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Plant species as driver to changes in nematode-based ecological indices and communities structure (Pinaceae species as a case study)

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Abstract

Nematodes are key components in the soil as some nematode groups are involved in various functions that support plant life and ecosystem health. Diversity and structure of their communities could be influenced by various factors. The current study was conducted on Pinaceae trees in the Syrian coastal region in order to identify and compare, via several nematode-based indices, diversity and structure of nematodes in communities according to different factors (Pinaceae species, pine origin, habitat types, and vegetation zones) to determine the most important factor affecting communities diversity and structure. A total of 469 root and associated soil samples were collected. A total of 62 nematode genera were identified, including 26 herbivores, 20 bacterivores, 6 predators, 6 fungivores, and 4 omnivores. 23 genera were recorded for the first time in Syria. Significant differences were observed in some indices among Pinaceae species (e.g. Maturity index 2–5, Plant Parasitic Index, Enrichment Index, Structure Index, Total number of individuls). NMDS analysis revealed a significant distinction of Pinaceae species based on the composition of their associated communities. Co-inertia analysis confirmed this association of some nematode genera to Pinaceae species (*Paratylenchus* to *P. nigra*, *Tylenchulus* to *C. libani*, and *Xiphinema* and *Promumtazium* to *P. halepensis*). These results conclude on the importance of plant species as the main factor affecting nematode diversity and their assemblage in communities. The trophic diversity recorded, along with higher maturity and structure indices under certain Pinaceae species, highlights the value of nematode communities as sensitive indicators of ecosystem stability.

Introduction

Studies of biological diversity in natural communities are of paramount importance because they are directly linked to the stability, resilience, and health of ecosystems, which in turn provide essential services for the survival and endurance of organisms. Soil represents one of the most important reservoirs of biodiversity. They have an ecological and economic importance due to they involved in various soil functions such as carbon and nitrogen cycling and organic matter decomposition and their role as agents for pest biological control strategies or as parasites on plants (Van der Hoogen et al. 2019; Hodda 2022). Soil nematode communities are characterized by a wide diversity: in their morphological features; their feeding habits (distinguished as bacterivores, fungivores, plant-parasites or herbivores, predators and omnivores (Yeates et al. 1993)); their life histories and their response to disturbances in the surrounding environment (assigned into five categories commonly known as colonizer-persister (c-p) groups) (Bongers 1990; Bongers and Bongers 1998; Melakeberhan et al. 2021). The analysis of nematode communities provides information on succession, changes in decomposition pathways in soil food webs, nutrient status, fertility, soil acidity, soil salinity and soil pollution (Ritz and Trudgill 1999; Bongers and Ferris 1999; Wilschut and Geisen 2021; Yang et al. 2021). For example, the dominance of bacterivore and fungivore nematodes in communities indicates rapid nutrient uptake and high nitrogen inputs by excreting nutrients in excess of their metabolic need, as organic and inorganic forms (i.e. NH4 + and PO4-), available to plants (Gebremikael et al. 2016). Conversely, a relative reduction in the abundance of omnivore and predator nematodes was observed in wheat fields, related to high nitrogen levels (Song et al. 2015). Several factors could affect the diversity of nematode and their composition of genera and species in communities, such as plant age and species (Háněl 2001; Peneva and Choleva 1994; Bardgett and Wardle 2010); climatic conditions (Armendâriz et al. 1996; Shao et al. 2023); geographical localities and altitude (Deimi and Metkowski 2017; Kashyap et al. 2022); and some edaphic factors as soil pH, nutrients, soil patches, etc. (Un nisa et al. 2021).

The Pinaceae trees are native to the Northern Hemisphere, but very distributed worldwide, especially in the Mediterranean, the Middle East, Asia, and the southwestern United States around orchards, gardens, parks, and in forests (Ya and Slavin 2008; Taylor et al. 2009). Pinaceae family includes 11 genera and more than 220 species. *Abies* (firs), *Picea* (spruce), *Tsuga* (hemlock), *Cedrus* (ceder) and *Pinus* (pines) are the most common and widely distributed genera (Farjon 2010). Different nematode genera and species were reported worldwide in association with different Pinaceae species: 33 genera in New Zealand (Yates 1990); 48 species in Bulgaria (Peneva and Choleva 1994); 21 genera and 56 species in Spain (Armendâriz et al. 1996); 47 genera in Germany (Háněl 2001); 21 species in India (Negi et al. 2009); 11 species in China (Fang et al. 2012); 17 species in Iran (Deimi and Metkowski 2017);42 and 62 species in Russia and Finland respectively (Sushchuk and Matveeva 2020); 10 genera and 33 species in France (Ali et al. 2021); 32 genera in Greece (Karmezi el al. 2023); and recently, 44 genera were identified in Turkey (Öztürk 2025).

In Syria, no report on nematode communities associated to Pinaceae trees is available so far. A survey of three Pinaceae species (*Pinus*, *Abies* and *Cedrus*) was conducted along Syrian coastal region in order to: (*i*) determine the identity, frequency, population density, diversity and structure of nematode communities associated with these Pinaceae species, (*ii*) compare nematode diversity and structure between plant species, pine origins, habitat types (forests, villages, cities and seaside) and vegetation zones according to the altitude above the sea level.

Materials and methods

Site description

This survey was conducted in the Syrian coastal region, which stretches along the western edge of the country along the Mediterranean Sea, between latitudes 35°–45° East and 36°–43° North. The region encompasses fertile plains, plateaus, and high mountains, covering an area of approximately 5,100 square kilometers, divided into two governorates: Latakia and Tartous. Each governorate is divided into several districts: four in Latakia (Latakia, Jableh, Al-Qardaha, and Al-Haffa) and five in Tartous (Tartous, Baniyas, Safita, Sheikh Badr, and Al-Dreikish). According to elevation above sea level and to temperature and humidity gradients, the coastal region of Syria could be divided into four Zones (Nahal 2010): (*i*) Thermo-Mediterranean (0–299 m), characterized by a warm to hot climate in summer (25–30°C) and moderate in winter, with annual rainfall ranging between 400–600 mm, by a natural vegetation typically Mediterranean, including *P. halepensis* and *Ceratonia siliqua*. (*ii*) Eu-Mediterranean (300–599 m), characterized by a moderate climate (20–27°C in summer and 2–8°C in winter), an annual rainfall (500–700 mm) and by forests of *P. brutia*, adjacent to *Quercus calliprinos*, *Q. infectoria* and *Prunus dulcis*. (*iii*) Supra-Mediterranean (600–899 m), where the climate becomes cooler (18–24°C in summer and 0–5°C in winter), and precipitation levels of 700–1000 mm annually. The dominant plant species in this zone include *P. brutia* and *Quercus cerris*. (*iv*) Montane-Mediterranean (900 m and above) is characterized by cool

summer (15–20°C), very cold winter (< 0°C) with regular snowfall, and annual precipitation exceeding 1000 mm. It is dominated by montane forests of *C. libani*, *A. cilicica*.

The presence of Pinaceae trees in the Syrian coastal region is as native (*Pinus brutia, P. halepensis, C. libani* and *A. cilicia*), or exotic / introduced species (*P. canariensis, P. radiata, P. nigra* and *P. pinaster*). Given the wide distribution of Pinaceae in the Syrian coast, samples were collected from four different habitat types (the place from where the tree was sampled): forests, rural areas, cities and seaside.

Sampling

The sampling was continuous from July 2023 to October 2024, from 26 and 25 sites in Latakia and Tartous, respectively. 469 samples (239 soil samples and 230 root samples) were collected in total **(**Table 1, Fig. 1**).**

Table 1
Localization of the sampling sites and corresponding codes and Pinaceae trees surveyed.

Region	Area	Site	Code	Latitude N	Longitude W	Pinaceae species
Latakia	Al-Haffah	Al-Haffah Hospital Forest	HA	35.60814183	36.05792912	*P. canariensis*
						P. radiate
		Al-Shurdub Forest	SH	35.59989667	36.05685438	*P. brutia*
		Balata Forest	BF	35.62943895	36.13533567	*P. brutia*
		Cedar and Shuh Reserve	CSR	35.59995918	36.2191561	*A. cilicica*
						C. libani
		Katif Al-Ezer Forest	KAF	35.6078369	36.18698435	*A. cilicica*
						C. libani
		Mzeraa	MZ	35.5332039	36.07168258	*P. canariensis*
		Salmah	SA	35.68683516	36.14130911	*P. pinea*
						P. pinaster
						C. libani
		Samandil	SAM	35.59959095	35.96570558	*P. pinea*
	Al-Qardaha	Al-Balat Area	ABA	35.51829184	36.15816139	*P. nigra*
		Al-Jawba	AJ	35.46497836	35.90188178	*P. canariensis*
		Al-Qardaha	AQ	35.45723126	36.05916669	*P. pinea*
		Al-Rrahbat Area	RR	35.5944535	36.19458456	*P. nigra*
		Beit Zantout	BZ	35.48987195	36.17299486	*P. nigra*
						C. libani
		Stamo	ST	35.47987242	35.92661323	*P. pinea*
						P. canariensis
	Latakia	Al-Hanadi	HAN	35.48754123	35.86358092	*P. brutia*
						P. halepensis
		Al-Shaati Al-Azraq	ZRQ	35.57540941	35.74619239	*P. radiate*
		Al-Shurta Forest (Qasr Versay)	SFQ	35.48996988	35.87874862	*P. brutia*
		Bassa	BS	35.5076873	35.84643608	*P. pinea*
						P. canariensis
		Buqa	BU	35.53541597	35.80708267	*P. brutia*
						P. pinea
						P. canariensis
						P. nigra
						A. cilicica
						C. libani
		Mashqita	MSH	35.66227876	35.9073306	*P. brutia*
		Sanawbar Jabla	SAJ	35.48311096	35.88436776	*P. pinea*
						P. canariensis
		Tishreen University	TI	35.52281282	35.80739316	*P. pinea*
						P. canariensis
						P. radiata
						C. libani
	Jableh	Al-Hikmiah	KMI	35.35361065	36.02517093	*P. pinea*

		Kfar Dbil	KFR	35.36796916	36.05054334	*P. brutia*
						P. pinea
		Matwar	MT	35.34285328	36.12723625	*P. brutia*
		Siyannu	SI	35.36020797	35.96479261	*P. brutia*
						P. pinea
Tartous	Al- Dreikish	Al-Naby Mataa□s Forest	NMT	34.95844514	36.25464777	*P. brutia*
						P. pinea
						P. halepensis
						A. cilicica
						C. libani
		Hamein	HN	34.90213945	36.04781632	*P. brutia*
		Maamoura	MAA	34.93714105	36.22211989	*P. brutia*
						P. pinea
	Al- Sheikh Badr	Al-Qumsyah	QU	35.05205608	35.98626127	*P. brutia*
		Bieuzrayiyl forest	YI	34.99589166	36.00703276	*P. brutia*
		Birmanat Ra'ed	BI	34.99646086	36.03898229	*P. pinea*
		Kawkab Al-Hwa	KW	34.9192778	36.08665164	*P. brutia*
	Baniyas	Al-Bayda	BY	35.12553282	35.94936847	*P. halepensis*
		Al-Hattaniyah	HAT	35.13689272	36.09519513	*P. halepensis*
		Al-Mawlaa Hasan Mountain	HAS	35.10762113	36.17633001	*P. brutia*
						C. libani
		Bayt Al-Myssrah	MY	35.1367539	36.11996801	*P. brutia*
		Hamaam Wasal	SL	35.07818996	36.08625402	*P. pinea*
		Maidan Forest (Al-Qadmus Hospital)	ID	35.10763562	36.14939661	*P. brutia*
	Safita	Al-Naby Saleh□s Mountain	SAL	34.92340364	36.27215267	*P. brutia*
						P. halepensis
						C. libani
		Al-Sayidah□s Mountain	SYY	34.86639061	36.23457504	*P. pinea*
						C. libani
		Sabbah	SB	34.90346902	36.23656939	*P. pinea*
						P. brutia
		Sirstan Forest	TAN	34.85279352	36.05211969	*P. halepensis*
	Tartous	Al-Awainiyah	AWA	34.95741684	35.96728541	*P. pinea*
		Al-Suwda	WD	34.99377011	35.94498169	*P. brutia*
		Bimalaka	IM	34.93462902	35.97420849	*P. brutia*
		Dir Al-Shaykh Saed	DIR	34.92709313	35.92889795	*P. canariensis*
						C. libani
		Eimrit	MR	34.85210138	35.9046778	*P. brutia*
		Khirbat Al-Faras	FAR	34.95039697	36.01229209	*P. halepensis*
		Ras Al-Turkman	TRK	34.94759986	36.35811119	*P. pinea*
		Taeshor	TE	34.85210138	35.9046778	*P. halepensis*

Soil samples were taken using a small shovel from the upper rhizosphere (5–30 cm deep, inhabited by polymorphic roots) after removing the surface layer. Weeds or other plants were avoided during sampling to prevent any potential influence on the nematode community structure. Sampling methods varied between forests, rural sites, cities, and seaside areas. For forests, each one was divided into several random sections according to its surface; several

subsamples (4–6) were randomly taken from each section (without taking into account any nematode symptoms). These subsamples were mixed to obtain a single representative sample of 500 grams per section. For other habitat types, several subsamples were taken from individual trees, and the subsamples from each tree were combined to form a composite sample of 500 grams. The number of representative samples per site varied according to the forest area and tree density. Root samples were taken at the same time as soil samples. They were wrapped in a paper towel moistened with water to keep moisture and to ensure that nematodes (if present) remained alive.

Nematode extraction, identification and quantification

A 250-cm^3 wet aliquot was taken from each soil sample for nematode extraction using the modified Baermann funnel method (Walker and Wilson 1960). For root samples, they were carefully washed under running tap, weighed, cut into small pieces (1–2) cm and then put for extraction as for soil samples. The extracted nematodes were enumerated in 5-cm^3 counting chambers (Merny and Luc 1969) and identified to the genus level under a microscope (OPTIKA B-195, Italy) at ≥ x40 magnification, using several taxonomic keys (Yeates et al. 1993; Stirling and Stirling 2023; Siddiqi 1986; Andrássy 2007; Mai and Mullin 2018). The population levels were expressed per dm^3 of fresh soil. For more morphological details, some nematode specimens were picked up from suspension, heat-killed, fixed in TAF solution and observed under a light microscope connected to a digital camera (OPTIKA B10, Italy).

Analyses of nematode diversity

Firstly, each nematode genus was allocated into five trophic groups: bacterivores, fungivores, herbivores (distinguished as moss feeders, root hair feeder, ectoparasites, semi-endoparasites, migratory endoparasites, sedentare parasites), omnivores and predators, as defined by Yeates et al. (1993), using the online program "NINJA: An Automated Calculation System for Nematode-Based Biomonitoring" (Sieriebriennikov and Ferris 2014).

Several nematode-based indices were also used: Maturity Index (*MI*), Maturity Index 2–5 (*MI*-2-5), Sigma Maturity Index (*∑MI*), Plant Parasitic Index (*PPI*), Channel Index (*CI*), Basal Index (*BI*), Enrichment Index (*EI*) and Structure Index (*SI*). They were also calculated via NINJA. Additionally, three taxonomical indices were applied: the total number of nematodes in a sample (*N*); the genus richness (*G*) (number of genera in a sample); the Shannon-Wiener diversity index (*H'*= −Σp*i*ln*p*i*; where p*i* is the proportion of individuals of the genus (*i*), it quantifies the local diversity or the heterogeneity of diversity (*H'* ranges from 0 to *ln*(G)).

The dominance of each genus was estimated, according to the model developed by Fortuner and Mirnyi (1973), by modeling its abundance *A* (the total population density of the genus in the complete samples (expressed as logarithm)) and its frequency *F* (the number of samples where the genus was detected, expressed as %), According to the model, thresholds were defined: a genus was considered unabundant when *A* < 2.30 (i.e., the total abundance of the genus < 200 individuals (Log 200 = 2.30)), and abundant when *A* ≥ 2.30. On the other hand, a genus present in at least 30% of the samples was considered frequent (*F* ≥ 30%), and occasional or less frequent when *F* < 30%.

Statistical analyses

All statistical analyses were done using R version 3.3.2 (R Core Team 2016). Each index variable was first checked for its distribution type in order to identify the error family. Logarithmic transformation was applied on the total number of nematodes (*N*) to improve the distribution of this variable. A model element selection process was chosen according to the criterion of Akaike (AIC) using the MASS package (Venables and Ripley 2002). The used model was selected according to the low value of AIC.

Mean values of indices were analyzed by one-way ANOVA, between the nine Pinaceae species studied, pine origins (as native or exotic), habitat types (forests, rural areas, cities and seaside) and between the four vegetation zones (thermo-Mediterranean, Eu-Mediterranean, supra-Mediterranean and Montane-Mediterranean). Tukey test was then used for pair-wise multiple comparisons between the significant variables according to ANOVA results. Differences obtained at *P* < 0.05 were considered significant.

In order to inspect if the different Pinaceae species affect the nematode composition in communities, a nonmetric multidimensional scaling (NMDS) analysis was conducted. The dissimilarity matrix was based on the total abundance of all genera within the community. A Bray-Curtis dissimilarity metric was used to determine effect of plant species on nematode communities' distances between the sampling points, for which the metaMDS function was used (R vegan package; Oksanen 2015). "Adonis" function was used to determine if groups are significantly different, using permutation/randomization methods with 999 times on the similarity matrix. One-way ANOVA was then applied to check the assumption of homogeneity of multivariate dispersion. Venny analysis was used via the application Venny v2.1 (Oliveros 2015) in order to identify the common and unique nematode genera across the different Pinaceae species studied.

To assess the correlation of nematode genera to the Pinaceae species, a Co-Inertia Analysis CIA (Dray et al. 2003) was applied between plant species and genera data. The scarcest nematode genera (with total abundance or density less than 1%) were excluded from the dataset prior to running the analysis. These different multivariate analyses and graphs were performed using the *ade4* library (Dray and Dufour 2007).

Results

Dominance of nematode genera in samples and on Pinaceae species

A total of 62 nematode genera, belonging to 33 families and 10 orders have been identified during this survey (Table 2). These genera were distinguished as five trophic groups: 26 herbivores, 20 bacterivores, 6 predators, 6 fungivores, and 4 omnivores. According to their abundance and frequency within the samples set, these 62 nematode genera were allocated into three groups according to the threshold defined by the model (as explained above) (Fig. 2). The first group (right upper quadrant) included 14 genera which were the most abundant and frequent (i.e. genera found in more than 30% of the samples and with a total population density more than 200 individuals/dm^3 of soil): *Aphelenchoides*, *Cephalobus*, *Eudorylaimus*, *Aphelenchus*, *Helicotylenchus*, *Xiphinema*, *Paratylenchus*, *Mononchus*, *Plectus*, *Ditylenchus*, *Acrobeles*, *Filenchus*, *Pratylenchus* and *Promumtazium*. 45 genera (identified in less than 30% of the samples and with a total of more than 200 individuals/dm^3 of soil) abundant but less frequent belonged to the second group (left upper quadrant). This group included: *Tylenchulus, Rhabditis, Rotylenchulus, Polenchus, Monhystera Aglenchus, Malenchus, Dorylaimus, Tylencholaimus, Gracilacus, Rotylenchus, Trichodorus, Tylocephalus, Eumonhystera, Longidorella, Tylenchorhynchus, Diploscapter, Mesodorylaimus, Prismatolaimus, Tylenchus, Panagrobelus, Mylonchulus, Acromadora, Steinernema, Longidorus, Zygotylenchus, Chromadorina, Aprutides, Mesocriconema, Seinura, Clarkus, Acrobeloides, Irantylenchus, Aporculaimus, Chiloplacus, Mesorhabditis, Alaimus ,Teratocephalus, Pellioditis, Merlinius, Chronogaster, Heterodera, Psilenchus, Neopsilenchus* and *Phasmarhabditis.* The third group (left lower quadrant) included genera with low frequency (found in less than 30% of samples) and low population density (less than 200 individuals/dm^3 of soil). This group was only represented by three genera: *Meloidogyne*, *Ogma* and *Paratrichorous*.

Table 2
List of nematodes genera associated to Pinaceae trees on the coastal region of Syria with indication to their trophic and *cp*-value groups.

Trophic group	Order / Family	Genus	Genus code (*cp*-value)	Trophic group	Order / Family	Genus	Genus code (*cp*-value)
Herbivores	**Dorylaimida**			**Bacteriovores**	**Chromadorida**		
	Dorylaimidae	*Longidorella**	Dorella (5)		**Chromadoridae**	*Chromadorina**	Chroma (3)
		Longidorus	Longi (5)		**Enoplida**		
		Xiphinema	Xiph (5)		**Alaimidae**	*Alaimus*	Ala (4)
	Triplonchida				**Monhysterida**		
	Trichodoridae	*Paratrichodorus*	P-tricho (4)		**Monhysteridae**	*Monhystera*	Mon (1)
		Trichodorus	Tricho (4)			*Eumonhystera**	Eum (1)
	Tylenchida				**Plectida**		
	Criconematidae	*Mesocriconema**	Meso_cr (3)		**Chronogastridae**	*Chronogaster**	Chrono (3)
		*Ogma**	Ogm (3)		**Plectidae**	*Plectus*	Ple (2)
	Heterodoridae	*Heterodera*	Hetero (3)			*Tylocephalus*	Tylo (2)
	Hoplolaimidae	*Helicotylenchus*	Heli (3)		**Teratocephalidae**	*Teratocephalus**	Tera (3)
		Rotylenchus	Roty (3)		**Rhabditida**		
	Meloidoginidae	*Meloidogyne*	Melo (3)		**Cephalobidae**	*Acrobeles*	Acro (2)
	Paratylenchidae	*Paratylenchus*	P-tylen (2)			*Acrobeloides*	A_oides (2)
		Gracilacus	Gra (2)			*Cephalobus*	Ceph (2)
	Pratylenchidae	*Pratylenchus*	Praty (3)		**Diploscapteridae**	*Diploscapter*	Dip (1)
		Zygotylenchus	Zygo (3)		**Panagrolaimidae**	*Panagrobelus*	Pana (1)
	Psilenchidae	*Neopsilenchus**	Neo (2)		**Rhabditidae**	*Chiloplacus*	Chilo (2)
		Psilenchus	Psi (2)			*Mesorhabditis**	Meso_rha (1)
	Rotylenchulidae	*Rotylenchulus*	R-chulus (3)			*Pellioditis**	Pello (1)
	Telotylenchidae	*Merlinius**	Mer (3)			*Phasmarhabditis**	Phasma (1)
		Tylenchorhynchus	Tylencho (3)			*Rhabditis*	Rhab (1)
	Tylenchidae	*Aglenchus*	Agl (2)		**Steinernematidae**	*Steinernema*	Ste (2)
		*Irantylenchus**	Ira (2)		**Triplonchida**		
		*Malenchus**	Mal (2)		**Prismatolaimidae**	*Prismatolaimus**	Pris (3)
		*Polenchus**	Pol (2)	**Fungivores**	**Aphelenchida**		
		Tylenchus	Tyl (2)		**Aphelenchoididae**	*Aphelenchoides*	Aphoi (2)
	Tylenchulidae	*Tylenchulus*	T-chulus (3)			*Aprutides**	Apr (2)
Predators	**Aphelenchida**				**Aphelenchidae**	*Aphelenchus*	Aph (2)
	Aphelenchoididae	*Seinura*	Sei (2)		**Tylenchida**		
	Chromadorida				**Anguinidae**	*Ditylenchus*	Dity (2)
	Chromadoridae	*Achromadora**	Achro (3)		**Tylenchidae**	*Filenchus**	Fil (2)
	Dorylaimida				**Dorylaimida**		
	Qudsianematidae	*Eudorylaimus*	Eudo (4)		**Tylencholaimidae**	*Tylencholaimus**	T-laimus (4)
	Mononchida			**Omnivores**	**Dorylaimida**		
	Mononchidae	*Mononchus*	Mono (4)		**Aporcelaimidae**	*Aporcelaimus**	Apo (5)
		*Clarkus**	Cla (4)		**Dorylaimidae**	*Dorylaimus*	Dory (4)
	Mylonchulidae	*Mylonchulus*	Mylo (4)			*Mesodorylaimus*	Meso-do (5)

(*) Genera recorded for the first time in Syria.

Trophic group	Order / Family	Genus	Genus code (*cp*-value)	Trophic group	Order / Family	Genus	Genus code (*cp*-value)
Herbivores	**Dorylaimida**			**Bacteriovores**	**Chromadorida**		
					Tylencholaimidae	*Promumtazium**	Promum (4)
(*) Genera recorded for the first time in Syria.							

Diversity of nematode communities associated to Pinaceae trees in Syrian coastal region

Several ecological and biomonitoring indices were measured to assess nematode diversity. These indices were compared between Pinaceae species; pine origins; habitat types and vegetation zones (Table 3). The ANOVA results showed significant differences in some indices especially according to Pinaceae species and pine origins (Table 3A, 3B).

Table 3

Mean values of taxonomic and functional diversity indices and metabolic activity analysis of soil nematode communities associated with pine species along t
test ($p < 0.05$).

Index name	A						
	Pinaceae species						
	A. cilicica	*C. libani*	*P. brutia*	*P. canariensis*	*P. halepensis*	*P. nigra*	*P. pinaster*
Maturity Index	2.71 ± 0.37	2.50 ± 0.42	2.46 ± 0.52	2.38 ± 0.40	2.53 ± 0.49	2.35 ± 0.42	2.54 ± 0.36
Maturity Index 2–5	2.72^{a}±0.37	2.61^{ab}±0.37	2.63^{ab}±0.44	2.45^{ab}±0.36	2.74^{a}±0.41	2.44^{ab}±0.33	2.54^{ab}±0.36
∑MI (Sigma Maturity Index)	2.77 ± 0.33	2.70 ± 0.48	2.65 ± 0.61	2.63 ± 0.43	2.85 ± 0.60	2.41 ± 0.31	2.45 ± 0.27
Plant Parasitic Index	3.13^{ab}±0.90	3.17^{ab}±0.84	3.08^{ab}±0.84	3.03^{ab}±0.67	3.51^{a}±0.88	2.48^{b}±0.27	2.34^{b}±0.31
Channel Index	95.14^{ab}±06.37	68.30^{b}±04.52	72.31^{ab}±04.18	81.22^{ab}±03.39	58.02^{b}±04.44	77.34^{ab}±03.89	100.00^{a}±0.00
Basal Index	29.13^{ab}±02.52	33.85^{ab}±02.38	28.98^{ab}±03.75	37.34^{ab}±01.17	24.53^{b}±03.85	38.88^{ab}±02.49	41.03^{a}±03.18
Enrichment Index	23.40^{ab}±04.05	32.12^{ab}±02.94	42.79^{ab}±02.93	40.41^{ab}±02.85	48.84^{a}±03.96	34.40^{ab}±02.66	17.39^{b}±01.85
Structure Index	66.44^{a}±05.37	58.56^{ab}±02.36	56.06^{ab}±02.91	46.76^{ab}±02.78	64.42^{a}±02.24	46.34^{ab}±05.65	52.52^{ab}±02.57
Total number of individuals	948.31^{ab}±03.69	2301.27^{a}±04.93	742.09^{b}±03.94	931.04^{b}±03.78	1046.77^{ab}±03.36	1136.22^{ab}±05.73	1044.57^{ab}±04.5
Shannon Index H'	2.00 ± 0.22	1.78 ± 0.48	1.77 ± 0.40	1.76 ± 0.55	1.85 ± 0.30	1.91 ± 0.35	1.59 ± 0.37
Richness S	11.69 ± 0.09	11.95 ± 0.95	10.66 ± 0.28	11.40 ± 0.21	12.15 ± 0.19	12.83 ± 0.14	9.43 ± 0.14

Index name	C					D
	Habitat					Vegetation zon
	Beach	City	Forest	Village	P (ANOVA)	Eu-mediterranean
Maturity Index	2.05 ± 0.07	2.54 ± 0.45	2.47 ± 0.47	2.49 ± 0.48	0.518	2.64 ± 0.50
Maturity Index 2–5	2.05 ± 0.07	2.56 ± 0.44	2.63 ± 0.40	2.60 ± 0.43	0.209	2.70 ± 0.46
Sigma Maturity Index	2.14 ± 0.10	2.70 ± 0.40	2.61 ± 0.51	2.75 ± 0.56	0.132	3.00^{a}±0.65
Plant Parasitic Index	3.00 ± 0.07	2.92 ± 0.61	3.04 ± 0.85	3.17 ± 0.81	0.458	3.55^{a}±0.99
Channel Index	100.00^{a}±0.00	92.03ab ± 0.07	67.39^{b}±0.11	82.58ab ± 0.62	0.001	87.85 ± 02.50
Basal Index	57.73 ± 01.59	36.10 ± 01.45	29.64 ± 01.21	31.32 ± 01.64	0.066	27.15 ± 01.38
Enrichment Index	38.56 ± 0.66	32.66 ± 01.88	41.25 ± 01.47	39.17 ± 01.17	0.276	40.62^{ab}±01.83
Structure Index	9.01 ± 0.74	52.52 ± 02.70	58.69 ± 02.15	54.83 ± 02.50	0.034	60.61 ± 05.85
Total number of individuals N	488.00 ± 07.54	1002.92 ± 10.72	1125.74 ± 09.85	802.72 ± 06.43	0.547	620.00 ± 35.15
Shannon Index H'	1.69 ± 0.33	1.86 ± 0.49	1.82 ± 0.36	1.78 ± 0.42	0.791	1.84 ± 0.36
Richness S	11.00 ± 0.82	12.16 ± 0.04	11.25 ± 0.27	11.20 ± 0.54	0.524	11.39 ± 0.04

The Maturity Index 2–5 (*MI* 2–5) and the Structure Index (*SI*) were significantly different between Pinaceae species ($p = 0.032$; $p = 0.011$, respectively). The highest values were respectively reported on *A. cilicica* (2.72; 66.44) and *P. halepensis* (2.74; 64.42), while the lowest value was recorded on *P. radiata* (2.35;

35.18). Significant differences between native and exotic species concerning *MI*2-5, *∑MI* (Sigma Maturity index) were also observed ($p < 0.001$; $p = 0.015$, respectively). The highest values were observed on the native (2.67; 2.71) compared to exotic pine (2.44; 2.52).

The Plant Parasitic Index (*PPI*) was also significantly different between Pinaceae species and pine origins ($p < 0.001$). This index was significantly higher on *P. halepensis* (3.51) compared to *P. pinaster* (2.34) and *P. nigra* (2.48). It was also higher on native (3.17) compared to exotic species (2.74). Channel Index (*CI*), Basal Index (*BI*) also showed significant differences between Pinaceae species ($p = 0.003$ and $p = 0.004$, respectively) and pine origins ($p = 0.024$ and $p < 0.001$). The highest values of *CI* and *BI* were recorded on *P. pinaster* and *P. radiata*, likewise, on exotic species. The Enrichment Index (*EI*) was significantly higher ($p = 0.002$) on *P. halepensis* (48.84) compared to *P. pinaster* (17.39). The total number of individuals (*N*) varied significantly between Pinaceae species ($p = 0.013$). The highest number of nematodes was counted on *C. libani* (2301 individuals /250 cm^3) and the lowest on *P. pinea*, *P. brutia* and *P. canariensis* (663, 742 and 931 individuals /250 cm^3 of soil).

Considering pine habitat types, the ANOVA analyses revealed nonsignificant differences except for the Channel Index ($p = 0.001$), which was significantly higher (100) in the seaside area compared to forests (67.39) (Table 3C).

The distribution of Pinaceae trees within different climatic levels (different vegetation zones) showed significant differences for three indices (Table 3D): *∑MI* ($p = 0.003$) which was highest within Eu-Mediterranean level (3) and lowest within the Montane-Mediterranean zone (2.57); *PPI* ($p < 0.001$) which was significantly higher in Eu-Mediterranean zone (3.55) compared to Supra-Mediterranean zone (2.81); and *EI* ($p = 0.004$), where the highest value was recorded in Thermo-Mediterranean zone (43.58), while the lowest value was reported in Montane- Mediterranean zone (28.80).

Nematode assemblage feeding structure on Pinaceae species in Syrian coastal region

According to their trophic preference, the fraction of soil nematodes was calculated using NINJA. The following trophic groups (herbivores, fungivores, bacterivores, predators and omnivores) were recorded. Herbivores, bacterivores and fungivores nematodes were the most frequent on all Pinaceae species, while omnivores and predatory nematodes were less frequent (Fig. 3A). The highest occurrence of herbivores was reported on *P. nigra* (42.1%) and the lowest was on *P. pinaster* (23.69%). The high occurrence of bacterivores (41.55%) was reported on *P. pinaster*, while the lowest was on *P. radiata* (24.26%). Fungivores nematodes were mostly present on *P. radiata* (33.31%), while they were less frequent on *C. libani* (9.96%). The highest occurrence of predatory and omnivores nematodes was detected on *P. pinaster* (14.59%), and on *C. libani* (2.88%), respectively. Omnivores nematodes were not reported on each *A. cilicica* and *P. radiata*.

Regarding the fraction of free-living nematodes (FLN) only, the analyses demonstrated that the bacterivores were dominant all Pinaceae species except on *P. pinea* and *P. radiata* where the dominance was for fungivore nematodes. The omnivore nematodes represented the lowest fraction among FLN. The highest occurrence of bacterivores was on *C. libani* (59.28%) and the lowest on *P. radiata* (37.75%) (Fig. 3B).

The % composition of herbivorous nematodes varied according to parasitism type (Fig. 3C). The epidermal / root-hair nematode group was the most dominant (72.02%) on *P. pinaster*, followed by the ectoparasitic nematode group (57.2%) on *A. cilicica*. The highest occurrence of semi-endoparasitic nematode group was on *P. radiata* (46.22%). The endoparasitic nematode groups (sedentary and migratory) were less frequent, they were especially reported on *C. libani* (21.52%) on *P. canariensis* (21.45%), respectively.

The % fractions of c-p (colonizer-persistent) and the p-p (plant-parasitic) values of, respectively, free-living and herbivorous nematodes, were also calculated. The results showed the predominance of c-p2 nematodes on all Pinaceae species, with the highest occurrence on *P. radiata* (81.21%) (Fig. 3D). Regarding the p-p groups, the dominance was alternated between the p-p2 and p-p3 groups. The p-p5 group was also well represented especially on *P. halepensis*, *A. cilicica*, *P. brutia* and *C. libani*. The p-p4 group was exclusively present on *P. canariensis*, *P. pinea*, *P. halepensis* and *P. brutia* (Fig. 3E).

Nematode community patterns associated to Pinaceae species in Syrian coastal region

The NMDS (Non-metric Multidimensional Scaling) axis provides a clear visual representation that the nematode communities reflect different patterns according to the Pinaceae species studied. According to the analysis (Fig. 4), the 9 Pinaceae species considered by the study could be regrouped into three groups: the first one included *A. cilicica* (Ac), *C. libani* (Cl), *P. canariensis* (Pc) and *P. pinea* (Pp*). P. brutia* (Pb) was grouped with *P. halepensis* (Ph) and *P. radiata* (Pr) in a distinct group. *P. pinaster* (Ppi) formed a group with *P. nigra* (Pn). These different groups of species were significantly different ($P < 0.001$; assumption of homogeneity of multivariate dispersion = 0,000032***).

To support this structuration of Pinaceae species into three groups, the % of common genera between plant species was investigated within each group using Venny analysis. Within the first group including *A. cilica*, *C. libani*, *P. canariensis* and *P. pinea*, Venn's diagram revealed 28 genera (49.1%) in common, and 1 unique genus for each of them (Fig. 5A). Considering the second group, *P. brutia* shared 28 genera (49.1%) in common with *P. halepensis* and *P. radiata*. 7 genera (12.3%) were only identified on *P. brutia*, 2 genera (3.5%) were exclusively detected on *P. halepensis* and 1 genus (1.8%) was uniquely present on *P. radiata* (Fig. 5B). According to the third group, 17 genera (42.5%) were detected in common between *P. nigra* and *P. pinaster*, while 21 genera (52.5%) seem to be specific to *P. nigra* and 2 others (5%) were exclusively identified on *P. pinaster* (Fig. 5C).

The correlations of nematode community genera to Pinaceae species were inspected by a Co-inertia analysis. According to the analysis, the proportion of variance attributed to the first two CIA axes was 38.93% and 27.99% (eigenvalues), respectively. The loading plot (Fig. 6) indicated that CIA1 axis was most closely related to *P. halepensis, P. nigra* and *C. libani* (positive values, located on the right side of the axes), in contrast to *P. brutia* (negative values, located on the left side of the axes). The analyses also indicated a significant contribution from *P. pinea* and *A. cilicia* (positive values) to CIA2 axis in contrast to *P. canariensis* (negative values). By projecting the nematode genera onto the loading plot, the analysis indicated that, according to CIA1 axis, *Paratylenchus* was mostly related to *P. nigra*, while, conversely, *Tylenchulus* was closely related to *C. libani*. *Xiphinema* and *Promumtazium* were mostly associated with *P.*

halepensis. According to the CIA2 axis, *Helicotylenchus* was associated with *P. pinaster*, and *Pratylenchus* was essentially associated with *P. canariensis*. *Cephalobus* and *Rhabditis* were associated with *P. brutia*, while *Aglenchus*, *Polenchus* and *Monhystera* seem to be a part of the community composition of *A. cilicica, P. radiata* and *P. pinaster*, in opposition to *Aphelenchus* essentially associated with *P. pinea.*

To confirm the association of nematode genera to Pinaceae species, as shown by the Co-inertia analysis, the population density of some of the most common nematode genera (selected according to their CIA1 and then their CIA2 eigenvalues) was compared between Pinaceae species. *Cephalobus* (10060 individuals) and *Rhabditis* (3488 individuals) were more abundant on *P. brutia* (Fig. 7A). Figure 7B showed high population density of *Xiphinema* (4520 individuals) and *Promumtazium* (2280 individuals) on *P. halepensis*. *Paratylenchus* was more abundant on *P. nigra* (5568 individuals), *Pratylenchus* were closely associated with *P. canariensis* (2608 individuals), while *Aphelenchus* was mostly higher on *P. pinea* (2676 individuals) (Fig. 7C).

Discussion

The main objectives of the present paper were to determine the identity, frequency, population density, diversity and structure of nematode communities associated with some Pinaceae species in the coastal region of Syria, and then compare, via several nematode-based indices, their diversity and structure between plant species, pine origins, habitat types and vegetation zones. This study is the first report on nematode communities associated with these trees from Syria. Twenty-three of a total of 62 genera were reported for the first time from the country. This high diversity of nematodes reported on Pinaceae trees is supported by the results of other surveys worldwide (Yates 1990; Peneva and Choleva 1994; Armendâriz et al. 1996; Deimi and Metkowski 2017; Ali et al. 2021; Karmezi el al. 2023; Öztürk 2025).

Several ecological and biomonitoring indices were applied and compared according to four different factors (plant species, pine origins, habitat types and vegetation zones), in order to expect how nematode communities could be affected by their surrounding environment and demonstrate the level of stability or disturbance within the studied communities. Some indices showed significant variation essentially between Pinaceae species (Table 3). The *MI2-5* index revealed higher values on *P. halepensis* and *A. cilicica*, indicating a mature community and a stable relatively undisturbed environment. A lower value was reported on *P. radiata* (referring to a simpler community structure subjected to disturbance by external factors) (Bongers 1990). That could be explained by the fact that *P. radiata* were sampled from localities subjected to disturbances (seashore or urban areas), whereas *P. halepensis* and *A. cilicica* were predominantly found in forests, far from human activities, susceptible to affect soil organisms' communities, including nematodes. The highest values of *PPI* were observed on *P. halepensis*, indicating a dominance of specialized plant-parasitic nematodes. That could be related to the high population densities of *Xiphinema* (*cp*-5) and *Promumazium* (*cp*-4) as shown by co-inertia analyses (Fig. 6) and confirmed in Fig. 7. Furthermore, *P. halepensis* plant may develop a dense and extensive root system, covering an area twice the size of its canopy, providing a suitable environment for parasitic nematodes (Andivia et al. 2019). In contrast, the low values of *PPI* reported on *P. pinaster* and *P. nigra*, reflecting either weak parasitic activity or a nutrient-poor environment (Du preez et al. 2022), could be related to the high population of *Paratylenchus* (c-p 2) associated with *P. nigra* (Fig. 7) as well as to the low population density of (p-p 4) and (p-p 5) groups (Fig. 3E).

The highest values of the *CI* (Channel Index) observed on *P. pinaster* and *P. radiata*, indicating a dominance of fungal decomposition and slower microbial activity, could be attributed to that these species growing in environments with low organic matter, which reduces bacterial activity and promotes fungal decomposition. Conversely, the low value reported on *P. halepensis* and *C. libani*, suggesting higher microbial activity and more balanced decomposition processes involving both fungi and bacteria, is likely due to the presence of roots rich in organic exudates (simple sugars and amino acids) as well as the availability of fresh nutrients which supports bacterial activity and bacterivores populations (Ferris et al. 2001).

The Enrichment Index (*EI*) (based on the abundance of opportunistic bacterivorus (*cp*-1) and fungivores (*cp*-2) nematodes) was significantly higher on *P. halepensis*. compared to *P. pinaster*, reflecting a greater availability of fresh organic matter under *P. halepensis* and a lower nutrient enrichment in soil under *P. pinaster*. The needles of *P. pinaster* characterized as hard, thick, rich in lignin and tannins, and therefore decompose slowly (More and Domingo 2000) could be the reason of the value. This suggests a relatively poor soil in readily available organic matter for microbial and bacterial activity, and consequently, a lower density of bacterial-feeding nematodes (Ferris et al. 2001). In contrast, the needles of *P. halepensis* decompose more rapidly, and this species is adapted to arid environments, releasing relatively more readily decomposable organic matter, which promotes microbial activity (Kurz et al. 2000(. In contrast to *EI*, The highest *BI* values were observed for *P. radiata* and *P. pinaster*, indicating the dominance of basal genera (genera characterised by low requirements, tolerant to nutrient-poor and stressed environements, e.g. *Cephalobus* (*cp*-2), *Aphelenchus* (*cp*-2) in our study, adapted to disturbed environments). Low value was reported on *P. halepensis*, suggesting a stable, resource-rich environment, and more diverse nematode communities (Ferris et al. 2001).

The *SI* (Structure Index) values were high on *P. halepensis*, *P. pinea*, and *A. cilicica*, reflecting a more complex and diverse food web, and low on *P. pinaster*, indicating a simplified community (Ferris et al. 2001).

Based on the above, indices' analyses of nematode communities associated to *P. halepensis* reflect a more stable (high *MI2–5*), nutrient-rich soil (high *EI*), with a high microbial activity and a diverse nematode community (high *SI*), and a decomposition typically follows a rapid and bacterial-dominated pathway (low *CI*). Furthermore, nematode communities were less dominanted by basal taxa, reflecting a more diverse functional structure (low *BI*). In contrast, nematode communities under *P. pinaster* and *P. radiata* indicate a more disturbed (low *MI2–5*) and nutrient-poor habitat types (low *EI*), with simpler food webs (low *SI*), dominated by slower fungal decomposition (high *CI*), and with a clear dominance of basal taxa (high *BI*).

Pine origins as native and exotic species revealed some significant differences in nematode community indices (Table 3B). Native species showed higher values for *MI 2–5*, Σ*MI*, *PPI* and *SI*, reflecting a more stable and complex nematode community structure, as well as a higher abundance of plant-parasitic nematodes, likely due to their long-term adaptation to the environment (Wasilewska 1997; Ferris et al. 2001). Conversely, *CI* and *BI* were higher under exotic species. The higher *CI* value indicates that organic matter decomposition in this soil is more dependent on fungi, while, a higher *BI* value indicates a higher

bacteria-feeding nematodes activity and a degraded environment poor in nutrients (Bongers and Ferris 1999), which is related to the nature of introduced species able to adapt to poor and dry soil conditions, especially *P. canareinsis* and *P. pinaster* (Nguyen-Queyrens et al. 2003; López et al. 2016).

Considering vegetation zones, three indices only (*MI*, *PPI* and *EI*) showed significant differences (Table 3C). This agrees with Xue et al. 2015, who found no direct relationship between altitude and functional indices of nematode communities. *MI* showed higher values in the Eu-Mediterranean zone and lower in the Montane-Mediterranean zone, reflecting a more complex nematode community at mid-elevations, potentially due to the availability of organic-rich soil and moderate organic matter decomposition, compared to the colder, higher altitudes that limit community activity and diversity. *PPI* index was also higher in the Eu-Mediterranean zone and lower in the supra-Mediterranean zone, suggesting that plant-parasitic nematodes are more abundant at mid-elevations due to favorable root activity and moderate environmental conditions, while their activity decreases at higher altitudes due to lower soil temperatures and altered physical properties. That could explain why the *EI* index showed higher values at lower altitude (thermo-Mediterranean zone) and lower values in the Montane-Mediterranean zone. This reflects the abundance of available food resources for nematodes in the lower zones, due to the rapid decomposition of organic matter at higher temperatures, compared to the colder, higher zones where decomposition is slower. This finding is consistent with the observations of Zhang et al. 2021, who stated that soils in lower-altitude areas exhibit greater nematode diversity and richness than those in higher altitudes, indicating a more sustainable and resilient ecosystem.

The above results showed the important role of tree species as the main factor driving the nematode diversity in communities, supporting the results of other findings (Bardgett and Wardle 2010; Cesarz et al. 2013). Nematode communities diversity and structure could be strongly influenced by tree species, either directly through the quality of leaf litter (e.g., carbon-to-nitrogen ratio) or root exudates, or indirectly through microorganisms that live in symbiosis with tree roots (Kondratow et al. 2019; Heděnec et al. 2023).

According to NINJA results, the trophic structure of nematodes in communities varied between Pinaceae species (Fig. 3A). Plant-parasitic nematodes were dominant in communities (42.1% of the total % nematodes). They were especially reported on *P. nigra*. its sensitivity to nematode infection in raison to a mal-adaptiveness with the coastal region environment Bacterial and fungal groups, ranked second and third, respectively, with higher occurrence on *P. pinaster* and *P. radiata*.

Among the free-living nematode communities, only bacterivores were dominant (59.28%) in the *C. libani* forest (Fig. 3B). That could be supported by the results of Čerevková et al. (2021), who found that bacterial-feeding nematodes are dominant in forests. These nematodes are actively involved in the organic matter decomposition and regulating bacterial communities, thus enhancing nutrient availability for plants (Bardgett and van der Putten 2014). Fungivores were especially reported on *P. radiata* (51.83%). Their high abundance could be attributed to soil acidification resulting from litter accumulation or the presence of mycorrhizal fungi (Háněl 2001; Sohlenius 2002). Regarding plant-parasitic nematodes only (Fig. 3C), root-feeding nematodes were the predominant species (72.02%), found on all tree species studied. This is consistent with Yeates and Bird (1994) and Ferris and Bongers (2006), who noted that Tylenchidae is among the most abundant soil organisms, comprising 30% of the total nematode population in soil samples. It is also consistent with Neher (2010), who found that these nematodes are widespread in diverse soil environments, reflecting their high adaptability and ability to thrive in various environments. Ectoparasitic nematodes were also dominant (57.2%). This is consistent with the findings of Öztürk (2025), who reported that ectoparasitic nematodes were the most abundant group after root hair feeder nematodes on trees, including Pinaceae. The sedentary parasitic group was dominant on *C. libani* (21.52%). This is likely due to the high population density of citrus nematodes *Tylenchulus semipenetrans.* The high prevalence of citrus nematode on *C. libani* could be explained by the proximity of some sampling sites to adjacent citrus farms.

Considering the c-p2 and p-p2 groups (Fig. 3D, 3E), they showed high prevalence across all plant species, indicating their ability to adapt and survive in diverse soil and plant environments, along with the availability of suitable microbial communities and essential nutrients. This is consistent with the results of Li et al. (2020), which demonstrate the higher abundance of these groups in various environments.

The NMDS axis (Fig. 4) supported our hypothesis that the plant species as the main factor is involved in the structuration of nematode genera in communities. It revealed a significant distinction (p-value = 0.001) of Pinaceae species based on the composition of their associated nematode communities. The Venny analysis (Fig. 5) showed the % of similarity between Pinaceae species and the common and unique nematode genera for each one. According to these analyses, it was observed that some species clustered in similar areas, indicating a relative similarity in their associated nematode communities, while other species occupied distinct positions, reflecting differences in the composition of these communities. *A. cilicica*, *C. libani*, *P. canariensis* and *P. pinea* clustered together (Fig. 4), and shared (49.1%) of nematode genera (Fig. 5A). The clustering of *P. pinea* with these three other species can be explained by its co-occurrence with *P. canariensis* in six of the sampling sites (Fig. 1). Its association with *C. libani* and *A. cilicica* is likely due to shared characteristics, such as deep root systems, phenolic acids exudates, in addition to their distribution in mid to high altitude areas. *P. brutia* was clustered with *P. halepensis* and *P. radiata* in a distinct group and shared (49.1%) of nematode genera (Fig. 5B). This association between *P. brutia* and *P. halepensis* can be partially explained by the similarity in terms of tree morphology, roots and secretions (Nikolić et al. 2024), and by the fact that they are two native species that spread in the same nursery soil in the study areas. This can be explained by the fact that *P. radiata* shares a common ground with *P. brutia* in one of the studied sites. Also, *P. radiata* was planted in another area of the study that was previously forested with *P. brutia*. A 42.5% of similarity was observed between *P. pinaster* and *P. nigra* (Fig. 5C), reflecting a certain level of structural similarity in the nematode communities, while each species retained its unique genera, The observed similarity can be attributed to the fact that both species are introduced and have been propagated and cultivated under identical conditions—within the same forest nursery and on the same soil type—for several years prior to their transfer to afforestation sites. Furthermore, both species were established using an open-system afforestation approach, characterized by relatively low canopy cover (less than 40–60% of the land area). Consequently, the wide spacing between trees exposes the soil more directly to environmental and climatic fluctuations, such as rainfall and solar radiation (Hanberry et al. 2018). This structuration could be related to the potential influence of plant species on soil microbial communities, supporting the hypothesis that each pine species creates a distinct biological environment that affects nematodes in terms of diversity, abundance, and ecological function. This finding aligns with Xu et al. (2023), who showed that the pine species has an impact on nematode community structure, and with Cesarz et al. (2013), who suggested that the

tree species itself is often more important than its diversity in determining the composition and diversity of nematode communities in forest ecosystems. It also agrees with Kitagami et al. (2024), who found that tree species identity, root characteristics, and soil environment influence the composition of associated nematode communities.

Co-inertia analysis was performed in order to identify the patterns of nematode community associated to each conifer species (Fig. 6). According to the analysis, *Paratylenchus* were essentially associated to *P. nigra*. This finding is consistent with the study by Peneva and Choleva (1994), who also recorded *Paratylenchus* on *P. nigra. C. libani* communities were predominantly composed of *Tylenchulus* due to their cultivation near citrus groves (i.e., in a different vegetative zone). The detection of *Tylenchulus* on root samples suggests that *Cedrus* trees are probably a new host for *Tylenchulus*, but further tests are required before confirmation. The analyses also showed the association of *Pratylenchus* to *P. canariensis*. This association was confirmed in Fig. 7. This is the first report on this association as literature reviews did not show any studies on the nematode communities associated with this tree species, possibly due to its very limited distribution outside its native range. The association of *Xiphinema* to *P. halepensis* is probably attributed to the unique forest nature of the study sites, characterized by their remoteness from human activities (agricultural practices, pesticides, etc.), which encourages nematode of c-p5 group (very sensitive to disturbances induced by human practices). The dominance of *Helicotylenchus* is due to the small number of specimens of this forest species and the identification of this genus in all of these specimens, which was previously identified for this *P. pinaster* species (Ali et al. 2021). The dominance of bacterial nematodes (*Cephalobus*, *Rhabditis*) on *P. brutia* and the prevalence of *Aphelenchus* on *P. pinea* could be attributed to the topsoil associated with these two pine species, composed of organic matter resulting from leaf litter accumulation and rapid decomposition of their needles, as well as the nature of the roots and the widespread presence of associated fungi. This agrees with Karmezi et al. (2023) on *P. brutia* and Öztürk (2025) on *P. pinea*. No preference for a specific nematode genus was observed either on *A. cilicica* or *P. radiata*, possibly due to the high abundance of Tylenchidae nematodes. These multivariate analyses indicate specific relationships between certain conifer species and specific nematode genera, with a clear distinction between plant-parasitic and free-living nematodes. They concluded that the structure of nematode communities varies across conifer species. Norton (1989) demonstrated that the host plant is the most important factor influencing nematode community composition, a finding later confirmed by subsequent studies (Yeates 1999; De Deyn et al. 2004). This distinction supports the hypothesis that plants directly influence the structure of microbial communities and provides a powerful tool for understanding complex ecological interactions within ecosystems (Han et al. 2021; Sun et al. 2022).

Conclusion

The current study concludes on a key role of Pinaceae species in the functional diversity of soil nematode communities. A high trophic diversity was reported, indicating high ecosystem stability and maturity. Significant differences were observed in some indices among Pinaceae species (e.g. MI 2–5, PPI, EI, SI, N). Elevated Maturity and Structure Indices under certain species (e.g. *P. halepensis*) further reflect well-structured and sustainable soil food webs, consistent with previous findings that permanent tree cover supports more stable nematode communities (Renčo et al. 2020). Nematode structure was also shown affected as distinct patterns according to Pinaceae species groups were reported. Tree-related factors (e.g. root exudates, decomposition leaves) could contributed to this variation.

Declarations

Conflict of interest

The authors declare that they have no conflicts of interest.

Ethics approval and consent to participate

the paper reflects the authors' own research and analysis in a truthful and complete manner.

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Author Contribution

Jaraa conducted the study, defined the nematode genera, wrote and reviewed the manuscript. Ali contributed to the genera definition and statistically analyzed the data. Shater contributed to identifying research sites and conducting fieldwork. Jaraa, Ali, and Shater all contributed to the final draft of the manuscript.

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Data Availability

This material is the authors' own original work, which has not been previously published elsewhere and has no conflict of interest.

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Figures

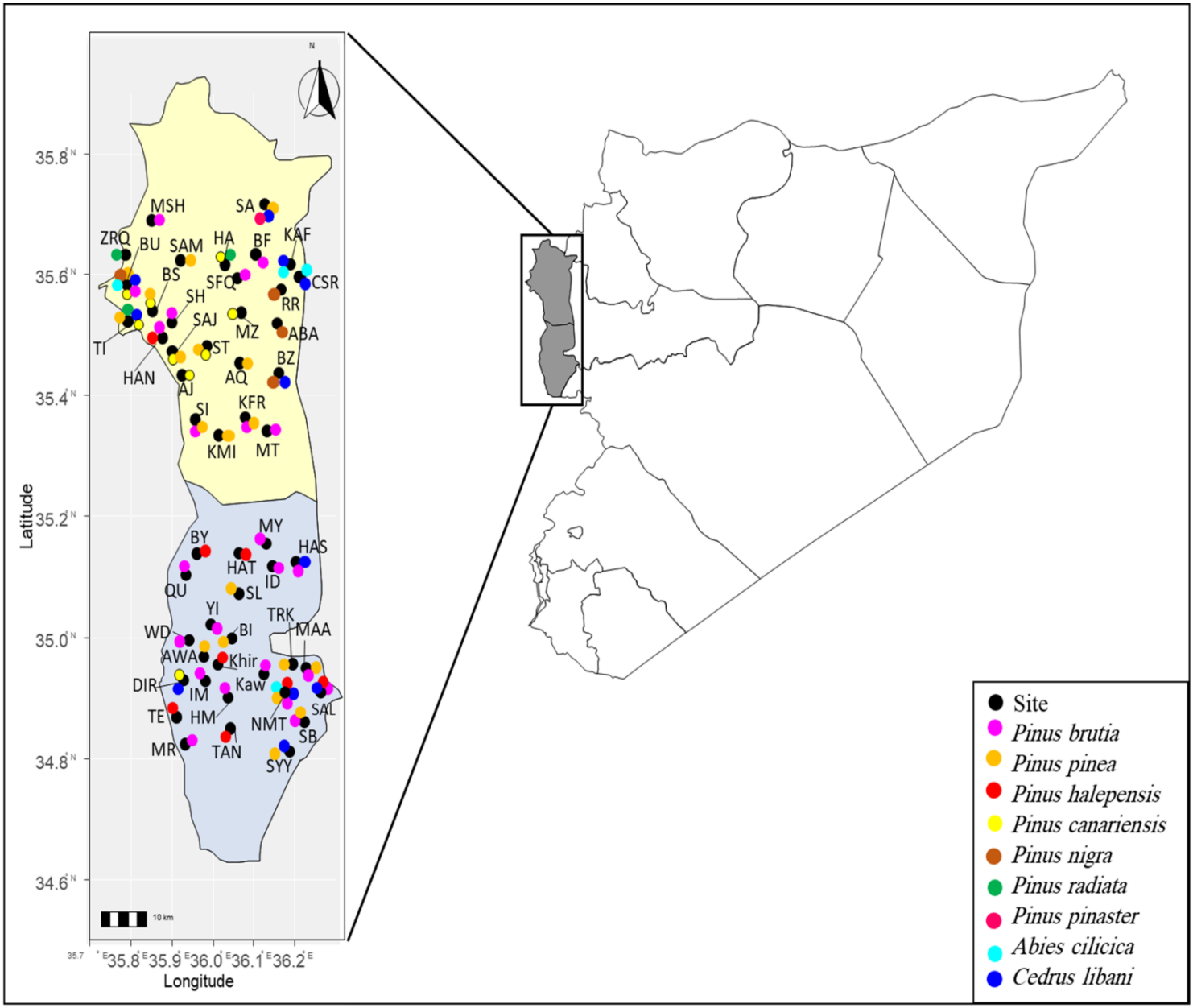


Figure 1

Sampled sites of Pinaceae on the Syrian coast.

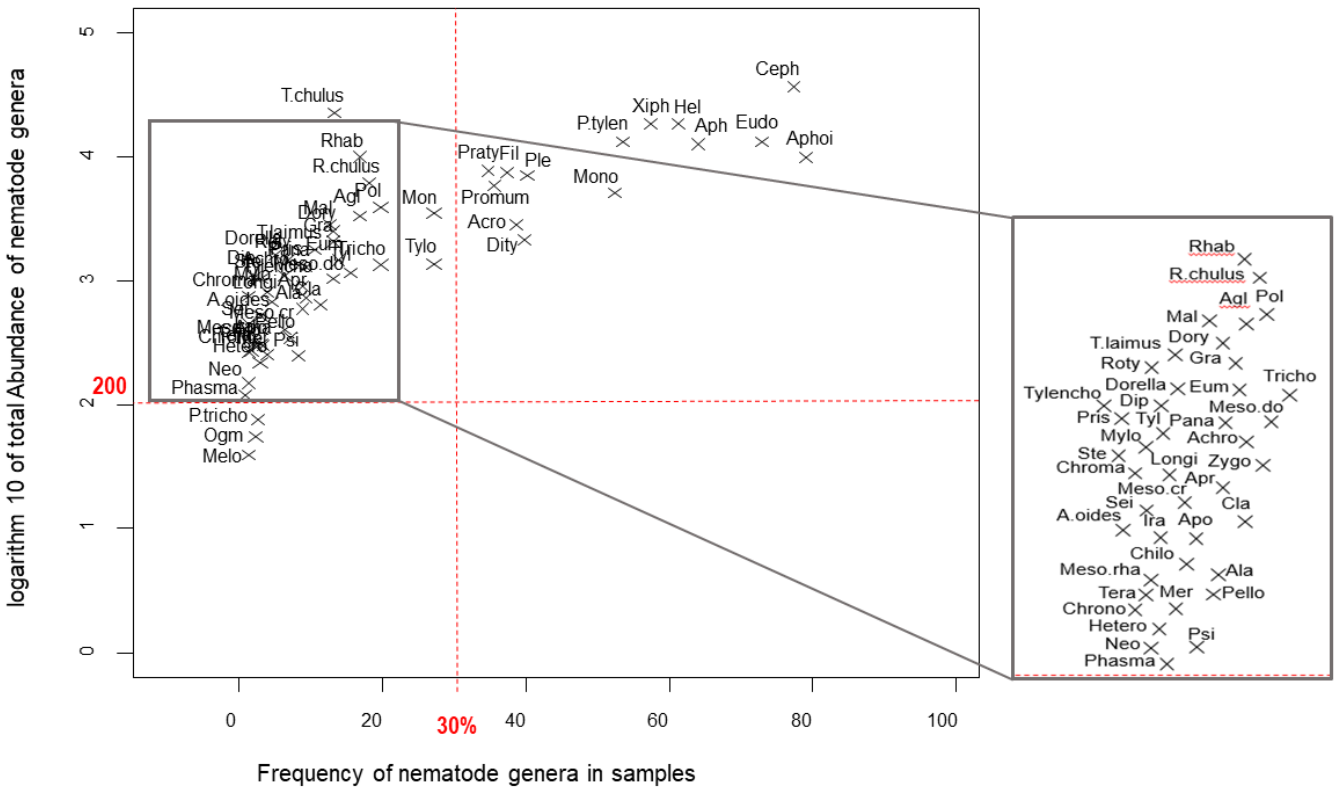


Figure 2

Dominance diagram of the nematode genera. Dotted lines indicate delineation (threshold) between low and high abundances and frequencies as described in (Fortuner and Merny 1973).

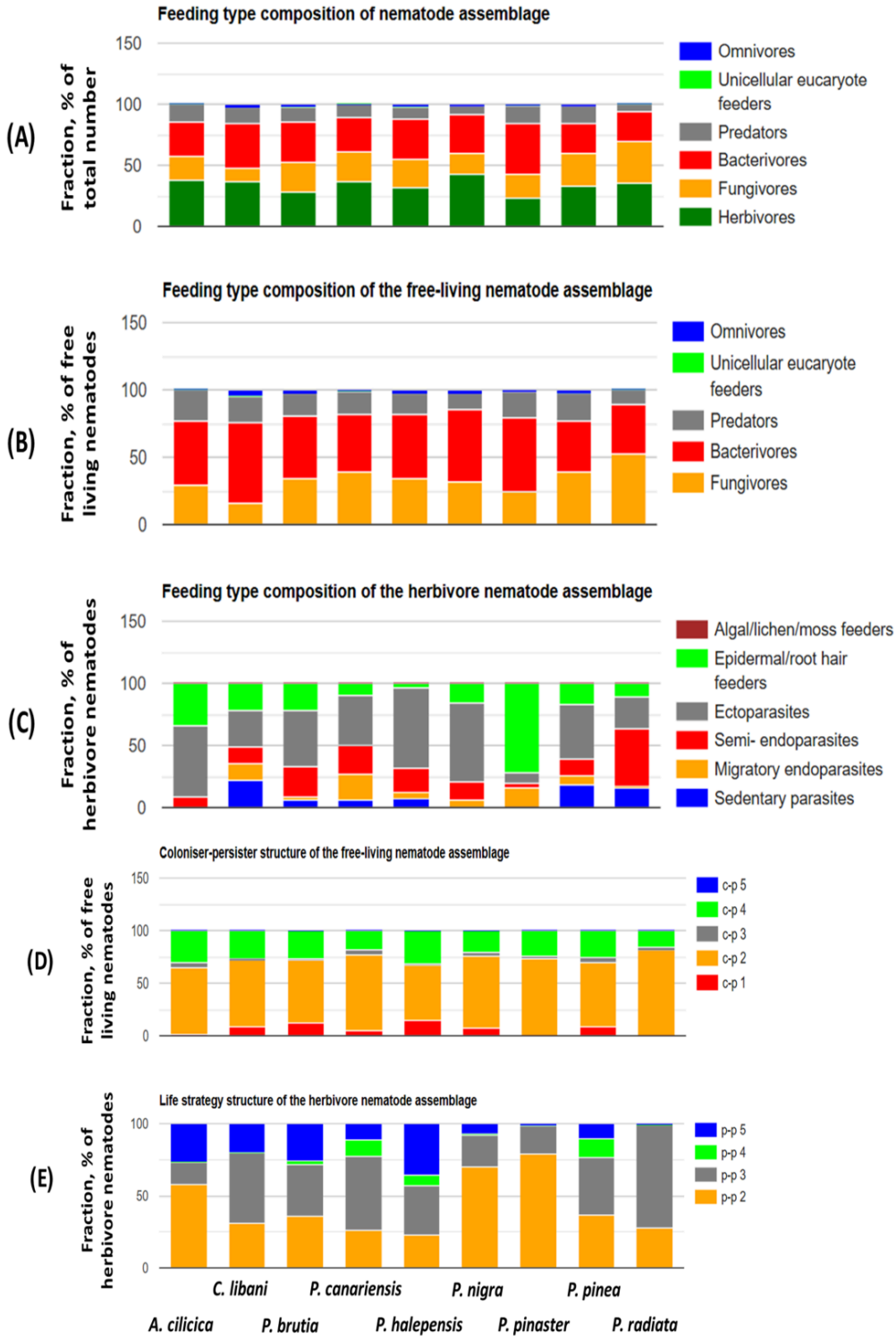


Figure 3

% Fraction of nematode communities occurred on Pinaceae species along the Syrian coast. (**A**) % Fraction of the total nematode numbers to their respective feeding group. (**B**) % Fraction of free-living nematodes. (**C**) % Fraction of herbivorous nematodes. (**D**) % Fraction of free-living nematodes according to their c-p (colonizer-persister) values. (**E**) % Fraction of PPNs according to their p-p (plant-parasitic) values.

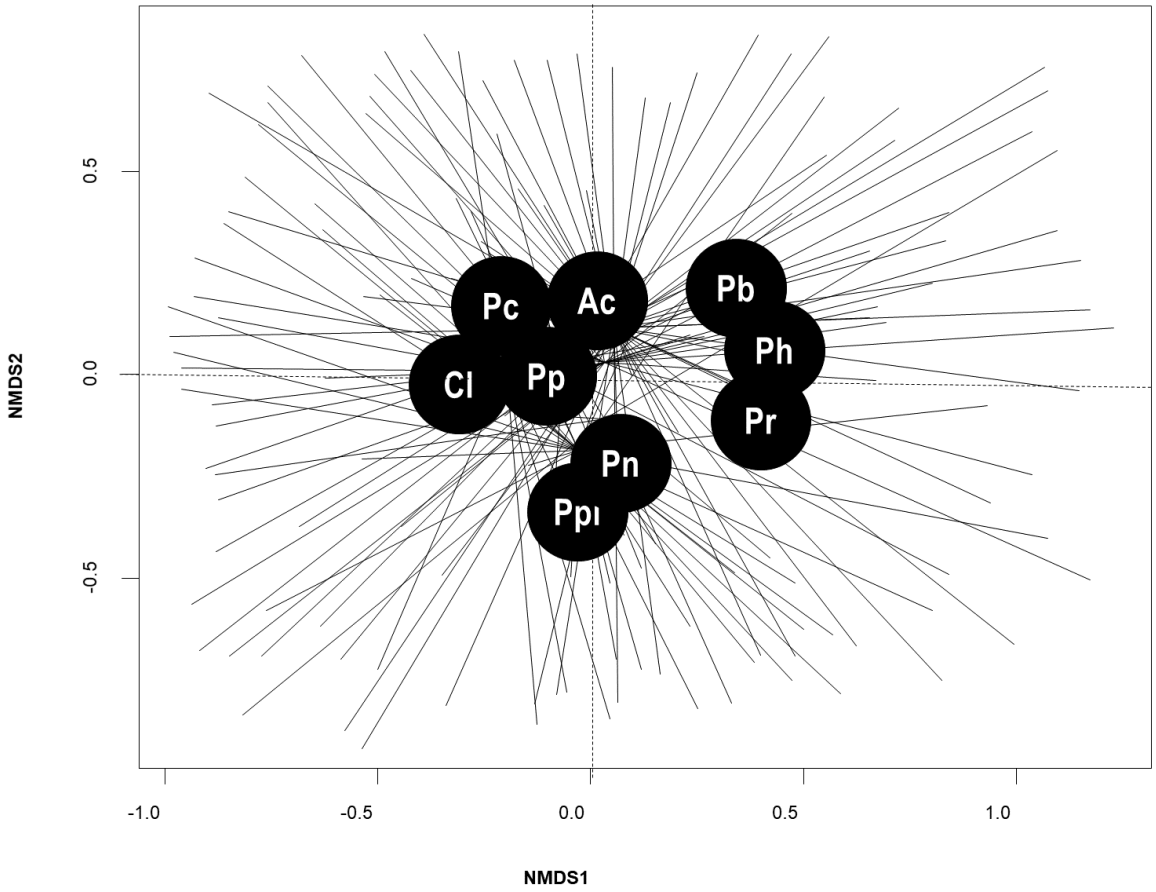


Figure 4

NMDS ordination analyse between nematode community structure and the different Pinaceae species sampled on the Syrian coast. Ac= *A. cilicica*, Cl= *C. libani*, Pb= *P. brutia*, Pc= *P. canariensis*, Ph= *P. halepensis*, Pn= *P. nigra*, Pp= *P. pinea*, Ppi= *P. pinaster*, Pr= *P. radiata*.

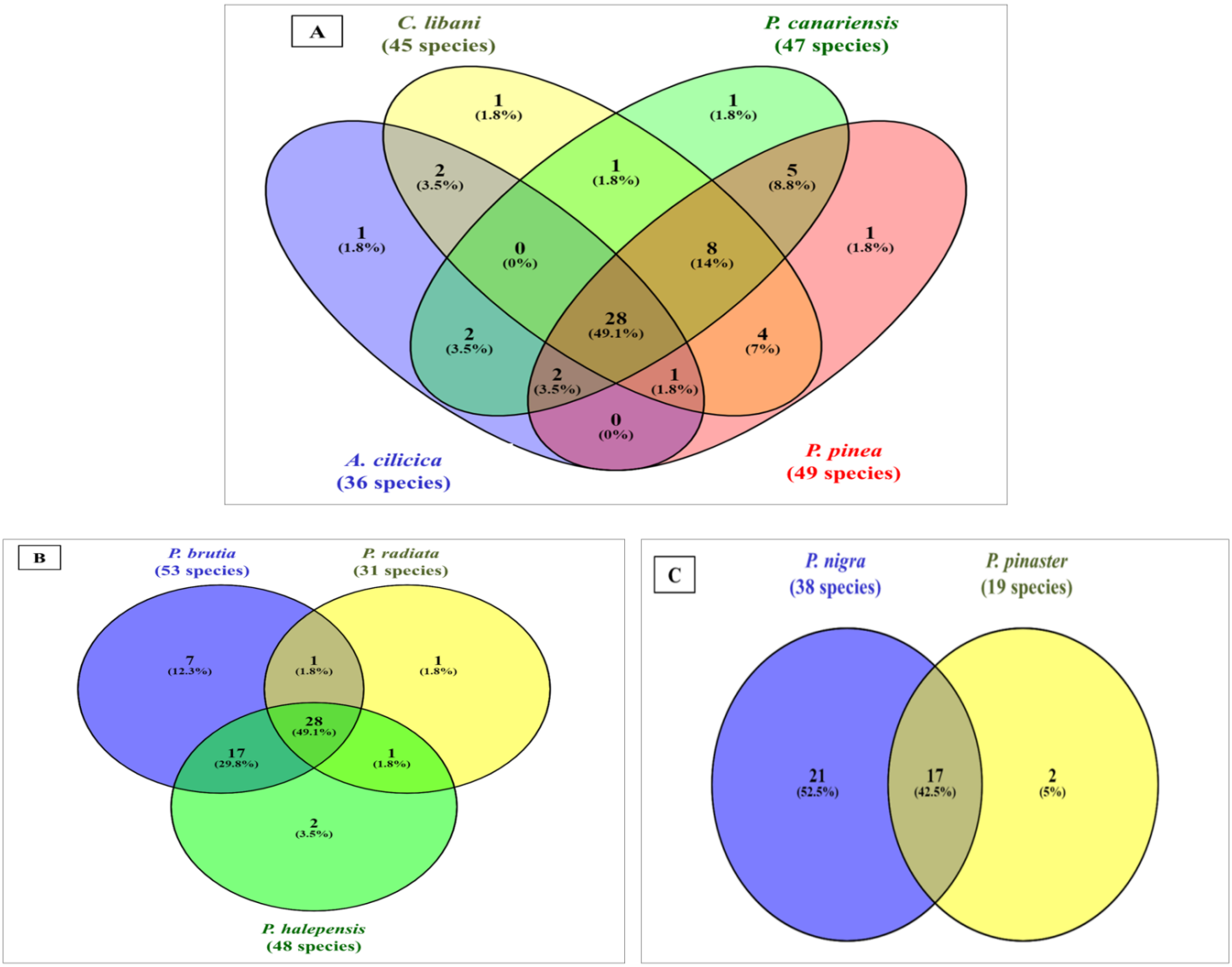


Figure 5

Venny diagram showing the common genera between Pinaceae groups (as shown in NMDS axis).

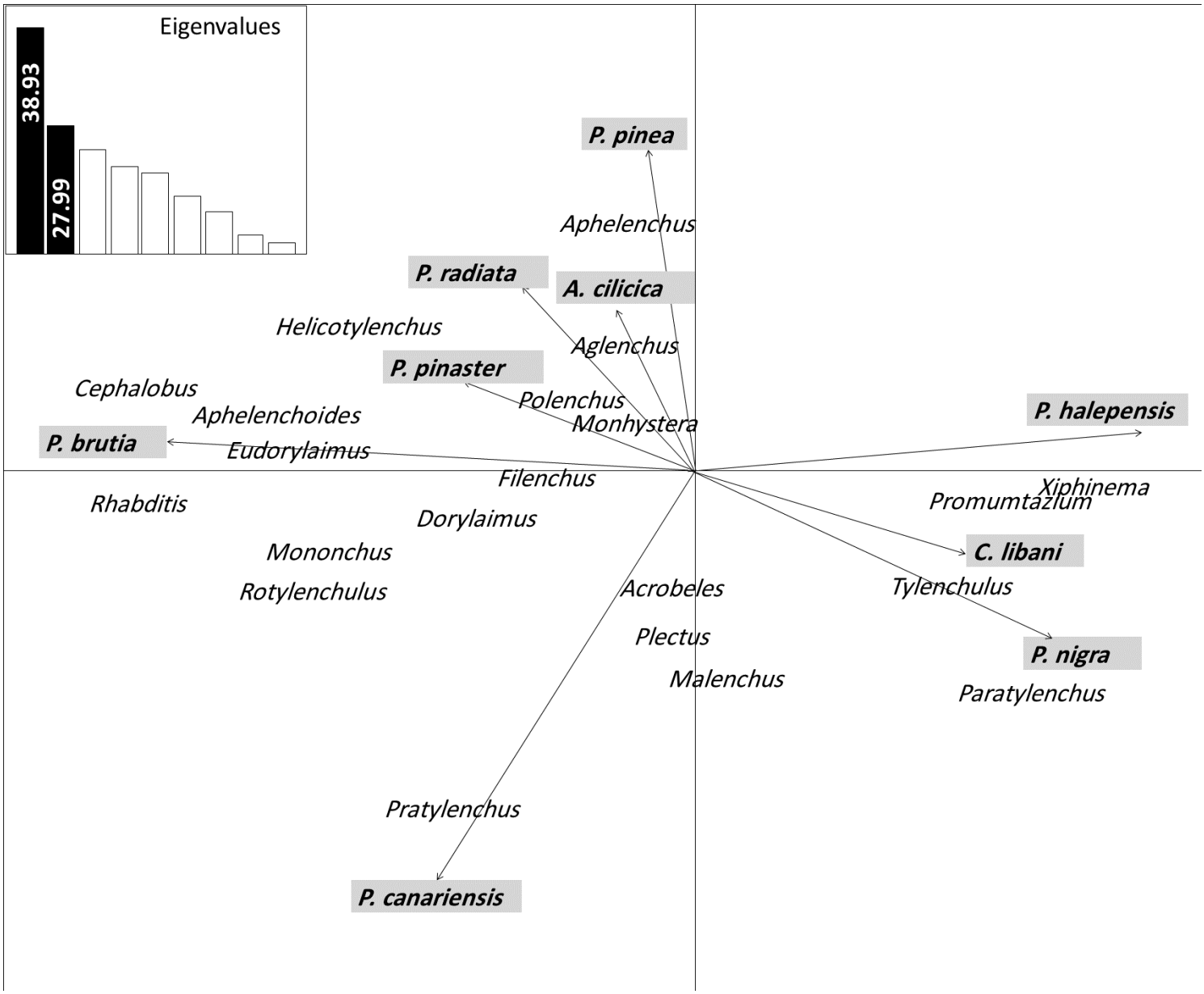


Figure 6

CIA loading axis for the nematode genera and Pinaceae species showing the structuration of nematodes genera according to plants species.

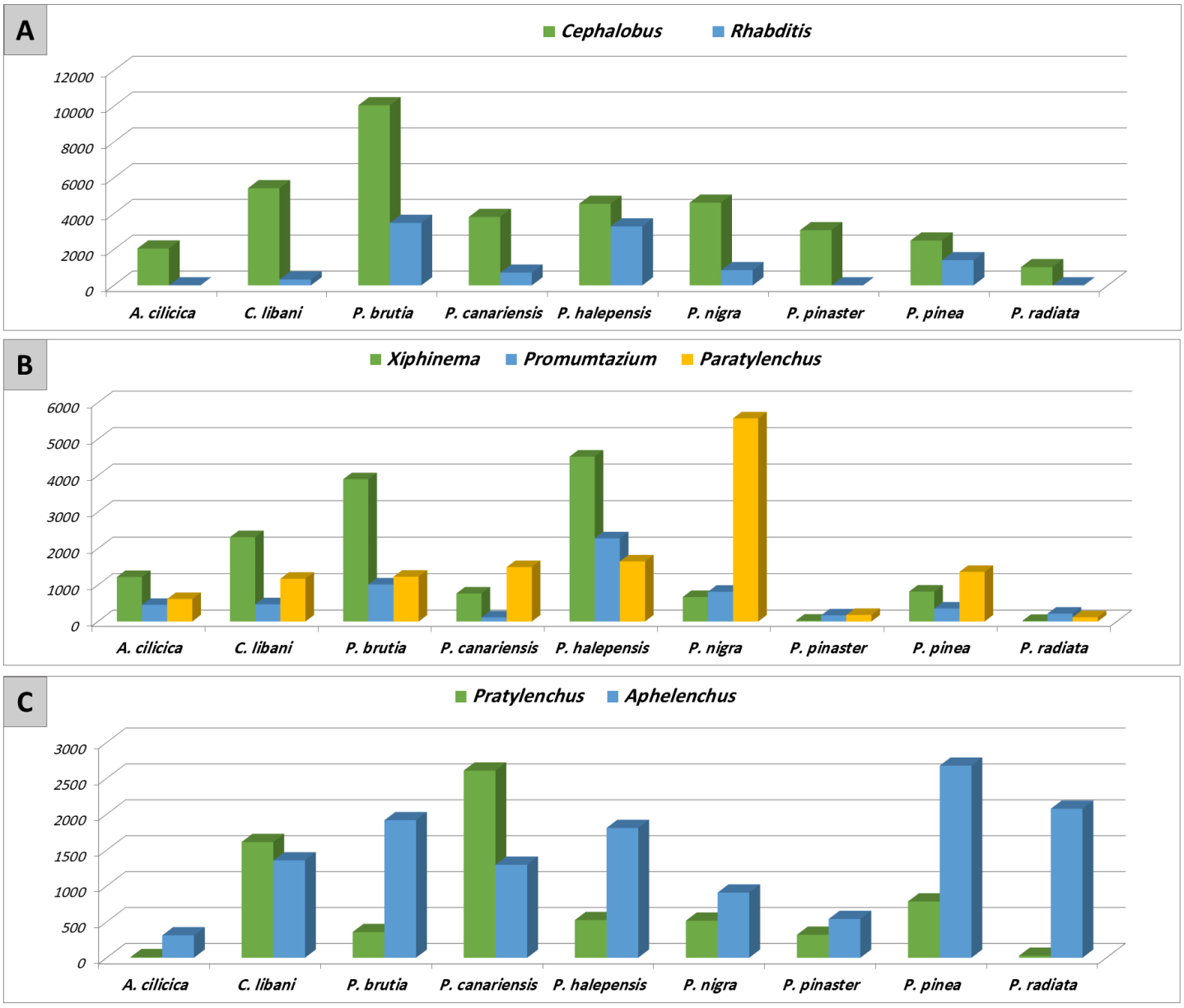


Figure 7

Comparisons of average number of nematodes (per 250 cm³ of soil) among different Pinaceae species, arranged according to their position on the CIA1 axis and then on the CIA2 axis, as shown in Figure 6.