and Jordan soils, ranging between 84-98, 66-79 and 68-69, respectively, and pointing to a fungal-dominated system. The site in France showed 8.1-8.5 ($P < 0.001$) low values, while the soil in Slovenia holds an intermediate position (Table 2), indicating bacterial decomposition at both sites (Ferris *et al*., 2001). Between seasons, the CI decreased in the soils of Slovenia ($P < 0.05$) and Spain ($P < 0.05$) from 37 to 21, and from 98 to 83, respectively. This decline between seasons is supported by the linear mixed model ($P < 0.01$; Suppl. Table S7).

As indicated by SI values under 52, the structure and complexity of the food webs were low, predominantly in autumn (Table 2). The Slovenian soils with a SI of

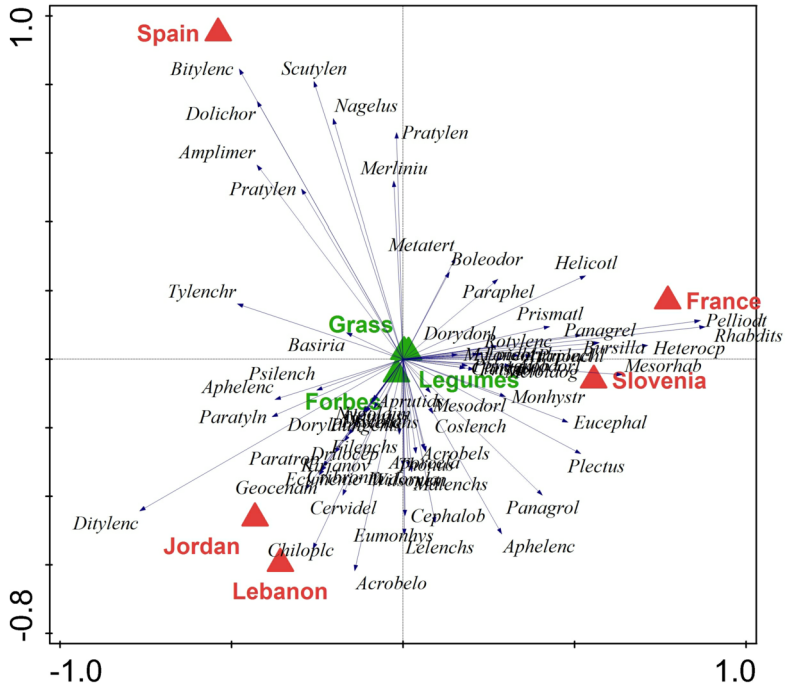


Fig. 1. Redundancy analysis (RDA) of grassland nematode community structure in the five Mediterranean regions France, Slovenia, Spain, Jordan and Lebanon. Presented are the nematode genera with relation to region (red) and forage plants (grasses, legumes, forbs; green).

Table 1. Similarity (%) in nematode community composition between the sites in France, Slovenia, Spain, Jordan and Lebanon, in autumn 2022 and spring 2023.

		Sørensen Index				Renkonen Index			
		France	Slovenia	Spain	Jordan	France	Slovenia	Spain	Jordan
Autumn	Slovenia	65.8				58.9			
	Spain	50.7	57.9			31.4	49.3		
	Jordan	51.9	62.8	53.8		40.8	55.2	44.9	
	Lebanon	59.5	62.9	54.3	72.5	38.7	61	44	85.4
Spring	Slovenia	73.1				50.5			
	Spain	48.2	48.8			28.3	37.7		
	Jordan	55.4	53.5	52.6		32	43.3	44.8	
	Lebanon	61.2	59.1	48.7	89.7	42.7	45	44.2	71.6

The shading from green to white represents higher similarity, while the shading from white to red represents lower similarity within one index. Presented are the identity of genera based on the Sørensen Index and the similarity in dominance structure according to the Renkonen Index.

33 displayed the highest values, while food webs in France and Jordan with a SI of 18 and 16, respectively, were strongly degraded ($P < 0.01$). In spring, food web structure in the Slovenian soils developed towards a maturing status (SI of 52; Ferris *et al.*, 2001), with again significantly higher SI compared to food webs in the soils of Spain, Jordan and Lebanon ($P < 0.001$). Between seasons, the food web structure increased from 18 to 37

Table 2. Nematode indices (±s.d.) in the soils of the five Mediterranean regions, France, Slovenia, Spain, Jordan and Lebanon.

		France	Slovenia	Spain	Jordan	Lebanon
Autumn	MI	1.5 ± 0.2b	2 ± 0.1a	2.2 ± 0.1a	2 ± 0.1a	2.1 ± 0.1a
	PPI	2.6 ± 0.2ab	2.5 ± 0.2ab	2.7 ± 0.1a	2.2 ± 0.1b	2.2 ± 0.1b
	CI	8.5 ± 6b	36.7 ± 13.5ab	98.3 ± 5.8a	67.7 ± 21.1ab	79 ± 16.7a
	BI	14.6 ± 9.1b	26.5 ± 7.2ab	50.6 ± 9.8a	52.7 ± 7.9a	52.1 ± 7.9a
	EI	84 ± 7.9a	51 ± 10.2ab	40 ± 3.5b	37 ± 8.7b	39.8 ± 10.3b
	SI	17.8 ± 10.8b	32.6 ± 11.2a	21.8 ± 15.8ab	16.4 ± 10.6b	25.1 ± 11.1ab
	H'	2.4 ± 0.3b	2.9 ± 0.1a	2.7 ± 0.1b	1.9 ± 0.6b	3.2 ± 1.5ab
Spring	MI	1.6 ± 0.2b	2.1 ± 0.1a	2.1 ± 0.1a	2.1 ± 0.1a	2 ± 0.1a
	PPI	2.6 ± 0.2ab	2.3 ± 0.1ab	2.8 ± 0.1a	2.2 ± 0.1b	2.3 ± 0.1b
	CI	8.1 ± 7.4b	21.1 ± 15.3b	83.8 ± 18.2a	69 ± 26.1a	65.8 ± 19.2a
	BI	15.3 ± 7.5b	39.7 ± 9.2ab	50.8 ± 7.4a	50.4 ± 5.3a	52.9 ± 7.3a
	EI	83.7 ± 10.5a	62.2 ± 11.8ab	42.7 ± 6.8bc	37.5 ± 12.4c	39.6 ± 9bc
	SI	36.7 ± 16.2ab	52.2 ± 8.3a	19.6 ± 13.8b	18.7 ± 8.6b	22.1 ± 8.7b
	H'	2.5 ± 0.4b	3.1 ± 0.1a	2.7 ± 0.2ab	2.4 ± 0.3b	2.3 ± 0.1b

Given are the maturity index (MI), plant parasite index (PPI), channel index (CI), enrichment index (EI), structure index (SI), and Shannon Diversity Index (H') in autumn and spring. Values within a row with the same letters are not significantly different according to Dunn-Bonferroni ($P < 0.05$).

and from 33 to 52 in the soils of France ($P < 0.05$) and Slovenia ($P < 0.01$), respectively, while the SI remained unchanged in the soils at the other three sites.

The graphical display of the functional metabolic footprints is given in Figure 2 as an area of equilateral rhomboid centred on the intersection of the EI and SI. The enrichment footprint was always highest in the soil in France, which was significant compared to Spain ($P < 0.001$; Suppl. Table S8). During the study period, larger enrichment footprints were observed in spring compared to autumn ($P < 0.05$), except for the Spanish soil. Similar seasonal shift occurred for the structure footprint, with a significant increase in spring in the soils in France ($P < 0.01$), Slovenia ($P < 0.05$) and Jordan ($P < 0.05$; Suppl. Table S8). As the functional metabolic footprint is maximised when the rhomboid shape becomes a square (Ferris *et al*., 2010), the soils in Slovenia and Jordan can be considered in metabolic balance (Fig. 2). With the structure footprint much smaller than the enrichment footprint, the food webs in the soils in France and Spain are in an unstable state.

The metabolic footprints of nematode trophic groups assign how much carbon is entering the soil food web by the respective pathway (Ferris *et al*., 2010). The biggest regional differences occurred for the bacterial footprint (Fig. 3; Suppl. Table S8). In autumn, the soils in France and Slovenia showed the highest, in Jordan and Lebanon intermediate, and in Spain the lowest values ($P < 0.001$). Comparably, in spring, the bacterial footprint was highest in the French and lowest in Spanish soils ($P < 0.001$). Regarding season, the bacterial footprint increased significantly by about 5 (France), 1.5 (Spain), and 2.5 (Jordan and Lebanon, respectively) in spring compared to autumn ($P < 0.05$).

The activity of fungal decomposer was highest in the eastern Mediterranean, whereas in the western regions, especially the Spanish soils, showed only a small fungal footprint at both sampling dates ($P < 0.001$; Fig. 3; Suppl. Table S8). Comparable to the bacterial channel and also in the fungal channel, more carbon was entering the food web in spring. This increase was about threefold in France, Jordan and Lebanon, and doubled in Spain ($P < 0.05$; Fig. 3). By contrast, the fungal footprint declined at the Slovenian site from 0.3 to 0.1 ($P < 0.001$).

In autumn, the herbivore footprint indicated a significant higher activity of plant feeders in the soils of Slovenia and Spain compared to France and Jordan, with Lebanon at intermediate position ($P < 0.001$; Fig. 3; Suppl. Table S8). In spring, at the site in Spain, the herbivore footprint was the highest and in Slovenia and Lebanon the lowest ($P < 0.001$). The herbivore footprint increased between seasons by five times in the French soil and doubled in the soils of Spain and Jordan ($P < 0.05$).

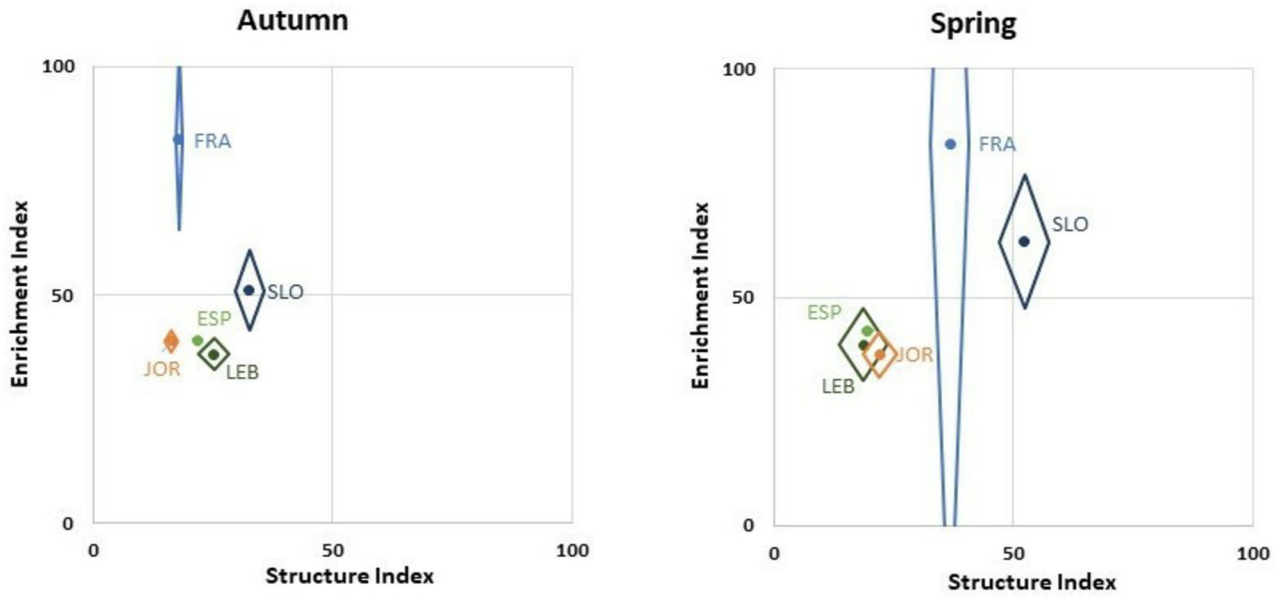


Fig. 2. Nematode faunal profile combined with the functional metabolic footprints in the soils of the five Mediterranean regions, France (FRA), Slovenia (SLO), Spain (ESP), Jordan (JOR) and Lebanon (LEB), in autumn and spring. The displayed rhomboids reflect the functional metabolic footprints with the scalar $k = 0.1$.

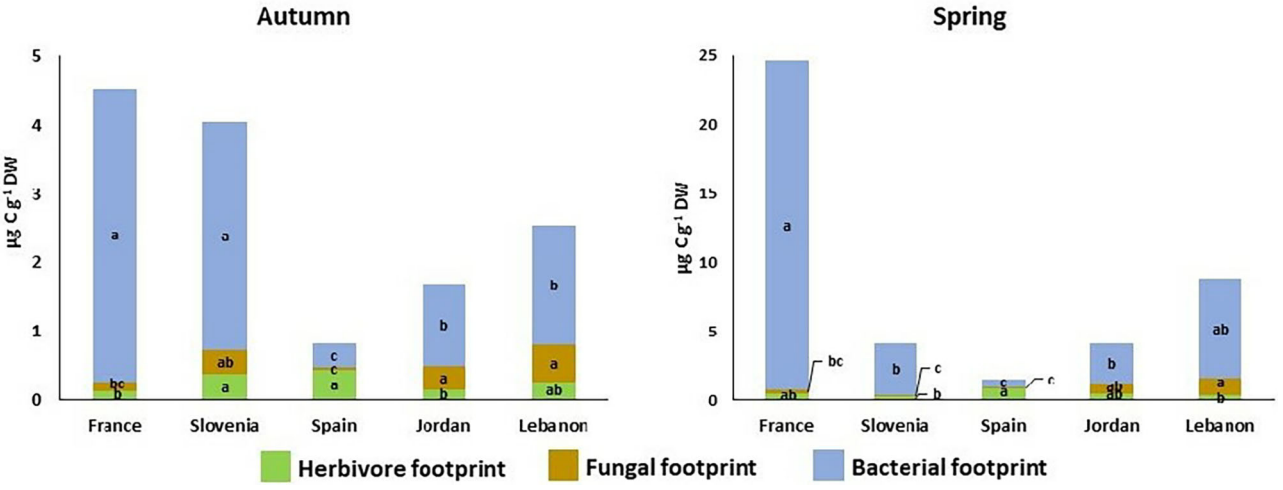


Fig. 3. The herbivore, fungal, and bacterial footprint in the soils of the five Mediterranean regions, France, Slovenia, Spain, Jordan and Lebanon. Given are the metabolic footprints in C (g DW)$^{-1}$ in autumn and spring. Values within one footprint and season with the same or no letters are not significantly different according to Dunn's test at $P < 0.05$.

Influence of plant functional groups

The linear mixed model revealed that the distribution of the nematode genera was only slightly affected by the presence of different plant functional groups (Table 3; Suppl. Table S9). Among plant-feeding nematodes, only *Basiria*, *Lelenchus*, *Malenchus* and *Tylenchus* were influenced. However, all reacted positively to the presence of grasses ($P < 0.05$, $P < 0.001$, $P < 0.05$, $P < 0.001$, respectively), where especially *L. perenne* fostered these nematodes. Furthermore, *Geocenamus*, which only occurred in the eastern Mediterranean, was fostered by

Table 3. Effects of plant functional group, plant identity and season on the abundance of nematodes.

	Plant functional group	Plant identity	Season
Acrobeles	8.19***	2.2*	0.69
Acrobeloides	0.39	0.58	14.03***
Allodorylaimus	0.04	1.12	6.73*
Aphelenchoides	0.53	1.2	4.3*
Aphelenchus	4.39*	1.32	4.17*
Aprutides	13.67***	4.17***	2.43
Basiria	3.94*	2.22*	0.78
Bursilla	25.05***	7.29***	2.76
Cephalobus	2.78	1.69	3.63*
Cervidellus	0.03	2.25	24.38***
Cribronema	2.19	2.56*	5.3*
Ecumenicus	28.22***	11.77***	8.9**
Eudorylaimus	0.54	0.36	24.47***
Eumonhystera	2.03	0.24	6.87*
Geocenamus	0.97	4.04***	0.25
Kirjanovia	9.73***	3.36**	2.05
Lelenchus	6.98**	2.43*	0.1
Malenchus	3.6*	0.94	1.49
Merlinius	0.29	0.64	5.18*
Mesodorylaimus	0.65	1.33	4.57*
Metateratocephalobus	0.02	0.7	5.31*
Monhystera	0.76	0.46	12.7***
Nagelus	0.52	0.61	10.78**
Nygolaimus	0.01	3.7**	2.16
Panagrellus	2.34	0.68	11.16**
Paratrophurus	0.04	1.15	5.94*
Pratylenchoides	0.51	2.17*	1.52
Prismatolaimus	0.08	0.72	5.59*
Pristionchus	0.05	1.14	5.42*
Rhabditis	10.27***	3.12**	7.92**
Rotylenchus	0.04	0.34	13.81***
Scutylenchus	0.37	1.49	9.93**
Tylenchorhynchus	0.11	0.41	21.26***
Tylenchus	6.52**	3.14**	4.5*
Wilsonema	0.84	0.89	9.21**

Presented are the F-values of linear mixed models of nematode genera with significant response. Asterisks indicate significant effect at $^{***}P < 0.001$; $^{**}P < 0.01$; and $^{*}P < 0.05$.

the grass *H. vulgare*, while *Pratylenchoides* responded positively to the grass *D. glomerata*.

Aphelenchus, a facultative root and fungal feeder, was influenced by plant functional group (Table 3), and reacted positively to the presence of grasses ($P < 0.05$). Among bacterial-feeding nematodes, the rare *Aprutides* ($P < 0.001$), *Acrobeles* ($P < 0.001$), and *Kirjanovia* ($P < 0.001$) were fostered by grass vegetation. Furthermore, the more common *Bursilla* ($P < 0.001$) and *Rhabditis* ($P < 0.001$) were positively related to the presence of legumes, yet *M. sativa* showed a significant negative impact on both genera.

The rare *Ecumenicus* was the only omnivorous nematode reacting to plant functional group (Table 3), showing a positive correlation with the presence of grasses ($P < 0.001$), but a negative correlation with *D. glomerata*. Predatory nematodes were not influenced by plant functional group.

The nematode indices were more responsive to a change in plant functional groups. The MI showed a

positive correlation with grasses (Suppl. Table S7; $P < 0.05$) and a negative correlation with legumes ($P < 0.001$). However, the presence of *M. sativa* had a positive effect on the MI. Forbs ($P < 0.05$) and grasses ($P < 0.001$) increased the CI, which was mainly mediated by *P. lanceolata* ($P < 0.05$). The EI was positively related to the presence of forbs ($P < 0.01$), but negatively to grasses ($P < 0.001$). This impact was reflected by all grass and forb species, except *D. glomerata*. Forbs also resulted in higher nematode diversity (H; $P < 0.001$), while the presence of legumes led to a decrease ($P < 0.01$). This was mainly due to *M. sativa* and *C. intybus*. The PPI and SI on the other hand were not influenced by plant functional group. For more information on the nematode indices, see Supplementary Table S10.

Finally, for the metabolic footprints, the composite footprint as well as the bacterial and enrichment footprint were positively corelated to the presence of legumes (Suppl. Table S7; $P < 0.01$, respectively), which was mainly a result of the presence of *M. sativa* and *O. viciifolia*.

Discussion

Regional differences shape nematode communities in Mediterranean grasslands

The local environment was identified as the main factor determining nematode community composition in the different Mediterranean regions. Based on their geographical proximity, the experimental sites in France, Slovenia and Spain can be allocated to the same west coast climate, while the fields in Jordan and Lebanon belong to the hot-summer Mediterranean climate (Lionello *et al*., 2006; Peel *et al*., 2007). This is reflected in the Sørensen and Renkonen indices, indicating the highest similarity between genera identity and dominance structure in the soils of Jordan and Lebanon, followed by France and Slovenia. It is well acknowledged that nematode communities are strongly influenced by the abiotic soil environment, *e.g.*, soil type, pH, moisture and organic matter (Xiong *et al*., 2021; Richter *et al*., 2023) as well as local climate conditions (Neher, 2010; Zhou *et al*., 2022). However, the nematode assemblages in the Spanish soil showed the lowest similarities with the other sites according to the Sørensen and Renkonen indices. During the study period, here the climate deviated from the long-term means (Sebastià *et al*., 2024), with a precipitation of 530 mm (compared to the series annual mean 854 mm) and temperature of 14°C (compared to the series annual mean 12°C). This likely induced adaptations within the nematode community, not apparent in France and Slovenia. That the Spanish soils do not group together with the other countries of the western Mediterranean is also visible through the BI, which is highest in the eastern Mediterranean and Spain. However, this is due to different reasons: a food web can become more basal (increased BI) due to limited resources, which was the case in the soils of Jordan and Lebanon, or due to adverse environmental conditions (Ferris *et al*., 2001). The latter applied to the Spanish soils during the severe drought in the experimental period (Ferris *et al*., 2001).

The affiliations assigned by genera identity and dominance structure of nematode assemblages were mirrored by the RDA. The experimental fields in France and Slovenia as well as those in Lebanon and Jordan clearly group together, while Spain is isolated. The similarities of France and Slovenia are likely due to comparable agricultural practices, together with sufficient rainfall and cold temperatures during winter. The nematode assemblages here were characterised by bacterial feeders belonging to c-p 1 and 2, especially genera of the family Rhabditidae, adapted to soils with a good nutrient status and tolerant to disturbance (Bongers, 1990). Moreover, they can survive harsh environmental conditions by entering a resistant dauer juvenile stage (Sohlenius, 1973). Rhabditidae are also active in colder soils (2-4°C), apparent at the French site with low temperatures in winter (Sohlenius, 1973; Anderson & Coleman, 1982) (see Suppl. Fig. S1).

Compared to western European agriculture, with its heavy use of machinery, pesticides and fertilisers, farming in the Near East is less intensive (Hole, 2007; Maudet *et al*., 2025). This difference, along with dry soil conditions, has shaped the nematode community in the soils of Jordan and Lebanon. The latter resulted in a higher presence of plant-feeding nematodes, and especially *Paratylenchus* was associated with these soils. They are considered opportunistic colonisers in permanent pastures, and prefer soils with low moisture and nutrients (Ciobanu *et al*., 2003). In addition, *Ditylenchus* was associated with the soils of Jordan and Lebanon. These nematodes can feed on both roots and fungi (Zheng *et al*., 2016), likely benefiting from the dry conditions (see Suppl. Fig. S1; Suppl. Table S1). Fungi are adapted to low soil moisture, and the high CI in these soils indicate fungal-dominated decomposition processes. Moreover, root- and fungal-feeding nematodes are less dependent on the water film

between soil particles (de Vries *et al*., 2018; Guo *et al*., 2021).

Root feeders were shown to benefit from the absence of predatory nematodes and thus a weakened top-down control in mesic grasslands after drought (Franco *et al*., 2019). This scenario was likely the driving factor for nematode community structure at the Spanish site, resulting in a very specific community pattern with no predators (Suppl. Table S4). These soils harboured great numbers of plant-parasitic nematodes, reflected in the highest proportional herbivore footprint across all experimental fields. Among them, the genus *Pratylenchus* infects a wide variety of host plants (Kanzaki *et al*., 2023). These nematodes are also well adapted to drought; while most nematodes prefer a soil water content of at least 5%, *Pratylenchus* can survive at 2% (Inomoto & Oliveira, 2008; Neher, 2010). Also, they can endure unfavourable conditions for up to 9 months in dead roots without a living host plant. *Scutylenchus*, another common genus in the Spanish soils, is capable of entering a dauer stage to survive lack of food or moisture (Hashemi *et al*., 2020). Likely, the other plant-feeding nematodes inhabiting the Spanish soils (*Bitylenchus*, *Pratylenchoides*, *Dolichorhynchus*) also possess some adaptations to withstand longer periods of drought (Womersley, 1987; McSorley, 2003).

Overall, the nematode communities in the different Mediterranean regions were primarily shaped by local conditions. The severe drought in Spain, in particular, allowed plant parasites to prosper, posing a threat to soil quality and health and thus to agriculture in this region.

Effects of Mediterranean climate on food web stability and decomposition channels

The seasonal climate differed greatly between the investigated regions. Most importantly, the eastern Mediterranean is distinguished by regular summer droughts, with precipitation mainly occurring in winter and early spring (Porqueddu *et al*., 2016). These (Jordan and Lebanon; Suppl. Fig. S1) showed low EI and SI areas, particular during summer dryness, comparable to nematode communities in an arid desert (Ferris, 2010). This reflects that microbial grazers, but also higher trophic levels, were hampered by low precipitation (Suppl. Fig. S1) together with the low nutrient content of the soil (Neher, 2010).

Summer dryness with low precipitation in combination with high temperature reduces the survival rate of nematodes by the fragmentation of their soil habitat (Neher, 2010), resulting in the low nematode population density in Jordan and Lebanon in autumn. Especially omnivores and predators are hampered by the disruption of their hunting grounds, while at the same time requiring years to recover (Okada & Harada, 2007). Despite the low structure and stability of the food web indicated by EI and SI, the soils of Jordan and Lebanon showed a surprisingly good metabolic balance regarding their functional metabolic footprints. The nematode communities in the eastern Mediterranean soils apparently can withstand the harsh summer conditions and maintain a certain level of metabolic activity and function. Vandegehuchte *et al*. (2015) reported that nematode communities from dry ecosystems are much better adapted to drought and can recover more quickly. From the higher trophic levels, normally susceptible to such changes, the genus *Eudorylaimus* seems to recover especially quickly from the summer drought.

As hypothesised, the dry climate in the eastern Mediterranean regions led to fungal dominated decomposition pathways, while the western Mediterranean was more bacterial dominated. This is further supported by the highest metabolic activity of the fungal channel in Jordan and Lebanon, which were comparable to other dry grasslands (Li *et al*., 2024). While bacteria depend on the water-filled pores between soil particles as habitat, fungi can grow in air-filed pores (Guan *et al*., 2021). Thus, fungi can cope better with low soil moisture, giving them an advantage in locations where drought re-occurs regularly (de Vries *et al*., 2018).

Considering the influence of winter rain, the metabolic footprints pointed towards an increased activity of the bacterial and fungal decomposition between autumn and spring. Generally, bacteria and bacterial-feeding nematodes are directly promoted by an increased soil water content (Neher, 2010; Guan *et al*., 2021). On the other hand, fungi and their nematode grazers may benefit from both winter rain and summer drought. During the vegetation season, AM fungi prosper due to the presence of host plants (Yang *et al*., 2010), whilst during plant dormancy in winter the saprotrophic fungi proliferate on plant residues from the last vegetation period (Rousk & Bååth, 2011).

The Spanish site, with nematode populations adapted to a mesic climate, responded differently to the severe drought occurring in the experimental period (Sebastià *et al*., 2024). Both food-web stability and metabolic activity were very low, resembling agricultural soil (Ewald *et al*., 2022). The degraded food web conditions, combined with the low unbalanced metabolic footprints, suggest a decline in the magnitude of ecosystem function and services

provided by nematode (Ferris, 2010). Thus, proposed climate change with more prolonged drought can be expected to lead to a permanent reduction in stability and activity of the soil micro-food web.

Effect of plant functional group on the nematode community

While only a few plant-feeding nematodes responded to the differences in plant functional groups, the direction of change was comparable: The presence of grasses, especially *L. perenne*, increased their numbers, supporting the hypotheses that the complex and large root systems of grasses are associated with plant feeders (Neher, 2010; Fleming *et al*., 2016). This is also in line with Viketoft *et al*. (2005), who reported that the presence of plant-feeding genera was greatest under grasses compared to legumes and forbs. However, the nematode genera linked to the change in plant functional group all belonged to the family Tylenchidae. They are ecologically responsive, opportunistic nematodes, which can react quickly to microhabitat variations caused by different plant cover (Bongers, 1990; Ou *et al*., 2005). Furthermore, Tylenchidae are more common in the upper root zone, where the changes in root traits are most pronounced (Ou *et al*., 2005).

Among microbial grazers, *Aphelenchus* also profited from the presence of grasses. These nematodes are plant-associated root and fungal feeders (Yeates *et al*., 1993), and can switch food sources depending on availability (Ruess *et al*., 2000; Zhang *et al*., 2020). This allows them to feed on either fungal hyphae or grass roots. Furthermore, in poor environments, grasses form symbioses with AM-fungi to increase the uptake of nutrients (Grayston *et al*., 2004). This was also shown by Harkes *et al*. (2021), where grasses increased the fungal community, subsequently leading to more fungal-feeding nematodes. The bacterial-feeding *Aprutides*, *Acrobeles* and *Kirjanovia* were also more common under grasses. Using different exudates, grasses create a specific bacterial community in their rhizosphere (Grayston *et al*., 1998), which might attract certain bacterial-feeding taxa (Viketoft *et al*., 2005).

In support of our hypothesis, *Bursilla* and *Rhabditis* were more common under legumes, which is in line with previous experiments (Viketoft *et al*., 2005). Legumes, often used as cover crops, are well known to enhance the bacterial channel through exudates, and in turn bacterial grazers such as nematodes (Zhao *et al*., 2014; Wang *et al*., 2024). However, these plants may influence bacterial feeders more directly. Horiuchi *et al*. (2005) stated that legumes actively attract bacterial-feeding nematodes through plant volatiles, released in order to bring rhizobia into the rhizosphere. Regarding the nematode indices, legumes are correlated with a lower CI, pointing towards a more bacterial dominated decomposition. Furthermore, the metabolic footprints associated with bacterial feeders (bacterial footprint, enrichment footprint) were also correlated to the presence of legumes, underlining the positive effect of these plants on the bacterial carbon and energy channel.

A positive effect of legumes on bacterial-feeding nematodes was especially visible in this experiment, while grasses fostered plant-feeding, but also some fungal- and bacterial-feeding genera. However, since grasses had an effect on multiple genera, belonging to different trophic levels, future research should investigate the interactions between grass forage plants and nematode communities in Mediterranean soils more closely.

Conclusion

This study, comparing western and eastern Mediterranean grasslands, is the first to examine nematode fauna under different forage plants in Jordan and Lebanon. Especially the local conditions shaped the nematode community, where reduced precipitation favoured plant- and fungal-feeding nematodes. A severe drought in Spain during the study period increased the occurrence of plant-feeding nematodes and decreased food web top-down control as well as the overall metabolic activity. This scenario is particularly relevant in the light of future climate change, which is expected to increase dry periods in the Mediterranean. The type of forage plant had minor effects on the structure and function of the nematode community during the 2 years of vegetation shift. For example, legumes enhanced some bacterial-feeding genera, while grasses provided a good environment for some plant parasites. However, the effect of different plant functional groups on nematodes was strongly modified by regional conditions, calling for locally adapted grassland management strategies.

Acknowledgements

We acknowledge the Partnership for Research and Innovation in the Mediterranean Area (PRIMA) for granting the SUSFORAGE project (PRIMA-Eranet-PCI2021-121971), and the associated national science foundations:

the Agencia Estatal de Investigación through the PCI 2021 call for PCI2021-121982 (M.T.S) and PCI2021-121971 (A.R.), MICIU/AEI /10.13039/501100011033 and EU NextGenerationEU/PRTR. We further acknowledge the Agence Nationale de la Recherche (ANR-21-PRIM-0014), the Slovenian Research Agency (Research programme P4-0072 for B.L. and P4-0133 for T.Ž.) as well as the German Aerospace Center (programme 01DH21020 for L.R.) for co-founding PRIMA project. We would also like to thank the many field and laboratory workers during the sampling campaign at the experimental fields in France, Slovenia, Spain, Lebanon and Jordan, as well as the Lebanese agricultural institute and the University of Balamand for providing the field and logistics.

References

Abu-Gharbieh, W., Karajeh, M. & Masoud, S. (2005). Current distribution of the root-knot nematodes (*Meloidogyne* species and races) in Jordan. *Jordan Journal of Agricultural Sciences* 1, 43-47.

Ali, E., Cramer, W., Carnicer, J., Georgopoulou, E., Hilmi, N.J.M. & Le Cozannet, G. (2022). Cross-Chapter Paper 4: Mediterranean Region. In: *Climate change 2022: Impacts, adaptation and vulnerability. Contribution of working group ii to the sixth assessment report of the intergovernmental panel on climate change*. Cambridge, UK, Cambridge University Press, pp. 2233-2272. DOI: 10.1017/9781009325844.021

Anderson, R.V. & Coleman, D.C. (1982). Nematode temperature responses: a niche dimension in populations of bacterial-feeding nematodes. *Journal of Nematology* 14, 69-76.

Askari, M.S. & Holden, N.M. (2014). Indices for quantitative evaluation of soil quality under grassland management. *Geoderma* 230-231, 131-142. DOI: 10.1016/j.geoderma.2014.04.019

Bardgett, R.D., Bullock, J.M., Lavorel, S., Manning, P., Shaffner, U., Ostle, N., Chomel, M., Durigan, G., Fry, E.L., Johnson, D. *et al.* (2021). Combatting global grassland degradation. *Nature Reviews Earth & Environment* 2, 720-735. DOI: 10.1038/s43017-021-00207-2

Baritz, R., Amelung, W., Antoni, V., Boardman, J., Horn, R., Prokop, G., Römbke, J., Romkens, P., Steinhoff-Knopp, B., Swartjes, F. *et al.* (2023). *Soil monitoring in Europe. Indicators and thresholds for soil quality assessments*. European Environment Agency Report 08/2022. DOI: 10.2800/956606

Bongers, T. (1987). *De nematoden van Nederland*. Utrecht, The Netherlands, Koninklijke Nederlandse Natuurhistorische Vereniging.

Bongers, T. (1990). The maturity index: an ecological measure of environmental disturbance based on nematode species composition. *Oecologia* 83, 14-19. DOI: 10.1007/BF00324627

Ciobanu, M., Geraert, E. & Popovici, I. (2003). The genera *Paratylenchus* Micoletzky, 1922 and *Gracilacus* Raski, 1962 in Romania (Nematoda: Tylenchulidae). *Nematologia Mediterranea* 31, 55-59.

Crotty, F.V., Blackshaw, R.P., Adl, S.M., Inger, R. & Murray, P.J. (2014). Divergence of feeding channels within the soil food web determined by ecosystem type. *Ecology and Evolution* 4, 1-13. DOI: 10.1002/ece3.905

de Vries, F.T., Griffiths, R.I., Bailey, M., Craig, H., Girlanda, M., Soon, H.G., Hallin, S., Kaisermann, A., Keith, A.M., Kretzschmar, M. *et al.* (2018). Soil bacterial networks are less stable under drought than fungal networks. *Nature Communications* 9, 3033. DOI: 10.1038/s41467-018-05516-7

Dietz, S., Herz, K., Gorzolka, K., Jandt, U., Bruelheide, H. & Scheel, D. (2020). Root exudate composition of grass and forb species in natural grasslands. *Scientific Reports* 10, 10691. DOI: 10.1038/s41598-019-54309-5

Du Preez, G., Daneel, M., De Goede, R., Du Toit, M.J., Ferris, H., Fourie, H., Geisen, S., Kakouli-Duarte, T., Korthals, G., Sánchez-Moreno, S. *et al.* (2022). Nematode-based indices in soil ecology: application, utility, and future directions. *Soil Biology and Biochemistry* 169, 108640. DOI: 10.1016/j.soilbio.2022.108640

Ehlers, B.K., Berg, M.P., Staudt, M., Holmstrup, M., Glasius, M., Ellers, J., Tomiolo, S., Madsen, R.B., Slotsbo, S. *et al.* (2020). Plant secondary compounds in soil and their role in belowground species interactions. *Trends in Ecology & Evolution* 35, 716-730. DOI: 10.1016/j.tree.2020.04.001

Erktan, A., Or, D. & Scheu, S. (2020). The physical structure of soil: Determinant and consequence of trophic interactions. *Soil Biology and Biochemistry* 148, 107876. DOI: 10.1016/j.soilbio.2020.107876

Ewald, M., Rusch, D., Rißmann, C., Trost, B., Theuerl, S. & Ruess, L. (2022). Effects of irrigation and fertilization practice on soil nematode communities in arable land. *Applied Soil Ecology* 177, 104546. DOI: 10.1016/j.apsoil.2022.104546

Ferris, H. (2010). Form and function: Metabolic footprints of nematodes in the soil food web. *European Journal of Soil Biology* 46, 97-104. DOI: 10.1016/j.ejsobi.2010.01.003

Ferris, H., Bongers, T. & de Goede, R.G.M. (2001). A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. *Applied Soil Ecology* 18, 13-29. DOI: 10.1016/S0929-1393(01)00152-4

Fleming, T.R., McGowan, N.E., Maule, A.G. & Fleming, C.C. (2016). Prevalence and diversity of plant parasitic nematodes in Northern Ireland grassland and cereals, and the influence of soils and rainfall. *Plant Pathology* 65, 1539-1550. DOI: 10.1111/ppa.12525

Franco, A.L.C., Gherardi, L.A., de Tomasel, C.M., Andriuzzi, W.S., Ankrom, K.E., Shaw, E.A., Bach, E.M., Sala, O.E. & Wall, D.H. (2019). Drought suppresses soil predators and

promotes root herbivores in mesic, but not in xeric grasslands. *Proceedings of the National Academy of Sciences of the United States of America* 116, 12883-12888. DOI: 10.1073/pnas.1900572116

Gardi, C., Tomaselli, M., Parisi, V., Petraglia, A. & Santini, C. (2002). Soil quality indicators and biodiversity in northern Italian permanent grasslands. *European Journal of Soil Biology* 38, 103-110. DOI: 10.1016/S1164-5563(01)01111-6

Grayston, S.J., Wang, S., Campbell, C.D. & Edwards, A.C. (1998). Selective influence of plant species on microbial diversity in the rhizosphere. *Soil Biology and Biochemistry* 30, 369-378. DOI: 10.1016/S0038-0717(97)00124-7

Grayston, S.J., Campbell, C.D., Bardgett, R.D., Mawdsley, J.L., Clegg, C.D., Ritz, K., Griffiths, B.S., Rodwell, J.S., Edwards, S.J., Davies, W.J. *et al.* (2004). Assessing shifts in microbial community structure across a range of grasslands of differing management intensity using CLPP, PLFA and community DNA techniques. *Applied Soil Ecology* 25, 63-84. DOI: 10.1016/S0929-1393(03)00098-2

Guan, P., Mahamood, M., Yang, Y. & Wu, D. (2021). Land conversion regulates the effects of long-term climate warming on soil micro-food web communities. *Agriculture, Ecosystems & Environment* 314, 107426. DOI: 10.1016/j.agee.2021.107426

Guo, X., Endler, A., Poll, C., Marhan, S. & Ruess, L. (2021). Independent effects of warming and altered precipitation pattern on nematode community structure in an arable field. *Agriculture, Ecosystems & Environment* 316, 107467. DOI: 10.1016/j.agee.2021.107467

Harkes, P., van Heumen, L.J.M., van den Elsen, S.J.J., Mooijman, P.J.W., Vervoort, M.T.W., Gort, G., Holterman, M.H.M., van Steenbrugge, J.J.M., Quist, C. & Helder, J. (2021). Characterization of the habitat- and season-independent increase in fungal biomass induced by the invasive giant goldenrod and its impact on the fungivorous nematode community. *Microorganisms* 9, 437. DOI: 10.3390/microorganisms9020437

Hashemi, K., Karegar, A. & Hamzehzarghani, H. (2020). Population dynamics of *Scutylenchus rugosus* under cultivation of maize and wheat and survival in dry fallow conditions. *Nematology* 22, 1079-1089. DOI: 10.1163/15685411-bja10012

Haugwitz, M.S., Michelsen, A. & Priemé, A. (2016). The legacy of climate change effects: previous drought increases short-term litter decomposition rates in a temperate mixed grass- and shrubland. *Plant and Soil* 408, 183-193. DOI: 10.1007/s11104-016-2913-2

Herz, K., Dietz, S., Gorzolka, K., Haider, S., Jandt, U., Scheel, D. & Bruelheide, H. (2018). Linking root exudates to functional plant traits. *PLoS ONE* 14, e0213965. DOI: 10.1371/journal.pone.0204128

Hole, F. (2007). Agricultural sustainability in the semi-arid Near East. *Climate of the Past* 3, 193-203. DOI: 10.5194/cp-3-193-2007

Horiuchi, J.-i., Prithiviraj, B., Bais, H.P., Kimball, B.A. & Vivanco, J.M. (2005). Soil nematodes mediate positive interactions between legume plants and rhizobium bacteria. *Planta* 222, 848-857. DOI: 10.1007/s00425-005-0025-y

Huang, X.-F., Chaparro, J.M., Reardon, K.F., Zhang, R., Shen, Q. & Vivanco, J.M. (2014). Rhizosphere interactions: root exudates, microbes, and microbial communities. *Botany* 92, 267-275. DOI: 10.1139/cjb-2013-0225

Ibrahim, S.K., Mama, M., Israel, A. & Ibrahim, L. (2017). The occurrence, distribution and control of potato cyst nematodes in Lebanon. *American Journal of Agricultural Science* 4, 51-57.

Inomoto, M.M. & Oliveira, C.M.G. (2008). Coffee-associated *Pratylenchus* spp. – ecology and interactions with plants. In: Souza, R.M. (Ed.). *Plant-parasitic nematodes of coffee*. Dordrecht, The Netherlands, Springer. DOI: 10.1007/978-1-4020-8720-2_4

Kanzaki, N., Banu, G. & Anes, K.M. (2023). Nematode problems in palms and their sustainable management. In: Khan, M.R. & Quintanilla, M. (Eds). *Nematode diseases of crops and their sustainable management*. New York, NY, USA, Academic Press, pp. 427-455. DOI: 10.1016/B978-0-323-91226-6.00017-1

Khanum, T.A., Mehmood, N. & Khatoon, N. (2021). Nematodes as biological indicators of soil quality in the agroecosystems. In: Bellé, C. & Kaspary, T.E. (Eds). *Nematodes - recent advances, management and new perspectives*. IntechOpen, pp. 1-12. DOI: 10.5772/intechopen.99745

Köppen, W. (1936). Das geographische System de Klimate. In: Köppen, W. & Geiger, G. (Eds). *Handbuch der klimatologie*. Bonn, Germany, Borntraeger, pp. 1-44.

Li, L., Luo, Z., Nian, L., Li, L., Niu, Y., Prasath, B.B., Haider, F.U., Zhang, Y., He, R. & Liu, J. (2024). Response of soil nematode community structure and metabolic footprint to nitrogen addition in alfalfa fields on the Loess Plateau. *Scientific Reports* 14, 17640. DOI: 10.1038/s41598-024-68393-9

Lionello, P., Malanotte-Rizzoli, P., Boscolo, R., Alpert, P., Artale, V., Li, L., Luterbacher, J., May, W., Trigo, R., Tsimplis, M. *et al.* (2006). The Mediterranean climate: an overview of the main characteristics and issues. In: Lionello, P., Malanotte-Rizzoli, P. & Boscolo, R. (Eds). *Developments in Earth and Environmental Sciences, vol. 4*. New York, NY, USA, Elsevier, pp. 1-26. DOI: 10.1016/S1571-9197(06)80003-0

Lu, Q., Liu, T., Wang, N., Dou, Z., Wang, K. & Zuo, Y. (2020). A review of soil nematodes as biological indicators for the assessment of soil health. *Frontiers of Agricultural Science and Engineering* 7, 275-281. DOI: 10.15302/J-FASE-2020327

Maudet, S., Brusse, T., Poss, B., Caro, G. & Marrec, R. (2025). Estimating landscape intensity through farming practices: an integrative and flexible approach to modelling farming intensity from field to landscape. *Ecological Modelling* 501, 110975. DOI: 10.1016/j.ecolmodel.2024.110975

McSorley, R. (2003). Adaptions of nematodes to environmental extremes. *Florida Entomologist* 86, 138-142. DOI: 10.1653/0015-4040(2003)086[0138:AONTEE]2.0.CO;2

Melakeberhan, H., Bonito, G. & Kravchenko, A.N. (2021). Application of nematode community analyses-based models towards identifying sustainable soil health management outcomes: a review of the concepts. *Soil Systems* 5, 32. DOI: 10.3390/soilsystems5020032

Neher, D.A. (2010). Ecology of plant and free-living nematodes in natural and agricultural soil. *Annual Review of Phytopathology* 48, 371-394. DOI: 10.1146/annurev-phyto-073009-114439

Okada, H. & Harada, H. (2007). Effects of tillage and fertilizer on nematode communities in a Japanese soybean field. *Applied Soil Ecology* 35, 582-598. DOI: 10.1016/j.apsoil.2006.09.008

O'Mara, F.P. (2012). The role of grasslands in food security and climate change. *Annals of Botany* 110, 1263-1270. DOI: 10.1093/aob/mcs209

Ou, W., Liang, W., Li, Q. & Wen, D. (2005). Vertical distribution of soil nematodes under different land use types in an aquic brown soil. *Pedobiologia* 49, 139-148. DOI: 10.1016/j.pedobi.2004.10.001

Paudel, S., Cobb, A.B., Boughton, E.H., Spiegal, S., Boughton, R.K., Silveira, M.L., Swain, H.M., Reuter, R., Goodman, L.E. & Steiner, J.L. (2021). A framework for sustainable management of ecosystem services and disservices in perennial grassland agroecosystems. *Ecosphere* 12, e03837. DOI: 10.1002/ecs2.3837

Peel, M.C., Finlayson, B.L. & McMahon, T.A. (2007). Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences* 11, 1633-1644. DOI: 10.5194/hess-11-1633-2007

Porqueddu, C., Ates, S., Louhaichi, M., Kyriazopoulos, A.P., Moreno, G., del Pozo, A., Ovalle, C., Ewing, M.A. & Nichols, P.G.H. (2016). Grasslands in 'Old World' and 'New World' Mediterranean-climate zones: past trends, current status and future research priorities. *Grass Forage Science* 71, 1-35. DOI: 10.1111/gfs.12212

Richter, A., Ewald, M., Hemmerling, C., Schöning, I., Bauhus, J., Schall, P. & Ruess, L. (2023). Effects of management intensity, soil properties and region on the nematode communities in temperate forests in Germany. *Forest Ecology and Management* 529, 120675. DOI: 10.1016/j.foreco.2022.120675

Rousk, J. & Bååth, E. (2011). Growth of saprotrophic fungi and bacteria in soil. *FEMS Microbiology Ecology* 78, 17-30. DOI: 10.1111/j.1574-6941.2011.01106.x

Ruess, L. (1995). Nematode fauna in spruce forest soils: a qualitative/ quantitative comparison. *Nematologica* 41, 106-124. DOI: 10.1163/003925995X00080

Ruess, L. (2024). Nematodes and their trophic interactions in the soil microbiome. In: Dunfield, K.E. (Ed.). *Understanding and utilizing soil microbiomes for a more sustainable agriculture*. Cambridge, UK, Burleight & Dodds Science Publishing, pp. 1-29.

Ruess, L., Michelsen, A., Schmidt, I.K. & Jonasson, S. (1999). Simulated climate change affecting microorganisms, nematode density and biodiversity in subarctic soils. *Plant and Soil* 212, 63-73. DOI: 10.1023/A:1004567816355

Ruess, L., Zapata, E.J.G. & Dighton, J. (2000). Food preferences of a fungal-feeding *Aphelenchoides* species. *Nematology* 2, 223-230. DOI: 10.1163/156854100508962

Sebastià, M.-T., Banagar, F., Palero, N., Ibáñez, M. & Plaixats, J. (2024). Quality production of sainfoin swards challenged by global change in mountain areas in the western Mediterranean. *Agronomy* 14, 6. DOI: 10.3390/agronomy14010006

Sohlenius, B. (1973). Structure and dynamics of populations of *Rhabditis* (Nematoda: Rhabditidae) from forest soil. *Pedobiologia* 13, 368-375. DOI: 10.1016/s0031-4056(23)02123-6

Steinauer, K., Heinen, R., Hannula, S.E., De Long, J.R., Huberty, M., Jongen, R., Wang, M. & Bezemer, T.M. (2020). Above-belowground linkages of functionally dissimilar plant communities and soil properties in a grassland experiment. *Ecosphere* 11, e03246. DOI: 10.1002/ecs2.3246

ter Braak, C.J.F. & Šmilauer, P. (2012). *Canoco reference manual and user's guide: software for ordination, version 5.0*. Ithaca, NY, USA, Microcomputer Power.

Tuel, A. & Eltahir, E.A.B. (2020). Why is the Mediterranean a climate change hot spot? *Journal of Climate* 33, 5829-5843. DOI: 10.1175/JCLI-D-19-0910.1

Vandegehuchte, M.L., Sylvain, Z.A., Reichmann, L.G., de Tomasel, C.M., Nielsen, U.N., Wall, D.H. & Sala, O.E. (2015). Responses of a desert nematode community to changes in water availability. *Ecosphere* 6, 1-15. DOI: 10.1890/ES14-00319.1

Viketoft, M., Palmborg, C., Sohlenius, B., Huss-Danell, K. & Bengtsson, J. (2005). Plant species effects on soil nematode communities in experimental grasslands. *Applied Soil Ecology* 30, 90-103. DOI: 10.1016/j.apsoil.2005.02.007

Viketoft, M., Bengtsson, J., Sohlenius, B., Berg, M.P., Petchey, O., Palmborg, C. & Huss-Danell, K. (2009). Long-term effects of plant diversity and composition on soil nematode communities in model grasslands. *Ecology* 90, 90-99. DOI: 10.1890/08-0382.1

Wang, J., Zhao, J., Yang, R., Liu, X. & Zhang, X. (2024). Interplanting leguminous shrubs boosts the trophic interactions of soil micro-food web in a karst grassland. *Soil Biology and Biochemistry* 188, 109224. DOI: 10.1016/j.soilbio.2023.109224

Wilson, M.J. & Kakouli-Duarte, T. (Eds). (2009). *Nematodes as environmental indicators*. Wallingford, UK, CAB International. DOI: 10.1079/9781845933852.0000

Womersley, C. (1987). A reevaluation of strategies employed by nematode anhydrobiotes in relation to their natural environment. In: Veech, J.A. & Dickson, D.W. (Eds). *Vistas on nematology*. Hyattsville, MD, USA, Society of Nematologists, pp. 165-173.

Xiong, D., Wie, C., Wang, X., Lü, X., Fang, S., Li, Y., Wang, X., Liang, W., Han, X., Bezemer, T.M. & Li, X. (2021). Spatial patterns and ecological drivers of soil nematode β-diversity in natural grasslands vary among vegetation types and trophic position. *Journal of Animal Ecology* 90, 1367-1378. DOI: 10.1111/1365-2656.13461

Yang, C., Hamel, C., Schellenberg, M.P., Perez, J.C. & Berbara, R.L. (2010). Diversity and functionality of arbuscular mycorrhizal fungi in three plant communities in semiarid Grasslands National Park, Canada. *Microbial Ecology* 59, 724-733. DOI: 10.1007/s00248-009-9629-2

Yeates, G.W., Bongers, T., de Goede, R.G., Freckman, D.W. & Georgieva, S.S. (1993). Feeding habits in soil nematode families and genera-an outline for soil ecologists. *Journal of Nematology* 25, 315-331.

Zhang, Y., Li, S., Li, H., Wang, R., Zhang, K.-Q. & Xu, J. (2020). Fungi-nematode interactions: diversity, ecology, and biocontrol prospects in agriculture. *Journal of Fungi* 6, 206. DOI: 10.3390/jof6040206

Zhao, J., Wan, S., Zhang, C., Liu, Z. & Zhou, L. *et al.* (2014). Contributions of understory and/or overstory vegetations to soil microbial PLFA and nematode diversities in Eucalyptus monocultures. *PLoS ONE* 9, e85513. DOI: 10.1371/journal.pone.0085513

Zheng, J., Peng, D., Chen, L., Liu, H., Chen, F., Xu, M., Ju, S., Ruan, L. & Sun, M. (2016). The *Ditylenchus destructor* genome provides new insights into the evolution of plant parasitic nematodes. *Proceedings of the Royal Society B: Biological Sciences* 283, 1835. DOI: 10.1098/rspb.2016.0942

Zhou, J., Wu, J., Huang, J., Sheng, X., Dou, X. & Lu, M. (2022). A synthesis of soil nematode responses to global change factors. *Soil Biology and Biochemistry* 165, 108538. DOI: 10.1016/j.soilbio.2021.108538

Supplementary Table S1. Soil properties and climate data during the experimental period of the five investigated Mediterranean regions.

	France	Slovenia	Spain	Jordan	Lebanon
Soil properties					
Sand (%)	51.33	30.355	41.073	n.a.	17.4
Silt (%)	17.895	36.22	25.323	n.a.	23.6
Clay (%)	30.775	33.425	33.603	n.a.	59
Texture	Sandy clay loam	Clay loam	Loam	n.a.	Clay
C org (%)	1.85	4.95	1.32	0.57	1.2
Organic matter (%)	3.19	8.54	2.27	0.98	2.07
N (%)	0.23	0.34	0.16	0.09	0.1
P (mg (kg DW)$^{-1}$)	48.78	7.71	9.45	38.16	49.43
pH	5.98	7.69	8.2	7.78	8.15
Water content (%)	21.25	22.25	6.92	8.81	8.57
Climate data					
Mean annual temperature (°C)	10.1	12.5	14.1	18.9	19.1
Mean annual precipitation (mm)	975	1178	530	417	602

n.a. = not available.

Supplementary Table S2. Density of the nematode genera and overall density in individuals (g DW)$^{-1}$ (±s.d.) in France of both sampling dates.

	Autumn			Spring		
	Grasses	Legumes	Forbs	Grasses	Legumes	Forbs
Achromadora	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Acrobeles	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Acrobeloides	1.1 ± 0.6	0.9 ± 0.5	0.8 ± 0.1	3.3 ± 1.3	2.4 ± 0.6	1.9 ± 0.3
Allodorylaimus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Anaplectus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.2
Aphelenchoides	0.2 ± 0.1	0.3 ± 0.3	0.2 ± 0.2	0.3 ± 0.3	1.8 ± 2.1	0.4 ± 0.5
Aphelenchus	1.2 ± 0.4	1 ± 0.5	0.8 ± 0.7	3 ± 1.1	1.8 ± 1.1	2.1 ± 1.3
Aporcelaimus	0.0 ± 0.0	0.0 ± 0.0	0 ± 0.1	0.1 ± 0.1	0.1 ± 0.2	0.0 ± 0.0
Basiria	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.2 ± 0.2	0.1 ± 0.1	0.0 ± 0.0
Boleodorus	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.3	0.5 ± 0.1	0.5 ± 0.2	0.5 ± 0.1
Bursilla	0.0 ± 0.0	0 ± 0.1	0 ± 0.1	0.2 ± 0.1	0.4 ± 0.4	0.0 ± 0.0
Cephalobus	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.3	0.1 ± 0.1	0.2 ± 0.2
Cervidellus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0 ± 0.1
Chiloplacus	0.0 ± 0.0	0.0 ± 0.0	0 ± 0.1	0.4 ± 0.1	0.1 ± 0.1	0.3 ± 0.3
Clarkus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.1 ± 0.1	0 ± 0.1
Coslenchus	0.1 ± 0.1	0.0 ± 0.0	0 ± 0.1	0.2 ± 0.3	0.2 ± 0.2	0.3 ± 0.1
Epidorylaimus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.2	0.0 ± 0.0	0.1 ± 0.1
Eucephalobus	0.2 ± 0.1	0.3 ± 0.3	0.2 ± 0.1	0.4 ± 0.3	0.6 ± 0.5	0.9 ± 0.3
Eudorylaimus	0.1 ± 0.1	0.1 ± 0.1	0.0 ± 0.0	0.8 ± 0.7	0.5 ± 0.2	0.3 ± 0.3
Eumonhystera	0.1 ± 0.1	0 ± 0.1	0.0 ± 0.0	0.6 ± 0.5	0.4 ± 0.5	0.4 ± 0.2
Filenchus	0.1 ± 0.2	0.3 ± 0.1	0.3 ± 0.3	0.9 ± 0.4	0.8 ± 0.7	0.5 ± 0.3
Helicotylenchus	0.6 ± 0.5	0.3 ± 0.2	1.3 ± 0.7	2.8 ± 2.1	1.7 ± 0.5	3.2 ± 3.3
Heterocephalobus	0.9 ± 1	0.2 ± 0.1	0.5 ± 0.3	0.5 ± 0.2	0.9 ± 0.5	0.4 ± 0.4
Lelenchus	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.2	*0.3 ± 0.1a*	*0.1 ± 0.1b*	*0.1 ± 0.1b*
Malenchus	0 ± 0.1	0.1 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Merlinius	0.0 ± 0.0	0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Mesodorylaimus	0.1 ± 0.1	0 ± 0	0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.2
Mesorhabditis	*0.7 ± 0.1c*	*4 ± 3a*	*2 ± 0.8b*	0.6 ± 0.4	0.3 ± 0.3	0.3 ± 0.3
Metateratocephalobus	0.0 ± 0.0	0.0 ± 0.0	0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Monhystera	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.2	0.2 ± 0.2	0.1 ± 0.1
Mononchoides	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.3	0.1 ± 0.2
Mylonchulus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Nagelus	0.0 ± 0.0	0 ± 0.1	0.0 ± 0.0	0.3 ± 0.3	0.1 ± 0.1	0.0 ± 0.0
Panagrellus	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	*0.2 ± 0.3ab*	*0.7 ± 0.2a*	*0.1 ± 0.2b*
Panagrolaimus	1.3 ± 1.3	0.5 ± 0.4	0.8 ± 0.5	5.5 ± 6	5.2 ± 3.1	2.9 ± 1.7
Paraphelenchus	*0.6 ± 0.7a*	*0 ± 0.1b*	*0.1 ± 0.1ab*	0.2 ± 0.3	0.4 ± 0.5	0.2 ± 0.2
Paratylenchus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.3	0.2 ± 0.2	0.1 ± 0.2
Pellioditis	0.3 ± 0.2	0.9 ± 0.3	0.6 ± 0.1	5.3 ± 6.6	2.7 ± 2.2	0.6 ± 0.4
Plectus	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.2	1.1 ± 0.6	0.7 ± 0.8	0.5 ± 0.3
Pratylenchoides	0 ± 0.1	0.0 ± 0.0	0.1 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0.1 ± 0.1
Pratylenchus	0 ± 0.1	0.1 ± 0.2	0.1 ± 0.1	0.1 ± 0.2	0.0 ± 0.0	0.2 ± 0.2
Prionchulus	0.1 ± 0.1	0.0 ± 0.0	0 ± 0.1	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Prismatolaimus	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.2	0.1 ± 0.2
Pungentus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.5	0.5 ± 0.2	0.3 ± 0.2
Rhabditis	0.7 ± 0.6	1.3 ± 0.4	1.3 ± 0.8	12.3 ± 10.1	11.5 ± 10.4	2.4 ± 1.2
Scutylenchus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.6	0.3 ± 0.4	0.1 ± 0.1
Thonus	0.0 ± 0.0	0 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	0.1 ± 0.1	0 ± 0.1
Tylenchorhynchus	0 ± 0.1	0 ± 0.1	0.2 ± 0.2	0.1 ± 0.1	0.2 ± 0.4	0 ± 0.1
Population density	9.5 ± 3.9	12 ± 4.3	10.7 ± 1.2	*43.6 ± 15.8a*	*37 ± 8.1ab*	*20.5 ± 5.6b*

Significant differences between plant functional groups in autumn and spring are indicated by different letters and marked in italics (Dunn-Bonferroni, $P < 0.05$).

Supplementary Table S3. Density of the nematode genera in individuals (g DW)$^{-1}$ (± s.d.) in Slovenia at both sampling dates.

	Autumn			Spring		
	Grasses	Legumes	Forbs	Grasses	Legumes	Forbs
Acrobeles	0.8 ± 0.6	1 ± 0.8	0.6 ± 0.4	*0.3 ± 0.2a*	*0.1 ± 0.1ab*	*0.0 ± 0.0 b*
Acrobeloides	2.3 ± 1.7	2.9 ± 2.4	2.3 ± 0.9	0.8 ± 0.2	0.8 ± 0.2	1 ± 0.4
Allodorylaimus	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.2	0.1 ± 0.1	0.2 ± 0.2
Anaplectus	0.1 ± 0.1	0.2 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0 ± 0.1
Aphelenchoides	1.8 ± 1.2	2.8 ± 1.5	1.5 ± 0.6	1 ± 0.8	1 ± 0.5	0.8 ± 0.3
Aphelenchus	1.4 ± 0.4	2.5 ± 0.8	2.5 ± 0.9	0.6 ± 0.5	0.6 ± 0.3	1.2 ± 0.2
Aporcelaimus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.1
Basiria	0.3 ± 0.3	0.4 ± 0.1	0.1 ± 0.2	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.2
Boleodorus	0.3 ± 0.3	0.4 ± 0.3	0.3 ± 0.4	0.2 ± 0	0.3 ± 0	0.3 ± 0.3
Bursilla	0.1 ± 0.1	0.0 ± 0.0	0 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	0 ± 0.1
Cephalobus	0.3 ± 0.3	0.3 ± 0.3	0.3 ± 0.1	0.2 ± 0.2	0.2 ± 0.1	0.1 ± 0.2
Cervidellus	0.1 ± 0.1	0.2 ± 0.2	0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Chiloplacus	0.1 ± 0.2	0.3 ± 0.3	0.2 ± 0.2	0.4 ± 0.2	0.1 ± 0.1	0.3 ± 0.2
Clarkus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0 ± 0.1	0.0 ± 0.0	0.1 ± 0.2
Coslenchus	0.1 ± 0.1	0.2 ± 0.2	0.1 ± 0.1	0 ± 0.1	0.1 ± 0.2	0.2 ± 0.3
Ditylenchus	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.2	0 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Dorydorella	0.2 ± 0.3	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.2	0.1 ± 0.2	0.2 ± 0.1
Epidorylaimus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0 ± 0.1	0.1 ± 0.3
Eucephalobus	1 ± 0.8	1.2 ± 0.4	0.7 ± 0.3	0.8 ± 0.9	0.8 ± 0.4	0.9 ± 0.4
Eudorylaimus	0.4 ± 0.5	0.4 ± 0.4	0.2 ± 0	0.9 ± 0.2	0.6 ± 0.2	0.7 ± 0.3
Eumonhystera	0.3 ± 0.3	0.7 ± 0.3	0.8 ± 0.6	0.3 ± 0.3	0.3 ± 0.2	0.3 ± 0.3
Filenchus	0.9 ± 0.8	1.1 ± 0.6	0.7 ± 0.2	1 ± 0.5	0.8 ± 0.3	0.4 ± 0.4
Helicotylenchus	1.6 ± 1.4	0.3 ± 0.3	0.4 ± 0.3	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Heterocephalobus	0.9 ± 0.5	0.6 ± 0.4	1.1 ± 1	1.1 ± 1	1 ± 0.3	0.6 ± 0.3
Lelenchus	0.4 ± 0.5	0.6 ± 0.6	0.3 ± 0.1	0.2 ± 0.1	0.0 ± 0.0	0.1 ± 0.1
Malenchus	0.2 ± 0.3	0.4 ± 0.4	0.4 ± 0.4	*0.1 ± 0.1b*	*0.5 ± 0.2a*	*0.1 ± 0.1b*
Merlinius	0.9 ± 0.2	0.2 ± 0.3	0.3 ± 0.6	0.1 ± 0.1	0.1 ± 0.1	0 ± 0.1
Mesodorylaimus	0.1 ± 0.3	0.2 ± 0.4	0.1 ± 0.1	0 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Mesorhabditis	1.4 ± 0.6	0.6 ± 0.4	1.1 ± 0.7	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Metateratocephalobus	0.4 ± 0.2	0.2 ± 0.3	0.4 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.0 ± 0.0
Monhystera	0.0 ± 0.0	0.1 ± 0.1	0 ± 0.1	0.4 ± 0.4	0.1 ± 0.2	0.1 ± 0.1
Mylonchulus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0 ± 0.1
Panagrellus	0.1 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.4	0.3 ± 0.1	0.6 ± 0.4
Panagrobelus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2	0 ± 0.1	0 ± 0.1
Panagrolaimus	0.6 ± 1.1	0.4 ± 0.2	0.4 ± 0.4	1 ± 0.6	0.4 ± 0.4	0.8 ± 0.6
Paraphelenchus	0.1 ± 0.2	0.1 ± 0.1	0.3 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Paratylenchus	0.1 ± 0.3	0.0 ± 0.0	0.1 ± 0.1	0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Pellioditis	0.3 ± 0.4	0.2 ± 0.2	0.1 ± 0.1	0.3 ± 0.4	0.3 ± 0.2	0.5 ± 0.3
Plectus	0.9 ± 0.5	1.4 ± 0.5	0.9 ± 1	1.1 ± 1	0.4 ± 0.3	0.4 ± 0.2
Pratylenchoides	0.2 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.1
Pratylenchus	0.7 ± 0.4	0.2 ± 0.1	0.4 ± 0.3	0.2 ± 0	0.2 ± 0.2	0.2 ± 0.1
Prionchulus	*0 ± 0.1ab*	*0.2 ± 0.2a*	*0.0 ± 0.0 b*	0.0 ± 0.0	0 ± 0.1	0.1 ± 0.1
Prismatolaimus	0.9 ± 0.4	0.5 ± 0.8	0.6 ± 0.6	0.4 ± 0.5	0.1 ± 0.1	0 ± 0.1
Pristionchus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2	0.0 ± 0.0	0.2 ± 0.2
Rhabditis	0.7 ± 0.6	0.3 ± 0.4	0.3 ± 0.2	0.7 ± 0.5	0.2 ± 0.1	1.1 ± 0.6
Rotylenchulus	0.5 ± 0.7	0.4 ± 0.5	0.4 ± 0.5	0.4 ± 0.3	0.4 ± 0.3	0.2 ± 0.2
Thonus	0.1 ± 0.1	0.4 ± 0.1	0.3 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.2
Wilsonema	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0.3 ± 0.2	0.2 ± 0.2	0.3 ± 0.2
Population density	21.7 ± 8.8	22.2 ± 5.4	18.7 ± 4.9	15 ± 6.2	11.3 ± 1.9	13.5 ± 4.7

Significant differences between plant functional groups in autumn and spring are indicated by different letters and marked in italics (Dunn-Bonferroni, $P < 0.05$).

Supplementary Table S4. Density of the nematode genera in individuals (g DW)$^{-1}$ (± s.d.) in Spain at both sampling dates.

	Autumn			Spring		
	Grasses	Legumes	Forbs	Grasses	Legumes	Forbs
Acrobeles	0.0 ± 0.0	0 ± 0.1	0.0 ± 0.0	0.1 ± 0.3	0.1 ± 0.2	0.0 ± 0.0
Acrobeloides	0.5 ± 0.3	1 ± 1.2	0.7 ± 0.2	0.9 ± 0.7	1.1 ± 0.4	1.5 ± 0.6
Amplimerlinius	0.1 ± 0	0.1 ± 0.1	0.1 ± 0.1	0.4 ± 0.6	0.2 ± 0.2	0.1 ± 0.1
Aphelenchoides	1 ± 0.4	1.2 ± 0.6	1.2 ± 0.4	1.3 ± 0.9	1.6 ± 0.7	1.1 ± 0.3
Aphelenchus	0.2 ± 0.1	0.4 ± 0.1	0.2 ± 0.2	0.5 ± 0.6	0.7 ± 0.6	0.3 ± 0.2
Basiria	0.3 ± 0.3	0.2 ± 0.1	0.1 ± 0.1	0.3 ± 0.3	0.2 ± 0.1	0.1 ± 0.1
Bitylenchus	0.4 ± 0.3	0.5 ± 0.1	0.3 ± 0.1	0.6 ± 0.6	0.6 ± 0.5	0.3 ± 0.3
Boleodorus	0.3 ± 0.2	0.3 ± 0.1	0.1 ± 0.1	0.7 ± 0.7	0.6 ± 0.4	0.3 ± 0.2
Cephalobus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0 ± 0.1	0.1 ± 0.1	0.2 ± 0.1
Chiloplacus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.2 ± 0.1	0.2 ± 0.2
Coslenchus	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Ditylenchus	0.2 ± 0.3	0.1 ± 0.1	0.1 ± 0.1	1 ± 0.5	0.8 ± 0.7	0.8 ± 0.5
Dolichorhynchus	0.2 ± 0.2	0.3 ± 0.3	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Dorydorella	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.2	0.0 ± 0.0	0.0 ± 0.0
Eucephalobus	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	*0.0 ± 0.0 b*	*0.3 ± 0.2a*	*0.1 ± 0.1b*
Eudorylaimus	0.1 ± 0.2	0.2 ± 0.4	0.1 ± 0.2	0.3 ± 0.3	0.1 ± 0.2	0.3 ± 0.2
Eumonhystera	0.0 ± 0.0	0.1 ± 0.2	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0 ± 0.1
Filenchus	0.4 ± 0.2	0.4 ± 0.1	0.3 ± 0.2	0.5 ± 0.4	0.2 ± 0.2	0.3 ± 0.2
Helicotylenchus	0.2 ± 0.1	0.2 ± 0	0.3 ± 0.1	0.0 ± 0.0	0.2 ± 0.2	0 ± 0.1
Heterocephalobus	0.0 ± 0.0	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.2	0 ± 0.1	0.0 ± 0.0
Lelenchus	0 ± 0.1	0.0 ± 0.0	0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Malenchus	0.1 ± 0.1	0.2 ± 0.2	0.1 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Meloidogyne	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0 ± 0.1	0.0 ± 0.0
Merlinius	0.2 ± 0.1	0.4 ± 0.5	0.1 ± 0.1	0.2 ± 0.2	0.3 ± 0.4	0.1 ± 0.1
Mesodorylaimus	0.0 ± 0.0	0.1 ± 0.1	0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Metateratocephalobus	0 ± 0.1	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	0.1 ± 0.1	0.0 ± 0.0
Nagelus	0.2 ± 0.2	0.1 ± 0.2	0.2 ± 0.2	0.6 ± 0.3	0.7 ± 0.4	0.9 ± 0.9
Panagrellus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0 ± 0.1	0.0 ± 0.0
Panagrolaimus	0.0 ± 0.0	0 ± 0.1	0.0 ± 0.0	0.2 ± 0.3	0.1 ± 0.3	0.2 ± 0.1
Paraphelenchus	0.0 ± 0.0	0.2 ± 0.3	0.1 ± 0.2	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0
Paratylenchus	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.4 ± 0.6	0.1 ± 0.1	0.2 ± 0.3
Pratylenchoides	0.4 ± 0.6	0.2 ± 0.3	0.2 ± 0.1	0.6 ± 0.4	0.3 ± 0.1	0.5 ± 0.4
Pratylenchus	1.2 ± 0.8	1.4 ± 1	0.9 ± 0.5	1.6 ± 1.3	2.1 ± 1.5	2.1 ± 1.6
Prismatolaimus	0.1 ± 0.2	0.2 ± 0.3	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Psilenchus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0
Rotylenchus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0 ± 0.1	0 ± 0
Scutylenchus	0.4 ± 0.3	0.5 ± 0.4	0.3 ± 0.2	0.9 ± 0.8	0.9 ± 0.7	0.8 ± 0.4
Thonus	0.1 ± 0.1	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Tylenchorhynchus	0.3 ± 0.3	0.5 ± 0.5	0.1 ± 0.1	0.7 ± 1.1	0.5 ± 0.5	0.5 ± 0.1
Wilsonema	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0 ± 0.1	0.0 ± 0.0
Population density	12.5 ± 5.9	15.2 ± 5.8	10.1 ± 4.5	12.5 ± 7	12.2 ± 4.8	11.1 ± 5.1

Significant differences between plant functional groups in autumn and spring are indicated by different letters and marked in italics (Dunn-Bonferroni, $P < 0.05$).

Supplementary Table S5. Density of the nematode genera in individuals (g DW)$^{-1}$ ($\pm$ s.d.) in Jordan at both sampling dates.

	Autumn			Spring		
	Grasses	Legumes	Forbs	Grasses	Legumes	Forbs
Acrobeles	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.8 ± 0.9	0.1 ± 0.2	0.2 ± 0.3
Acrobeloides	2.9 ± 0.8	2.1 ± 0.7	1.9 ± 1.3	6.9 ± 5	5.6 ± 4.2	6.7 ± 2.5
Alaimus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.2	0.0 ± 0.0	0.0 ± 0.0
Amplimerlinius	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4	0.1 ± 0.2
Aphelenchoides	0.3 ± 0.2	1.4 ± 1.5	0.6 ± 0.2	2.2 ± 1.9	1.5 ± 1.3	1.2 ± 0.3
Aphelenchus	1.3 ± 0.8	0.9 ± 0.4	0.6 ± 0.2	2.2 ± 2.3	2.2 ± 1.8	1.6 ± 1.7
Aporcelaimellus	*0.2 ± 0.2a*	*0.0 ± 0.0 b*	*0.0 ± 0.0 b*	0.1 ± 0.1	0.1 ± 0.1	0 ± 0.1
Aprutides	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Basiria	0.3 ± 0.4	0.4 ± 0.3	0.2 ± 0.3	0.2 ± 0.3	0.4 ± 0.4	0.1 ± 0.3
Boleodorus	0.4 ± 0.3	0.4 ± 0.4	0.3 ± 0.5	0 ± 0.1	0.1 ± 0.1	0.2 ± 0.3
Cephalobus	0.3 ± 0.2	0.3 ± 0.2	0.2 ± 0.2	1 ± 0.5	0.8 ± 0.6	0.6 ± 0.4
Cervidellus	0.3 ± 0.2	0.3 ± 0.2	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	0.1 ± 0.1
Chiloplacus	0.4 ± 0.3	0.7 ± 0.5	0.3 ± 0.2	0.6 ± 0.7	0.9 ± 0.3	0.7 ± 0.3
Coslenchus	0.3 ± 0.4	0.1 ± 0.2	0.2 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Cribronema	0.1 ± 0.1	0.2 ± 0.2	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0
Ditylenchus	1.4 ± 0.7	1.1 ± 0.4	1.6 ± 0.3	3.6 ± 2.3	3.5 ± 3.5	2.8 ± 0.9
Dorylaimellus	0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Drilocephalobus	*0.0 ± 0.0 b*	*0.1 ± 0.1a*	*0.0 ± 0.0 b*	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Ecumenicus	0.1 ± 0.1	0 ± 0.1	0.0 ± 0.0	0.3 ± 0.3	0.2 ± 0.3	0.1 ± 0.2
Eucephalobus	0.3 ± 0.4	0.1 ± 0.1	0.3 ± 0.1	0.2 ± 0.3	0.4 ± 0.3	0.4 ± 0.6
Eudorylaimus	0.2 ± 0.2	0.2 ± 0.3	0.1 ± 0.1	1.1 ± 0.4	1 ± 0.8	0.6 ± 0.4
Eumonhystera	0.2 ± 0.2	0.2 ± 0.2	0.1 ± 0.1	1.1 ± 1.1	1 ± 1.3	0.6 ± 0.7
Filenchus	0.6 ± 0.5	0.4 ± 0.2	0.9 ± 0.5	0.9 ± 0.3	1.4 ± 0.7	1.1 ± 0.3
Geocenamus	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	0.2 ± 0.3	0.2 ± 0.3	0.0 ± 0.0
Helicotylenchus	0.1 ± 0.1	0 ± 0.1	0 ± 0.1	0.4 ± 0.5	0.4 ± 0.6	0.0 ± 0.0
Heterocephalobus	0 ± 0.1	0.2 ± 0.2	0.1 ± 0.2	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.2
Kirjanovia	0.0 ± 0.0	0.2 ± 0.4	0.0 ± 0.0	0.5 ± 1	0.1 ± 0.1	0.1 ± 0.2
Lelenchus	0.2 ± 0.1	0.4 ± 0.4	0.4 ± 0.2	0.4 ± 0.7	0.2 ± 0.3	0.6 ± 0.2
Malenchus	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0	0.4 ± 0.4	0.2 ± 0.2	0.6 ± 0.2
Mesodorylaimus	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Mesorhabditis	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0 ± 0.1	0 ± 0.1	0.1 ± 0.2
Monhystera	0 ± 0.1	0 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Nygolaimus	0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Panagrellus	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Panagrolaimus	0.3 ± 0.3	0.4 ± 0.4	0.4 ± 0.3	0.4 ± 0.7	0.8 ± 0.7	1.4 ± 1
Paraphelenchus	0 ± 0.1	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Paratrophurus	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.1 ± 0.2	0.1 ± 0.1	0.1 ± 0.2
Paratylenchus	*0 ± 0.1b*	*0.1 ± 0.2ab*	*1.4 ± 2.2a*	1.9 ± 2.2	13.9 ± 16.9	0.1 ± 0.1
Plectus	0.1 ± 0.1	0.1 ± 0.1	0.3 ± 0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Pratylenchus	*0.1 ± 0.1b*	*0.1 ± 0.2b*	*0.7 ± 0.5a*	*0.1 ± 0.1ab*	*0.3 ± 0.2a*	*0.0 ± 0.0 b*
Prismatolaimus	0.0 ± 0.0	0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Psilenchus	0.0 ± 0.0	0 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Pungentus	0.0 ± 0.0	0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Thonus	0.1 ± 0.1	0.1 ± 0.1	0 ± 0.1	0.2 ± 0.1	0.0 ± 0.0	0 ± 0.1
Tylencholaimus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
Tylenchorhynchus	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2	0.9 ± 0.5	1 ± 0.6	0.3 ± 0.3
Tylenchus	0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.3	0.0 ± 0.0	0 ± 0.1
Wilsonema	0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	1.2 ± 0.9	1.1 ± 1.9	0.8 ± 1
Population density	10.7 ± 2.2	11.1 ± 2.2	11.7 ± 2.3	28.5 ± 11.3	37.5 ± 28.23	21.4 ± 6.8

Significant differences between plant functional groups in autumn and spring are indicated by different letters and marked in italics (Dunn-Bonferroni, $P < 0.05$).

Supplementary Table S6. Density of the nematode genera in individuals (g DW)$^{-1}$ (± s.d.) in Lebanon at both sampling dates.

	Autumn			Spring		
	Grass	Legumes	Forbs	Grass	Legumes	Forbs
Acrobeles	0.5 ± 0.7	0.1 ± 0.2	0.1 ± 0.1	0.5 ± 0.5	0 ± 0.1	0.4 ± 0.5
Acrobeloides	4.5 ± 2.2	2.5 ± 1.1	2.3 ± 1.7	8.8 ± 7.2	5.6 ± 2.3	17.4 ± 11.2
Alaimus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.3
Amplimerlinius	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1
Aphelenchoides	1.1 ± 0.9	1.6 ± 1.8	2.1 ± 1.2	3.5 ± 1.9	2.3 ± 1	6 ± 5.7
Aphelenchus	*3.1 ± 0.8a*	*0.9 ± 0.5b*	*0.8 ± 0.6b*	3.3 ± 2.6	1.2 ± 0.7	4.2 ± 3.9
Aporcelaimellus	0.3 ± 0.4	0 ± 0.1	0.1 ± 0.1	0.1 ± 0.2	0 ± 0.1	0.1 ± 0.2
Aprutides	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.2	0.0 ± 0.0	0.0 ± 0.0
Basiria	0.8 ± 0.8	0.4 ± 0.2	0.1 ± 0.1	0.2 ± 0.3	0.1 ± 0.3	0.2 ± 0.5
Boleodorus	0.6 ± 0.5	0.3 ± 0.3	0.2 ± 0.3	0.1 ± 0.2	0.2 ± 0.2	0.3 ± 0.3
Cephalobus	0.5 ± 0.3	0.4 ± 0.2	0.3 ± 0.3	0.6 ± 0.8	0.3 ± 0.4	0.8 ± 1
Cervidellus	0.5 ± 0.4	0.5 ± 0.1	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Chiloplacus	1.2 ± 0.5	0.8 ± 0.6	0.5 ± 0.3	*0.5 ± 0.3b*	*0.9 ± 0.3ab*	*1.6 ± 0.9a*
Coslenchus	0.6 ± 0.7	0.2 ± 0.2	0.6 ± 1	0.0 ± 0.0	0.2 ± 0.3	0.0 ± 0.0
Cribronema	0.2 ± 0.2	0.2 ± 0.2	0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4
Discolaimus	0.1 ± 0.1	0.0 ± 0.0	0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Ditylenchus	2 ± 0.7	1.5 ± 0.5	2.2 ± 2	4.5 ± 3.4	1.8 ± 1.4	8.6 ± 6.7
Dorylaimellus	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Drilocephalobus	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0 ± 0.1	0.0 ± 0.0	0.2 ± 0.3
Ecumenicus	0 ± 0.1	0 ± 0.1	0.0 ± 0.0	0.3 ± 0.4	0.0 ± 0.0	0.2 ± 0.2
Eucephalobus	0.5 ± 0.4	0.4 ± 0.3	0.4 ± 0.4	0.3 ± 0.3	0.1 ± 0.1	0.9 ± 1.7
Eudorylaimus	0.4 ± 0.4	0.5 ± 0.2	0.2 ± 0.3	1.1 ± 1.2	0.4 ± 0.2	2.6 ± 1.9
Eumonhystera	0.7 ± 0.5	0.3 ± 0.2	0.3 ± 0.4	*0.7 ± 0.3b*	*0.8 ± 0.9b*	*5.7 ± 4a*
Filenchus	0.3 ± 0.4	0.8 ± 0.3	0.8 ± 0.3	0.8 ± 0.4	0.6 ± 1	2.6 ± 1.9
Geocenamus	0.0 ± 0.0	0.1 ± 0.3	0.3 ± 0.5	0.2 ± 0.2	0.1 ± 0.2	0.1 ± 0.2
Helicotylenchus	0.1 ± 0.1	0.1 ± 0.2	0.2 ± 0.3	0.1 ± 0.2	0 ± 0.1	0.0 ± 0.0
Heterocephalobus	0.1 ± 0.1	0.4 ± 0.4	0.0 ± 0.0	0.2 ± 0.2	0.0 ± 0.0	0.1 ± 0.1
Kirjanovia	0.0 ± 0.0	0.2 ± 0.5	0.0 ± 0.0	0.6 ± 1.2	0.1 ± 0.2	0.2 ± 0.3
Lelenchus	0.5 ± 0.5	0.6 ± 0.4	0.6 ± 0.5	0.2 ± 0.2	0.3 ± 0.3	1.5 ± 1.8
Malenchus	0.3 ± 0.2	0.2 ± 0.2	0.2 ± 0.1	0.0 ± 0.0	0.3 ± 0.4	1.3 ± 1.3
Mesodorylaimus	0.1 ± 0.1	0.2 ± 0.2	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0 ± 0.1
Mesorhabditis	0.0 ± 0.0	0.1 ± 0.2	0.0 ± 0.0	0.1 ± 0.2	0.1 ± 0.1	2.7 ± 5.1
Monhystera	0.1 ± 0.1	0 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.2 ± 0.4
Nygolaimus	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Panagrellus	0.0 ± 0.0	0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Panagrolaimus	0.4 ± 0.3	0.4 ± 0.4	0.3 ± 0.2	0.6 ± 0.8	1.2 ± 0.7	31.1 ± 53.8
Paraphelenchus	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.2 ± 0.3
Paratrophurus	0.0 ± 0.0	0.0 ± 0.0	0 ± 0.1	0.2 ± 0.5	0.1 ± 0.1	0.2 ± 0.3
Paratylenchus	0.1 ± 0.1	0.3 ± 0.6	4.6 ± 8.9	0.4 ± 0.5	0.6 ± 0.5	1.3 ± 2.3
Plectus	0.4 ± 0.6	0.3 ± 0.1	0.6 ± 0.6	0 ± 0.1	0.2 ± 0.2	0.7 ± 1.3
Pratylenchoides	0.0 ± 0.0	0.1 ± 0.1	0.1 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Pratylenchus	0.0 ± 0.0	0.1 ± 0.2	1.5 ± 2.5	0.1 ± 0.2	0.1 ± 0.1	0.0 ± 0.0
Prismatolaimus	0.1 ± 0.1	0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Psilenchus	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Pungentus	0.1 ± 0.1	0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Rhabditis	0.0 ± 0.0	0.1 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Rotylenchus	0.0 ± 0.0	0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Thonus	0.5 ± 0.4	0.2 ± 0.2	0.1 ± 0.2	0.2 ± 0.2	0.1 ± 0.2	0.4 ± 0.5
Tylenchorhynchus	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.2	0.7 ± 0.5	0.6 ± 0.4	1 ± 0.9
Tylenchus	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4	0.1 ± 0.3	0.2 ± 0.3
Wilsonema	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.6 ± 1.1	0.0 ± 0.0	2 ± 2.2
Overall density	20.6 ± 7.5	15.4 ± 2.8	20 ± 17.3	29.9 ± 19.6	18.4 ± 4.1	58.7 ± 38.2

Significant differences between plant functional groups in autumn and spring are indicated by different letters and marked in itlaics (Dunn-Bonferroni, $P < 0.05$).

Supplementary Table S7. Effects of plant functional group, plant identity and season on nematode indices and metabolic footprint.

	Plant functional group	Plant identity	Season
MI	8.29***	2.8*	0.02
PPI	1.16	0.98	0.82
CI	6.37**	2.75*	10.2**
EI	5.49**	3.61**	4.02*
SI	0.58	0.5	8.92**
H	6.7**	3.17**	1.11
Herbivore footprint	2.12	1.52	10.61**
Fungal footprint	0.87	1.13	10.96
Bacterial footprint	5.42**	2.24*	12.46***
Composite footprint	4.6*	2.03	15.38***
Enrichment footprint	6.15**	2.4*	10.1**
Structure footprint	0.36	0.66	19.91***

Presented are the F-values of linear mixed models. Asterisks indicate significant effect at $^{***}P < 0.001$; $^{**}P < 0.01$; and $^{*}P < 0.05$; the absence of asterisks indicates no significant effect.

Supplementary Table S8. Metabolic footprints (μ g C (g DW)$^{-1}$ ($\pm$ s.d.)) in the soils of the five Mediterranean regions: France, Slovenia, Spain, Jordan and Lebanon.

		France	Slovenia	Spain	Jordan	Lebanon
Autumn	Herbivore	0.1 ± 0.1b	5.0 ± 6.1a	0.4 ± 0.2a	0.2 ± 0.1b	0.3 ± 0.3ab
	Fungal	0.1 ± 0.1bc	0.3 ± 0.1ab	0.1 ± 0.02c	0.3 ± 0.1a	0.5 ± 0.2a
	Bacterial	4.3 ± 1.6a	3.3 ± 1.9ab	0.4 ± 0.2c	1.2 ± 0.4bc	1.7 ± 1.0ab
	Enrichment	4.0 ± 1.7a	1.8 ± 1.4ab	0.1 ± 0.02c	0.5 ± 0.2bc	0.7 ± 0.4b
	Structure	0.1 ± 0.2b	0.6 ± 0.4a	0.2 ± 0.2b	0.3 ± 0.3ab	0.6 ± 0.6a
Spring	Herbivore	0.5 ± 0.3ab	1.3 ± 1.8a	0.8 ± 0.5ab	0.4 ± 0.5ab	0.3 ± 0.2b
	Fungal	0.3 ± 0.2bc	0.2 ± 0.1c	0.1 ± 0.1c	0.8 ± 0.5ab	1.1 ± 0.9a
	Bacterial	24.0 ± 22.7a	3.8 ± 2.4b	0.5 ± 0.2c	2.9 ± 1.4b	4.4 ± 3.9ab
	Enrichment	22.8 ± 22.7a	2.9 ± 2.0ab	0.2 ± 0.1c	1.0 ± 0.6b	1.6 ± 1.6ab
	Structure	0.8 ± 0.6a	1.1 ± 0.4a	0.2 ± 0.2b	0.7 ± 0.5a	1.0 ± 1.1a

Given are the herbivore, fungivore, bacterivore, enrichment and structure footprint in autumn and spring. Values within a row with the same letters are not significantly different according to Dunn-Bonferroni ($P < 0.05$).

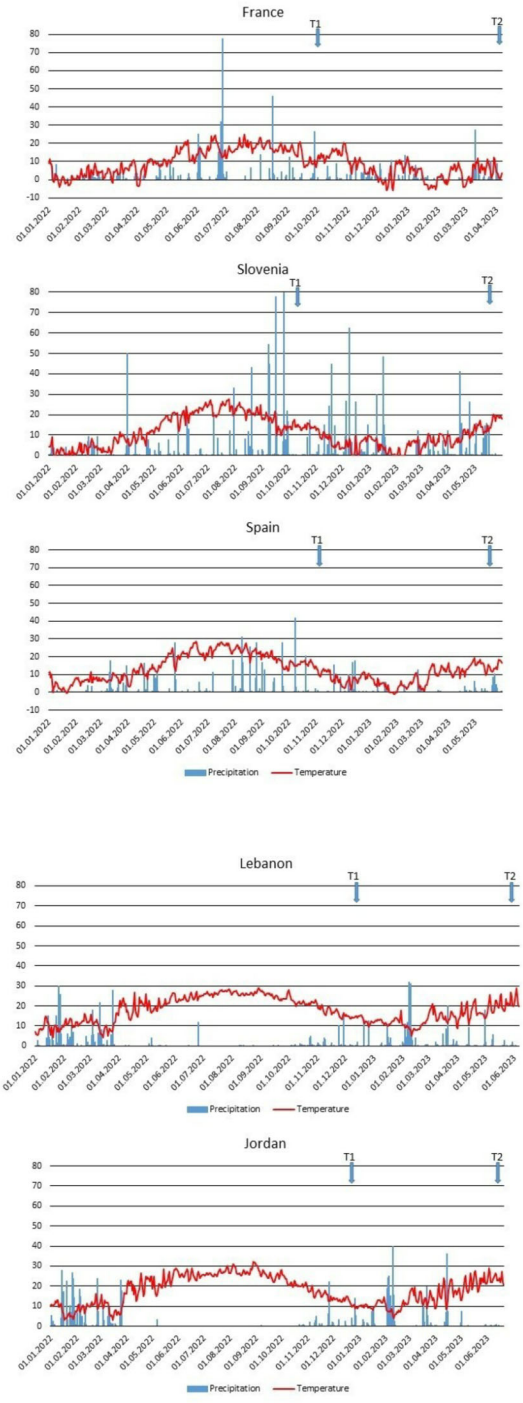
Supplementary Table S9. Effects of plant functional group, plant identity and season on the abundance of nematodes.

	Plant functional group	Plant identity	Season
Acrobeles	8.19***	2.2*	0.69
Acrobeloides	0.39	0.58	14.03***
Alaimus	0.94	0.89	1.96
Allodorylaimus	0.04	1.12	6.73*
Amplimerlinius	0.19	1.15	3.86
Anaplectus	0.1	0.51	0.03
Aphelenchoides	0.53	1.2	4.3*
Aphelenchus	4.39*	1.32	4.17*
Aporcelaimellus	2.14	1.81	1.45
Aprutides	13.67***	4.17***	2.43
Basiria	3.94*	2.22*	0.78
Bitylenchus	0.02	0.54	0.11
Boleodorus	0.3	0.93	0.25
Bursilla	25.05***	7.29***	2.76
Cephalobus	2.78	1.69	3.63*
Cervidellus	0.03	2.25	24.38***
Chiloplacus	0.27	2.05	9.05
Clarkus	0.41	0.26	3.11
Coslenchus	0.98	0.75	3.82
Cribronema	2.19	2.56*	5.3*
Discolaimus	1.5	1.07	2.08
Ditylenchus	0.57	0.97	12.05
Dolichorhynchus	0.03	1.13	3.75
Dorydorella	0.05	1.94	2.27
Dorylaimellus	1.4	0.84	2.37
Drilocephalobus	1.22	0.47	0.05
Ecumenicus	28.22***	11.77***	8.9**
Epidorylaimus	0.1	0.46	3.09
Eucephalobus	1.84	1.29	0.9
Eudorylaimus	0.54	0.36	24.47***
Eumonhystera	2.03	0.24	6.87*
Filenchus	2.39	0.97	7.33
Geocenamus	0.97	4.04***	0.25
Helicotylenchus	2.83	1.39	2.2
Heterocephalobus	0.37	1.53	0.04
Kirjanovia	9.73***	3.36**	2.05
Lelenchus	6.98**	2.43*	0.1
Malenchus	3.6*	0.94	1.49
Meloidogyne	0.02	0.53	3.23
Merlinius	0.29	0.64	5.18*
Mesodorylaimus	0.65	1.33	4.57*
Mesorhabditis	1.48	0.58	2.65
Metateratocephalobus	0.02	0.7	5.31*
Monhystera	0.76	0.46	12.7***
Mylonchulus	0.01	0.88	1.82
Nagelus	0.52	0.61	10.78**
Nygolaimus	0.01	3.7**	2.16
Panagrellus	2.34	0.68	11.16**
Panagrobelus	0.07	0.43	3.9
Panagrolaimus	1.53	0.62	2.63
Paraphelenchus	1.77	1.16	0.73

Supplementary Table S9. (Continued.)

	Plant functional group	Plant identity	Season
Paratrophurus	0.04	1.15	5.94*
Paratylenchus	0.26	0.97	1.29
Pellioditis	2.03	1.19	3.9
Plectus	1.76	1.09	0.01
Pratylenchoides	0.51	2.17*	1.52
Pratylenchus	1.82	2.03	0.01
Prionchulus	0.21	0.55	0.54
Prismatolaimus	0.08	0.72	5.59*
Pristionchus	0.05	1.14	5.42*
Psilenchus	0.7	1.01	0.1
Pungentus	0.01	1.42	2.97
Rhabditis	10.27***	3.12**	7.92**
Rotylenchus	0.04	0.34	13.81***
Scutylenchus	0.37	1.49	9.93**
Thonus	0.05	1.35	2.01
Tylenchorhynchus	0.11	0.41	21.26***
Tylenchus	6.52**	3.14**	4.5*
Wilsonema	0.84	0.89	9.21**

Presented are the F-values of linear mixed models of all nematode genera. Asterisks indicate significant effect at $***P < 0.001$; $**P < 0.01$; and $*P < 0.05$; the absence of asterisks indicates no significant effect.



Supplementary Fig. S1. Daily precipitation (mm) and daily mean temperature (°C) during the experimental period in the five Mediterranean regions France, Slovenia, Spain, Jordan and Lebanon. The blue arrows mark the soil sampling campaigns in autumn (2022; T1) and spring (2023; T2).

Supplementary Table S10. Nematode indices (± s.d.) in the soils of the five Mediterranean regions France, Slovenia, Spain, Lebanon and Jordan.

		France			Slovenia			Spain			Lebanon			Jordan		
		Grasses	Legumes	Forbs	Grasses	Legumes	Forbs	Grasses	Legumes	Forbs	Grasses	Legumes	Forbs	Grasses	Legumes	Forbs
Autumn	MI	1.6 ± 0.1	1.4 ± 0.2	1.5 ± 0.2	2 ± 0.1	2.1 ± 0.1	2 ± 0	2.2 ± 0.1	2.2 ± 0.2	2.1 ± 0.1	2.2 ± 0.1	2.1 ± 0.1	2.1 ± 0.1	2.1 ± 0.1	2 ± 0.1	2 ± 0.1
	PPI	2.6 ± 0.2	2.4 ± 0.2	2.7 ± 0.3	*2.6 ± 0.2a*	*2.3 ± 0.1b*	*2.5 ± 0a*	2.7 ± 0	2.8 ± 0.1	2.7 ± 0.1	2 ± *0b*	*2.1 ± 0.1ab*	*2.3 ± 0.1a*	2.1 ± 0.1	2.1 ± 0.1	2.3 ± 0.1
	CI	13.9 ± 6.3	5.6 ± 3.5	6 ± 4.8	*23.1 ± 6.1b*	*50 ± 9.9a*	*37.1 ± 7.2ab*	100 ± 0	95 ± 10	100 ± 0	82.5 ± 12.3	72.7 ± 26.2	81.8 ± 10.2	70.9 ± 24.5	71.6 ± 23.3	60.5 ± 19.5
	H'	2.6 ± 0.1	2.2 ± 0.3	2.5 ± 0.2	3 ± 0.2	2.9 ± 0.1	2.9 ± 0	2.7 ± 0.1	2.7 ± 0.2	2.6 ± 0.1	2.6 ± 0.2	2.8 ± 0.2	2.5 ± 0.2	2.5 ± 0.1	2.6 ± 0.1	2.6 ± 0.3
Spring	MI	1.5 ± 0.3	1.5 ± 0.3	1.7 ± 0.1	2.1 ± 0.2	2.2 ± 0.1	2.1 ± 0.1	2.1 ± 0.1	2 ± 0	2.1 ± 0.1	2.1 ± 0.1	2 ± 0.1	2.1 ± 0.1	2.2 ± 0.1	2 ± 0.1	2 ± 0.1
	PPI	2.5 ± 0.2	2.6 ± 0.1	2.6 ± 0.2	2.4 ± 0.1	2.3 ± 0.2	2.3 ± 0.1	2.7 ± 0.1	2.8 ± 0.1	2.9 ± 0	2.4 ± 0.2	2.3 ± 0.2	2.2 ± 0	2.3 ± 0.1	2.2 ± 0.2	2.1 ± 0.1
	CI	6.7 ± 7.7	6.8 ± 7.8	10.7 ± 8	16.3 ± 17.8	29.2 ± 16.2	17.8 ± 11.9	83.1 ± 16.2	89.2 ± 21.6	79 ± 20.5	82.8 ± 7.3	53.6 ± 15.8	59.4 ± 21.4	88.3 ± 13.5	68.1 ± 30.7	50.7 ± 20.8
	H'	2.4 ± 0.4	2.3 ± 0.6	2.7 ± 0.2	3.1 ± 0	3.2 ± 0.2	3.1 ± 0.2	2.7 ± 0.3	2.7 ± 0.2	2.6 ± 0.1	2.3 ± 0.1	2.3 ± 0.2	2.4 ± 0.2	2.5 ± 0.3	2.2 ± 0.3	2.4 ± 0.1

Given are the maturity index (MI), plant parasite index (PPI), channel index (CI) and Shannon diversity (*H'*) in autumn (2022) and spring (2023). Significant differences between plant functional groups within one region and season are indicated by different letters and marked in italics (Dunn-Bonferroni, $P < 0.05$).