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Legacy of plant-parasitic nematode communities from past ecosystems and shift by recent afforestation

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A B S T R A C T

Ancient ecological legacies and past land use changes may inform on the present structure of biological communities. However, regions providing such successive ecosystems are scarce. In France, the 'Landes de Gascogne' area provides such ecological shifts since a few ancient moorland, peatland and oak areas prior the afforestation with maritime pine (*Pinus pinaster*) 160 years ago still remain. Focusing on soil-borne parasites such as plant-parasitic nematodes (PPN), because forests were recently increasingly impacted by the introduction of intensive agriculture, this study is therefore aimed at comparing the diversity and the community patterns of these organisms at different scales (intra- and intersites) and between different successive ecosystems. The understory vegetation as well as the pedo-climatic characterization of the sampled sites were also considered. Common diversity indices were not impacted by this transition from ancient to past ecosystems. Although the most colonizer nematodes prevailed in all the ecosystems, PPN community structures significantly diverged between both ecosystems. In the logged pine forests, the sediment legacy could have primarily impacted the diversity. Moreover, the PPN diversity would mainly respond to the soil hydromorphicity that determined the associated understory vegetation. Consequently, a significant shift in community structure from moorlands to logged pine to logged pine forests was observed, regarding especially high pathogenic species such as *Pratylenchus* spp. Thus, analyzing PPN community structure highlights the PPN potential risk to consider during the introduction of intensive cropping systems.

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1. Introduction

Most of biodiversity studies focusing on land-use changes target present agrosystems to lead suitable management practices for protecting or restoring sustainable landscapes with special focus on soils (Greenland and Szabolcs, 2002). Managing soil quality became a new challenge in modern agriculture (Schjonning et al., 2004; Beniston et al., 2016), especially to improve soil suppressiveness to disease (Janvier et al., 2007; Sánchez-Moreno, 2016). Studies on soil impacts of ancient land-use changes are scarce and mostly focus on plant diversity and post-agricultural forests set during the previous centuries, instead of cultivated fields (80% of the current forest cover; Flinn and Vellend, 2005). Other ancient land-use changes also concern the afforestation of natural ecosystems, especially moorlands (Hester et al., 1991).

In the southwest of France, the 'Landes de Gascogne' area was submitted to an overall afforestation 160 years ago (Regulation June 19, 1857; Sargos, 1997). However, at the end of the last glacial period and after the accretion of Atlantic sands throughout the Aquitaine basin, increasing rainfalls have turned this region into swamplands supporting hygrophilous and mesophilous trees (oak, alder, birch, willow, hazel). During the same period, peatlands developed mostly in valley floors. Today, a few peatlands are located near the lakes, and other rare sites are located in riverbeds that most often correspond to old dead branches (Maizeret, 1998). They come from accumulation of plant matter, whose decomposition is incomplete. These processes were dated to about 5000 years ago (Gayet and Marambat, 1995). Today, relic peatlands and moorlands are very rare. Such sites of peatlands are located in the Leyre and the Le-Naou ('Parias' peatland). They mostly host Cyperaceae (*Eriophorum angustifolium, Schoenus nigricans*) and Poaceae (*Molinia caerulea*), and at a lesser extent Ericaceae (*Erica ciliaris*, *E. tetralix*). The deciduous forests have then disappeared in favour of moorlands because of the increasing development of itinerant pasture in these forests. Moorlands remain in three protected places occupied by French military camps ('Souge', 'Cazeaux' and 'Poteau'). The main habitats are wet and mesophilous moorlands (50%), natural pine forests (20%) and oak forests (15%). They are mostly inhabited by Ericaceae (*E. ciliaris, E. tetralix, Calluna vulgaris*), Poaceae (*M. caerulea*), Cyperaceae (*S. nigricans*) and Fabaceae (*Ulex minor*). Some patrimonial plants such as *Carum verticillatum* (Apiaceae), *Genista anglica* (Fabaceae), *Gentiana pneumonanthe* (Gentianaceae), *Serratula tinctoria* (Asteraceae) are relatively common there. The natural pine and oak forests are wet environments dominated by *M. caerulea* and *Pteridium aquilinum* (Dennstaedtiaceae), respectively.

Since the 19th century, the establishment of human populations in this area has required soil fixing with massive introduction of maritime pine (*Pinus pinaster*, Pinaceae). In wetlands, soil drying was improved by digging drains to rivers, and by the maritime pine. Maritime pine has been shown to contribute to the drying up and today, it covers more than 900,000 ha (FIBA, 2006). The major consequence of the afforestation has been the disappearance or rarefaction of biotopes as evidenced by the comparison with the ancient flora (Clavaud, 1881; Timbal and Maizeret, 1998). The low altitude of this area and the reliance of its hydrogeology to the Atlantic Ocean make a permanent water table at shallow depth. Seasonal fluctuations of the water table define three typological groups of pine forest ecosystems from dry to wet conditions (Demounem, 1979): (*i*) the dry forest mainly distributed near the rivers (which act as drains) or where the water table is more than 2-m deep, and mostly dominated by *E. cinerea* and *C. vulgaris*; (*ii*) the mesophilous forest characterized by intermediate levels of the water table, and dominated by *Pteridium aquilinum*; (*iii*) the wet forest distributed in the wide interfluves where the water table fluctuates between the soil surface in winter and 1.5 m deep in summer, and dominated by *M. caerulea* and *U. minor*. So, peatlands, moorlands and forests share many plant species in common, but at different levels of dominance depending on the dryness/wetness conditions.

Among all soil-borne pests of plants, plant-parasitic nematodes (PPN) are known to contribute significantly to plant production losses (Nicol et al., 2011; Sasanelli et al., 2018). Mainly, most PPN appear to have broad capacity to adapt to different environments (Bird et al., 2015). In addition, ecosystem types are significant in shaping soil nematode and microbial communities and affecting soil properties (Renčo et al., 2020). A descriptive approach based on the comparison of different ecosystems including moorlands and forests spotted exclusive DNA restriction fragments profiles of total nematode communities (Donn et al., 2008). It was established that the succession from moorland to birch forest clearly increased the abundance of PPN (especially *Helicotylenchus* spp. and *Paratylenchus* spp.) as a result of changes in both plant diversity as well as soil properties associated with tree invasion (Keith et al., 2006). Several PPN species were detected in the 'Landes de Gascogne' pine forests, regardless of the dryness/wetness conditions and therefore of the vegetation type (Baujard et al., 1979b). Trichodoridae and Hoplolaimidae nematodes would be more frequent in the wet and mesophilous forests while Criconematidae nematodes would mainly found in the dry forests. However, no evidence of pathogenicity of these PPN families was detected on pine (Baujard et al., 1979b). The texture of the upper soil horizons and their organic content influence the diversity of free-living nematodes diversity (especially fungal feeders, bacterial feeders), but not PPN diversity (Baujard et al., 1979b; Scotto La Massèse and Boulbria, 1980).

Nematode functional groups are also impacted by the ecosystems they inhabit. Nevertheless, comparing different forests and grasslands in Natura2000 sites, revealed that colonizer nematodes prevailed in forests, whereas persisters abounded in grasslands (Ciobanu and Popovici, 2015). Moreover, anthropogenic activities in forests are able to unbalance nematode

communities (Neher et al., 2005). Kalinkina et al. (2016) compared different land uses in forests and established that the proportion of PPN among all soil nematodes was higher under introduced trees than natural forests.

The present study focussed on the response of the PPN communities to a global land-use legacy (ancient peatlands, moorlands, pine and oak forests, and more recent afforestation). More specifically, we explored the potential drivers that may influence the community assemblages through examining interactions between PPN, vegetation, soil and climate according to a synchronic analysis in different aged ecosystems. This study is a first step towards understanding the impacts of moorland-to-forest shift on the diversity of PPN communities, evaluating how this diversity will be structured according to the environmental specificities, and providing information about the PPN risk that could appear in intensive crops introduced 60 years ago in the forest ecosystems after deforestation.

2. Materials and methods

2.1. Site description

The 'Landes de Gascogne' region is located in the south-west of France. It is delimited by the Atlantic Ocean to the west, by the River Garonne to the northeast and by the River Adour to the south. Five ecosystems were surveyed for nematode analyses (Table 1; Fig. 1):

- Peatlands: from two relic sites (site 4 'Langue' and site 7 'Parias'), dominated by *M. caerulea*) and by *M. caerulea* and *Sphagnum* sp.), respectively.
- Moorlands: from two relic sites (site 8 'Poteau1' and site 9 'Poteau2') (in the NATURA2000 area) characterized by wet (*M. caerulea*) and mesohygrophilous (*E. ciliaris* and *E. scoparia*) vegetation, respectively.
- An oak forest (*Quercus robur*, Fagaceae): from a wet relic site located in the 'Poteau' camp (site 10 'Poteau3') where *P. aquilinum* was the dominant understory plant.
- A natural pine forest (*P. pinaster*) from a wet site located in the 'Poteau' camp (site 11 'Poteau4').
- Logged pine forests: mostly dispersed in the 'Landes de Gascogne' Regional Natural Park which were moorlands prior to afforestation. Samples were taken from two wet sites (site 5 'Bel-Air' and site 6 'La Trougne'); three mesohygrophilous sites (site 1 'Ombrières', site 2 'Belle-Viste' and site 3 'Lagassey') and from two dry sites (site 4 'Langue' and site 7 'Parias').

2.2. Soil sampling

Soil sampling took place in 2010. In each site, five sampling points (five replicates) were marked every 10 m along a 50 m long transect. At each sampling point, several rhizospheric soil subsamples were collected using a 2-cm diameter gouge auger from 5 to 60 cm depth, around the plant species that dominated. The collected samples were gathered in a polyethylene bag to form a 500-cm3 reference soil sample for each sampling point. A total of 165 soil samples were recovered.

2.3. Nematode extraction and quantification

All nematode analyses were performed in the nematode quarantine area (French Government Agreement No 80622) of the Research Unit, 'Centre de Biologie pour la Gestion des Populations' (Montpellier, France). A 250-cm^3 wet soil aliquot of every sample was used for nematode extraction using the elutriation procedure (Seinhorst, 1962). PPN belonging to Dorylaimida, Triplonchida and Tylenchida orders were enumerated in 5-cm^3 counting chambers (Merny and Luc, 1969) under a

Table 1
Localisation of the sampling sites and corresponding ecosystems surveyed.

Site	Latitude N	Longitude W	Map	Ecosystems				
	(decimal°)	(decimal°)	code	Peatland	Moorland	Oak forest	Pine forest	
							natural	logged
Ombrières	44.75	−0.85	1					m
Belle-Viste	44.66	−0.76	2					m
Lagassey	44.34	−0.86	3					m
Langue	44.27	−0.78	4	w				d
Bel-Air	44.25	−0.91	5					w
La Trougne	44.36	−0.52	6					w
Parias	44.30	−0.45	7	w				d
Poteau1	44.25	−0.39	8		w			
Poteau2	44.24	−0.33	9		m			
Poteau3	44.23	-0.31	10			w		
Poteau4	44.20	−0.29	11				w	

d = dry; m = mesophilous; w = wet.

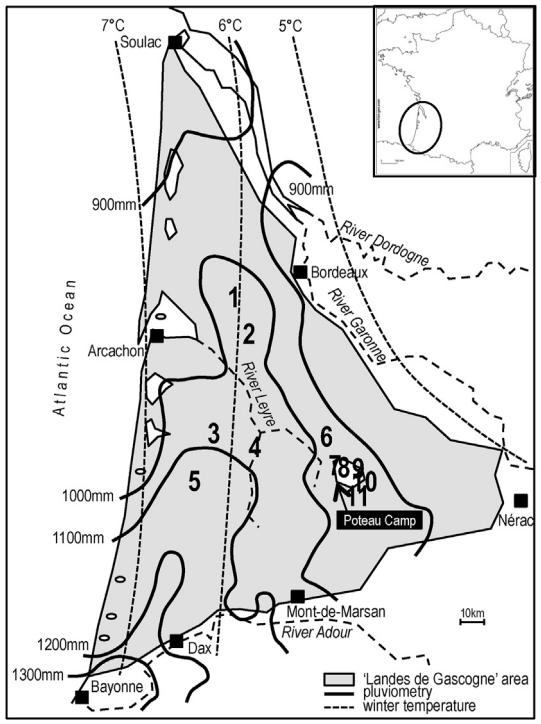


Fig. 1. Map of the sites surveyed. Encoding for sites is listed in Table 1.

stereomicroscope (≥x60 magnification). Mobile stages of nematodes (juveniles, males and females) were first identified at the genus level based on dichotomous keys (Mai and Mullin, 1996) and then at the species level with morphological genus-specific keys. Concerning specific identification, the nematode suspensions were preserved in a mixture of formalin and glycerine (De Grisse, 1969). The adult specimens were processed according to Seinhorst method (van Benzoijen, 2006) and then mounted onto slides (Cobb, 1917) for microscopic observation. Nematode population levels were expressed per dm^3 of fresh soil.

2.4. Nematode ecological indices

Several ecological indices were calculated to assess the diversity of PPN community:

a) Taxonomical diversity: total number of PPN per dm^3 of soil (N); species richness (S = number of species in a community); local diversity defined by the Shannon-Wiener index ($H' = -\sum p_i ln p_i$, where p_i is the proportion of individuals in species) and evenness ($E = H'/lnS$, which quantifies how species within communities are numerically alike, E varies between 0 and 1); Species richness and evenness were displayed according to Rank Abundance Curves (Magurran, 2007); Morisita's overlap index (Grassle and Smith, 1976) that measures β diversity (dissimilarity between samples) while taking into account the contribution of rare species.
b) Functional diversity: PPN species detected in communities were distributed into life-strategy groups according to the colonizer/persister value (*cp*-value) of the family to which they belong (Bongers, 1990). Functional diversity was described by calculating: (*i*) the plant-parasitic index (PPI = $\Sigma cpi ni/N$), which quantifies the plant-feeding diversity of the communities; (*ii*) the relative mean abundance (%) of each *cp*-value class in a community calculated as follows: $Rcpi = cpini/N$.
c) The structure of PPN communities was designed at the genus level. Afterwards, PPN community structures were described according to multivariate statistical analyses.

2.5. Data analyses

Data were log-transformed before analysis to improve normality. These diversity indices were calculated using the Vegan Library (Oksanen et al., 2016). Mean values were analysed by one-way ANOVA and Wilcoxon (nonparametric test) was then used for pair-wise multiple comparisons. Differences obtained at $P < 0.05$ were considered to be significant. The Morisita's overlap index was performed using BiodivR1.2 analysis display free software (Hardy, 2010). Principal Component Analysis

(PCA, Chessel et al., 2004) was carried out on nematode genera data in order to describe PPN community patterns. A k+1 multivariate method and a MultiBlock Partial Least Squares (MBPLS, Bougeard et al., 2011) were used to explored the potential drivers (in relation to vegetation, soil and climate characteristics) that could influence the nematode assemblage in community. These different multivariate analyses and graphs were performed using *ade4* library (Dray and Dufour, 2007). Different environmental variables were defined (Table 2). For the mean temperatures, the minimal data was only considered because 10 of the 11 sites were submitted to the same maximal isotherm. In order to avoid outlier patterns for genera, scarcest genera (with total abundance less than 1%) were excluded from the dataset prior to running the analysis. In order to examine if the different ecosystems affect nematode community structures, a nonmetric multidimensional scaling ordination analysis (NMDS) was conducted. The dissimilarity matrix was based on the total abundance of all genera within the communities. A Bray-Curtis dissimilarity metric was used to determine the effects of ecosystems on the nematode community distances between the sampling points, for which the metaMDS function was used (Oksanen, 2015). The "Adonis" function was used to determine if groups are significantly different, using permutation/randomization methods with 999 runs on the similarity matrix. A one-way ANOVA was then applied to check the assumption of homogeneity of multivariate dispersion. All statistical analyses were performed using R version 3.3.2 (R Core Team, 2016).

3. Results

3.1. Diversity of the plant-parasitic nematodes in all ecosystems

Forty-five species belonging to 24 genera and 13 families were detected across the surveyed sites (Table 3). *Bitylenchus bryobius* (Telotylenchidae) was the only common species detected in all the ecosystems surveyed. Tylenchidae and Hoplolaimidae families were highly diversified, represented by 15 and 11 species, respectively. Among all the ancient ecosystems, the highest PPN diversity, 13 species recorded especially represented by Hoplolaimidae species, was noted in peatlands. Interestingly, *Hirschmanniella* sp. (Pratylenchidae) was detected in the peatland located at site 7 'Parias'. PPN communities were less diversified (6–10 species) in moorlands, oak and natural pine forests in comparison to the logged pine forests (up to 29 species). This ecosystem mostly hosted Criconematidae species, especially in wet conditions, and *Pratylenchus* species, especially in mesophilous environments.

According to soil population levels analysed by Fortuner and Merny (1973), all the ecosystems appeared highly infested ($N \geq 200$ nematodes/dm^3 of soil), except for the dry logged pine forests (Table 4). High levels of *Pratylenchus* populations were detected in logged pine forests (up to 3400 nematodes/dm^3 of soil). In each ecosystem, the mean species richness (S) was rather low with less than five species. The local diversity (H') was low and the evenness (E) indicated that species were quite uniformly distributed in communities. The taxonomical indices were homogeneous across ecosystems. The rank order abundance curves indicated that the logged pine forests exhibited more homogeneous species diversity (longer curve = more richness; lower slope = more evenness) than the other ecosystems (Fig. 2).

Considering the functional diversity of the PPN (cp-value ≥ 2; Bongers, 1990), the most persistant species (cp-4 and cp-5 nematodes) were rare anywhere (Table 5). Consequently, all the ecosystems surveyed hosted quite exclusively colonizers nematodes (cp-2 and cp-3). The cp-3 nematodes were dominant everywhere, but the cp-3/cp-2 ratios significantly prevailed

Table 2
Environmental variables analysed and their corresponding codes.

e	Code	Variable	Code
Ecosystem		*Climate data*	
Peatland	PEA	mean minimal temperature	
Moorland	MOO	5–6 °C	5_6
Oak forest	OAK	6–7 °C	6_7
Natural pine forest	NPF	mean annual rainfall	
Logged pine forest	LPF	900–1000 mm	900_1000
Type of forest		1000–1100 mm	1000_1100
Dry	D	1100–1200 mm	1100_1200
Mesophilous	M	*Soil data*	
Wet	W	Clay (0–2 μm)	Cla
Understorey plants		Fine silts (2–20 μm)	fSi
Calluna vulgaris	Cal	Coarse silts (20–50 μm)	cSi
Erica scoparia	Eri	Fine sands (50–200 μm)	fSa
Frangula alnus	Fra	Coarse sands (200–2000 μm)	cSa
Molinia caerulea	Mol	Calcium	Ca
Pseudarrhenatherum longifolium	Pse	Sodium	Na
Pteridium aquilinum	Pte	Magnesium	Mg
Rubus fruticosus	Rub	Nitrogen	N
Ulex minor	Ule	Phosphorus	P
		Potassium	K
		Organic matter	OM
		pH H_2O	pH

Table 3
Plant-parasitic nematode taxa detected in the 'Landes de Gascogne' ecosystems surveyed.

Orders and families	Species	Ecosystems							
(cp-value)		Peatland	Moorland		Oak	Natural	Logged pine forest		
			mesophilous	wet	forest	pine forest	dry	mesophilous	wet
Dorylaimida									
Longidoridae (5)	*Xiphinema* sp.		+				+	+	+
Triplonchida									
Trichodoridae (4)	*Paratrichodorus pachydermus*			+	+		+	+	+
	Trichodorus velatus							+	
	Trichodorus sp.							+	
Tylenchida									
Anguinidae (2)	*Ditylenchus* sp.						+		
Criconematidae (3)	*Hemicriconemoides* sp.				+	+	+	+	+
	Macroposthonia xenoplax							+	+
	Ogma aquitanense								+
Ecphyadophoridae (2)	*Lelenchus leptosoma*						+	+	+
Hemicycliophoridae (3)	*Loofia thienemanni*			+	+	+	+		+
Heterodoridae (3)	*Heterodera* sp.					+	+		+
Hoplolaimidae (3)	*Helicotylenchus californicus*	+	+	+	+	+	+	+	+
	H. exallus	+					+	+	+
	H. pseudorobustus	+					+	+	+
	Helicotylenchus sp.	+					+	+	+
	Rotylenchus agnetis	+					+		+
	R. goodeyi	+					+		+
	R. ouensensis	+					+		
	R. pumilus	+							
	R. quartus								
	R. robustus								
	Rotylenchus sp.								
Paratylenchidae (2)	*Paratylenchus projectus*						+	+	
Pratylenchidae (3)	*Hirschmanniella* sp.	+						+	+
	Pratylenchus crenatus							+	
	P. fallax							+	
	P. pseudopratensis							+	
	Pratylenchus sp.								
Psilenchidae (2)	*Psilenchus* sp.								+
Telotylenchidae (3)	*Bitylenchus bryobius*	+	+	+	+	+	+	+	+
Tylenchidae (2)	*Aglenchus agricola*	+	+	+	+	+	+	+	+
	Allotylenchus excretorius	+	+	+	+		+	+	+
	Basiria tumida	+					+	+	+
	Coslenchus turkeyensis						+	+	+
	Filenchus acutus							+	+
	F. discrepans							+	+
	F. facultativus							+	+
	F. filiformis								+
	F. hamatus								+
	F. misellus								+
	F. uliginosus								
	Filenchus sp.								
	Malenchus acarayensis								
	M. bryophilus								
	Neopsilenchus magnidens								

in favour of *cp*-3 nematodes in mesophilous environments (moorlands and logged pine forests) while it failed in dry logged pine forests. In that way, PPI value was significantly higher in mesophilous conditions (moorlands and logged pine forests) than in dry logged pine forests.

3.2. Plant-parasitic nematode community patterns in all ecosystems

Looking at PPN community patterns, the PCA analysis (Fig. 3) clearly distinguished the PPN communities related to *Pratylenchus*, *Basiria* and *Filenchus* genera in logged pine forests from those more related to *Aglenchus*, *Helicotylenchus*, *Bitylenchus*, *Rotylenchus* and *Trichodorus* genera in the ancient ecosystems (natural pine and oak forests, moorlands and peatlands). *Ogma*, *Malenchus*, *Loofia* and *Allotylenchus* genera were more related to some logged pine forest sites. Significantly, contrasted PPN community structures were observed between natural and logged pine forests, while peatlands and moorlands hosted similar communities.

Table 4
Taxonomical diversity indices (mean values) in plant-parasitic nematode communities detected in the 'Landes de Gascogne' ecosystems (N = total number of nematodes; S = species richness; H' = local diversity; E = evenness), (P-value according to ANOVA analysis).

Ecosystems	*N*	*S*	*H'*	*E*
Peatland	1078	3.56	0.57	0.45
Mesophilous moorland	854	3.75	0.52	0.42
Wet moorland	2723	5.00	0.79	0.51
Oak forest	654	4.40	0.69	0.49
Natural pine forest	1272	3.20	0.63	0.49
Dry logged pine forest	248	2.89	0.56	0.52
Mesophilous logged pine forest	1544	3.57	0.62	0.55
Wet logged pine forest	1134	4.33	0.94	0.63
P-value	*0.594*	*0.059*	*0.265*	*0.858*

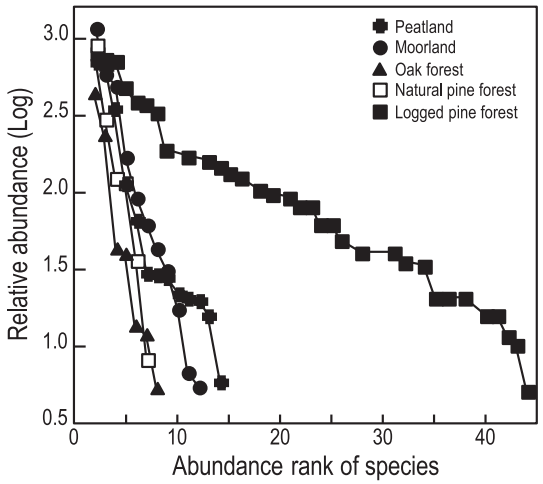


Fig. 2. Rank order abundance curves for nematode communities encountered in the different ecosystems surveyed.

Table 5
Functional diversity in plant-parasitic nematode communities detected in the 'Landes de Gascogne' ecosystems (R*cp*-i = relative mean abundance of nematodes (mean % values) in each *cp*-i class in communities), PPI= Plant Parasitic Index. The letters (*a, b*) indicate significant differences among the variables measured according to ANOVA and Wilcoxon tests, $P < 0.05$.

Ecosystems	R*cp*-2	R*cp*-3	R*cp*-4	R*cp*-5	PPI
Peatland	17.00 *ab*	82.99 *ab*	0	0 *b*	2.83 *ab*
Mesophilous moorland	4.41 *b*	94.52 *a*	0	1.1 *a*	2.98 *a*
Wet moorland	17.76 *ab*	82.04 *ab*	0.2	0 *b*	2.82 *ab*
Oak forest	38.15 *ab*	61.15 *ab*	0.7	0 *b*	2.63 *ab*
Natural pine forest	23.41 *ab*	76.58 *ab*	0	0 *b*	2.77 *ab*
Dry logged pine forest	41.11 *a*	59.66 *b*	0	0 *b*	2.67 *b*
Mesophilous logged pine forest	9.17 *b*	90.03 *a*	0.9	0 *b*	2.94 *a*
Wet logged pine forest	29.89 *ab*	77.62 *ab*	0.4	0 *b*	2.86 *ab*
P-value	*0.0365*	*0.0453*	*0.837*	*0.000659*	*0.0132*

Focusing on the afforestation of the moorlands, the PCA analysis confirmed contrasted communities between moorlands and logged pine forests especially because of the presence of *Pratylenchus*, *Basiria* and *Allotylenchus* genera in the logged pine forests while these genera were not detected in moorlands (Table 3; Fig. 4). Other genera, such as *Helicotylenchus, Rotylenchus, Trichodorus* and *Filenchus* did not contribute to the community patterns.

3.3. Plant-parasitic nematode diversity in logged pine forests

The distribution of the PPN communities was only investigated in the logged pine forests. High diversity overlaps in communities were observed within each site (Morisita index up to 1) along the sampling transects, except in sites 4 ('Langue') and 6 ('La Trougne') where species were more dispersed (Fig. 5). The diversity dissimilarity between sites (Table 6) revealed that most of PPN communities did not overlap with each other (Morisita index down to 0), except between sites 3 ('Lagassey'), 4 ('Langue') and 6 ('La Trougne') on one hand, and between sites 5 ('Bel Air') and 7 ('Parias') on the other hand.

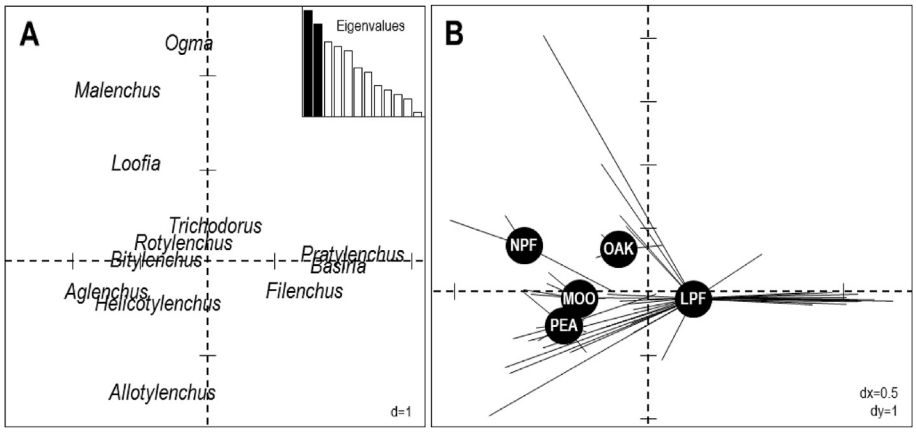


Fig. 3. Plant-parasitic nematode community patterns in the ecosystems surveyed. (A) PCA loading plot for the nematode genera. (B) Score plot for the samples according to each ecosystem. Codes for ecosystems are listed in Table 2.

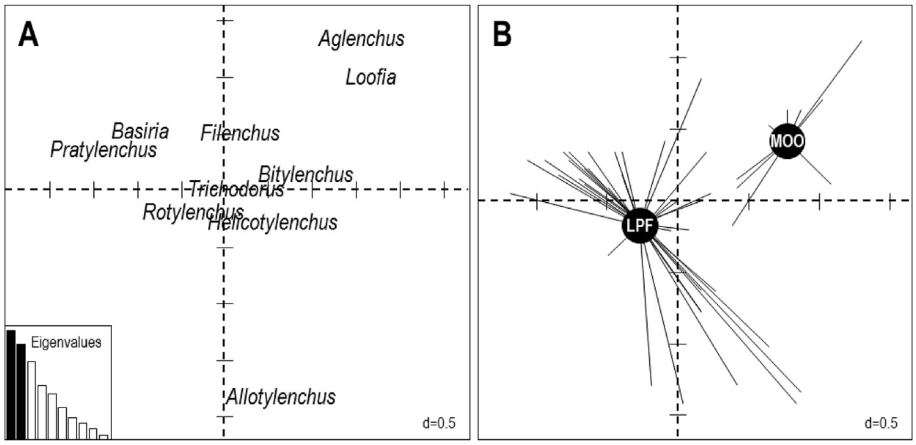


Fig. 4. Plant-parasitic nematode community patterns in moorlands and in logged pine forests. (A) PCA loading plot for the nematode genera. (B) Score plot for the samples according to each ecosystem. Codes for ecosystems are listed in Table 2.

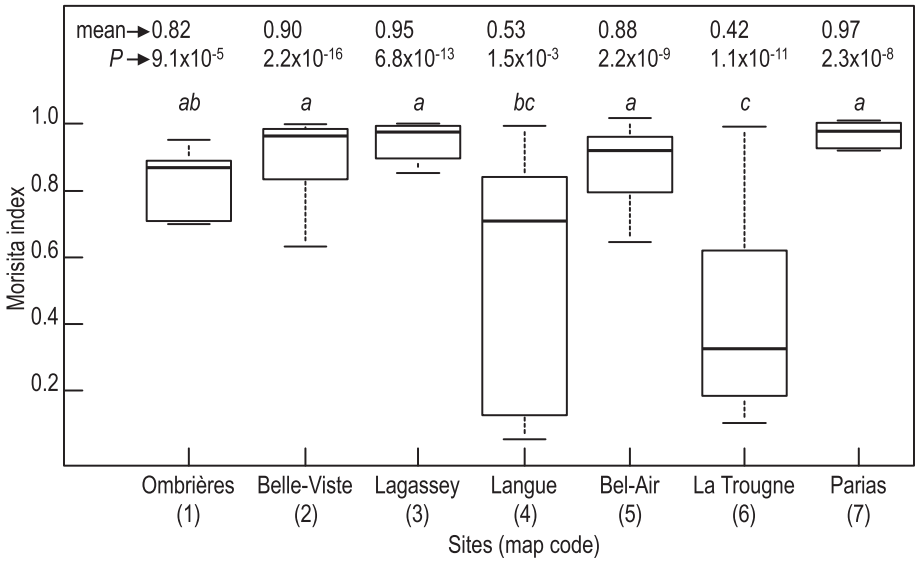


Fig. 5. Species diversity dissimilarity between samples (Morisita's overlap index) in each logged pine forest site. Different letters (a–c) indicate significant differences between sampling sites according to ANOVA, $P < 0.05$.

Table 6
Species diversity dissimilarity between logged forest sites (Morisita's overlap index).

Sites (map code)	Ombrières (1)	Belle-Viste (2)	Lagassey (3)	Langue (4)	Bel Air (5)	La Trougne (6)
Belle-Viste	0.2603					
Lagassey	0.0059	0.0014				
Langue	0.1038	0.0696	**0.9441**			
Bel Air	0.1981	0.0020	0.0002	0.0012		
La Trougne	0.0000	0.0000	**0.9828**	**0.9202**	0.0000	
Parias	0.1758	0.0000	0.0158	0.0130	**0.8024**	0.0183

Considering the PPN community patterns, the genus *Helicotylenchus* did not contribute to MBPLS analysis, while the genus *Bitylenchus* contributed to it but as a lesser extent (Fig. 6A). The first axis of the analysis clearly distinguished the genus *Allotylenchus* from the other genera whose contributions differed according to the second axis: *Filenchus* and *Basiria* genera related to positive values, and *Trichodorus, Pratylenchus, Rotylenchus* related to negative values. The MBPLS analysis distinguished the soil variables from the understorey vegetation variables (Fig. 6B). Considering the soil factors only, the MBPLS 1 axis clearly indicated the influence of a textural gradient with the sand variables (cSa and fSa) related to its positive values, and the silt (cSi and fSi) and clay (Cla) variables related to its negative values. Soil nutrients (N, P, K, Ca, Mg, Na) and organic matter (OM) variables were associated with finest textured soils. Considering the vegetation variables, the MBPLS 1 axis separated two groups of plants (Fig. 6B): *P. longifolium* (Pse), *P. aquilinum* (Pte) and *M. caerulea* (Mol) from *E. scoparia* (Eri), *R. fruticosus* (Rub), *U. minor* (Ule) and *F. alnus* (Fra). The analysis showed a highest contribution of *C. vulgaris* (Cal), *M. caerulea* (Eri) and *U. minor* (Ule) than of *E. scoparia* (Eri) and *R. fruticosus* (Rub). The score plot of the samples displayed a significant opposition between the dry forests from the mesophilous and the wet forests according to the first axis (Fig. 6C). However, the second axis separated the samples according to the rainfall gradient (Fig. 6D) and to the minimal temperatures (Fig. 6E).

The NMDS analysis confirmed that the nematode communities reflect different patterns according to these different ecosystems. Patterns in both logged and natural pine forest seemed to be the same. On the other hand, oak, heathland and peatland ecosystems exhibited different patterns form each other (Fig. 7). These different groups ecosystems were significantly different ($P < 0.001$).

4. Discussion and conclusion

Among soil nematodes, PPN are the most important one due to their real threat on agriculture (Neher, 2010). Although several studies focused on soil nematodes (both plant parasitic and free-living forms), they mostly aimed at evaluating soil health, by estimating ecological descriptors (Wilson and Kakouli-Duarte, 2009; Maurya et al., 2020), than examining species and population shifts in nematode communities able to change their overall pathogenicity (Mateille et al., 2008). Moreover, the diversity of PPN communities is much more explored in agrosystems than in natural ecosystems, and nematodes have been proposed as indicators to detect changes in response to environmental impacts (Renčo et al., 2020).

Our study highlighted the detection of 45 PPN species belonging to 24 genera. This richness is less than that previously detected by Baujard et al. (1979b) who recorded 80 obligate plant-parasitic species, but most of them were unidentified to species level. Different nematode taxa listed here have already been recorded in previous studies (Baujard et al., 1979a, b; Scotto La Massèse and Boulbria, 1980). These common species may form the basis of the communities present in the 'Landes de Gascogne' area. Nevertheless, this survey adds species that are reported for the first time in this region, especially those belonging to the Tylenchidae family. The pine specific species *Bursaphelenchus xylophilus* (syn. *B. lignicolus*) already reported by Baujard et al. (1979a) in this region was not detected. Scotto La Massèse and Boulbria (1980) suggested that *Ogma aquitanense* (syn. *Criconema aquitanense*) is an endemic species. This is a recent record of this species in Europe after that of Flis et al. (2014). Moreover, *Bitylenchus bryobius* (Telotylenchidae), which was the only species detected in all the ecosystems surveyed, is likely to be adapted to these ancient ecosystems long time ago. This is the first record of this species in France, while the Fauna Europaea (www.fauna-eu.org) reported it in Germany, Poland and The Netherlands. As observed by Baujard et al. (1979b), most of the PPN identified in this study were ectoparasitic nematodes (*Helicotylenchus, Paratrichodorus, Paratylenchus, Rotylenchus, Trichodorus, Xiphinema*, etc.). These nematodes are present in almost all ecosystems, making difficult to establish a link between their presence and the typology of the ecosystem or the host plant. The only endoparasites identified were *Hirschmaniella*, *Pratylenchus* and *Heterodera* species, which are known for their high pathogenicity on different crops (Bernard et al., 2017).

Although the diversity indices are often linked to the abundance of species, we find that most of them, such as species richness, local diversity and evenness, did not differ significantly between the different ecosystems as reported by Arpin and Ponge (1986). The richness in PPN communities was low (less than 10 species) in moorlands, oak and natural pine forests while it was high in logged pine forests that exhibited up to 29 PPN species. Both high richness and evenness in logged pine forests were confirmed by the rank order abundance curves. This low richness could be explained by the lower sampling size (according to available sites) done in the ancient ecosystems (up to 10 samples for peatlands, moorlands, oak and natural pine forests) compared to logged pine forests (up to 100 samples). Indeed, Mateille et al. (2011) estimated that the optimal diversity was detected when the sampling size reached 20 samples per site at least. Moreover, we can hypothesize that the rich

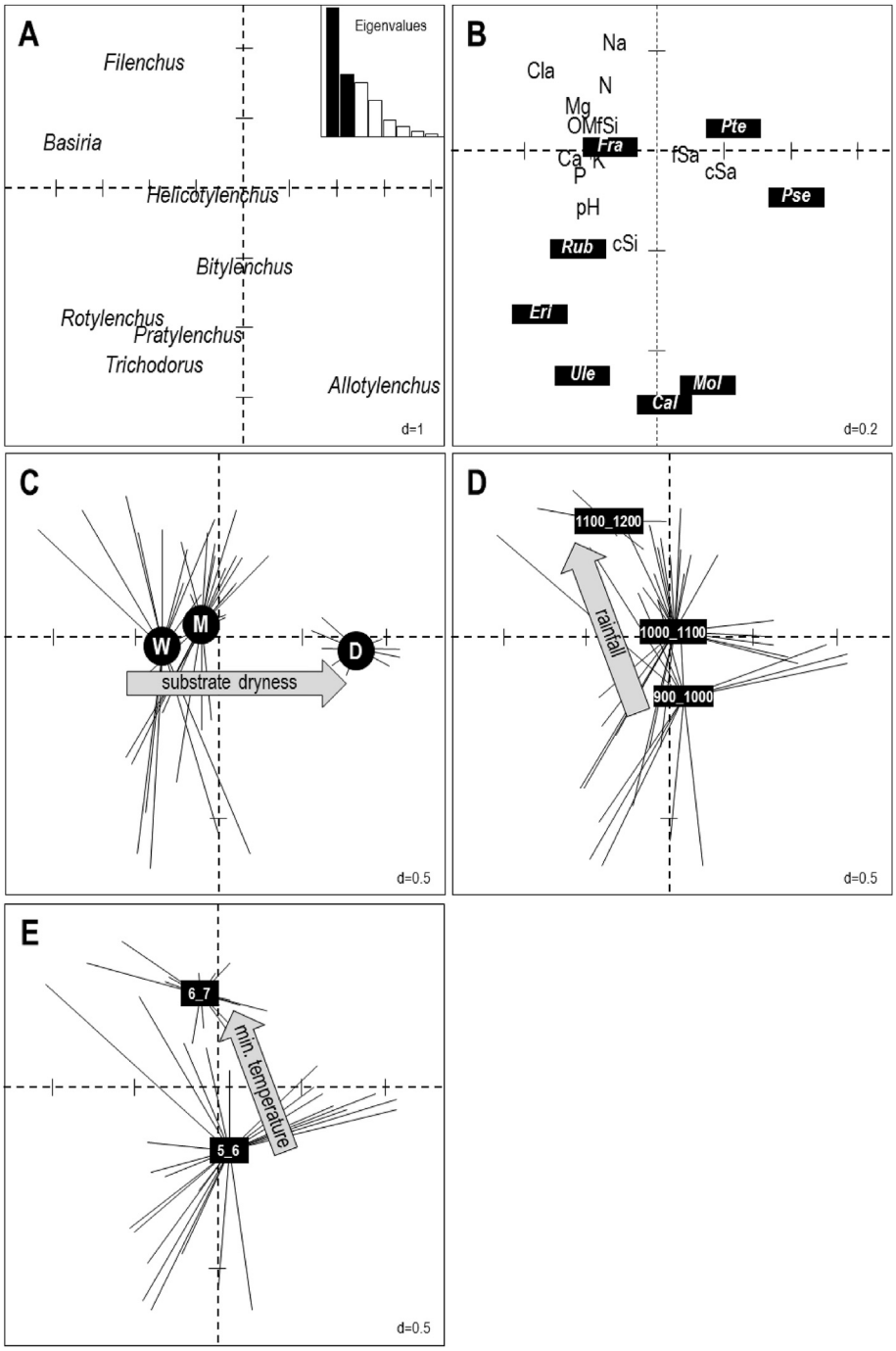


Fig. 6. MBPLS analysis between plant-parasitic nematode communities and understorey vegetation, soil factors, substrate dryness and climate in logged pine forests. (A) PCA loading plot of the nematode genera. (B) PCA loading plot of the understorey vegetation and soil factors. (C) Score plot for the samples according to the forest typology. (D) Score plot for the samples according to the mean annual rainfall. (E) Score plot for the samples according to the mean minimal temperature. Codes for ecosystems are listed in Table 2.

understorey plant diversity (especially in logged pine forests) impacts the structure of PPN communities, as confirmed by the MBPLS analyses.

The PPN diversities were very homogeneous in each logged forest site, with some exception (sites 4 and 6). However, they differed between sites and correspond to a latitudinal distribution that has no relation with other variables (climate and vegetation), unless it was impacted by the latitudinal sediment legacy as hypothesized by Mateille et al. (2011). Furthermore, coming back to the geographical distribution of the sites indicated that the PPN community dissimilarity was related to the site latitude, while the longitude location had no effect, even between very distant sites (e.g., sites 5 and 7).

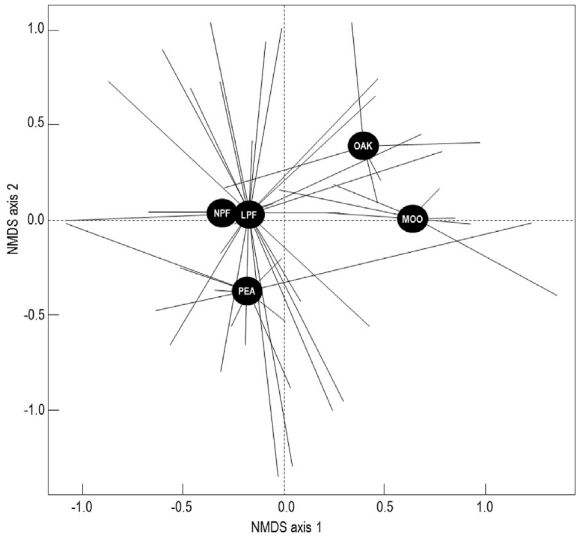


Fig. 7. NMDS ordination analyse between nematode community structure and the different ecosystems. Codes for ecosystems are listed in Table 2.

Considering the PPN communities patterns, the PCA analyses showed some contrasted community assemblages (*Pratylenchus*, *Basiria* and *Filenchus* versus *Helicotylenchus* and *Rotylenchus*; *Ogma* and *Loofia* versus *Allotelenchus*). This opposition could be explained either by the competition between PPN species, the different climatic and soil requirements, or food preferences. Based on PPN abundance in the different ecosystems, the great variability in their community composition is explained by different types of competition established between the nematodes themselves or between them and the other soil organisms (Piskiewicz et al., 2007, 2008).

The structure of the nematofauna is influenced by numerous edaphic, climatic, and phytosociological factors (Scotto La Massese and Boulbria 1980). Furthermore, the nematode species respond differently to moisture and temperature changes, which consequently modify the structure of their communities (Papatheodorou et al., 2004; Pen-Mouratov et al., 2004). The results demonstrated an important role of the hydromorphic typology of the ecosystems on the structure of the PPN communities. Indeed, communities were clearly different in moorlands and in logged pine forests on one hand, and in dry, mesophilous and wet forests on the other hand. *Loofia thienemanni* (syn. *Hemicycliophora thienemanni*) was detected in dry pine forests, which contradicts the observation of Scotto La Massese and Boulbria (1980) who concluded a strict association of this species with very humid areas. However, our results supported their observations about the specificity of some species such as *O. aquitanense* and *Helicotylenchus californicus* to humid conditions. The occurrence of *Hirschmanniella* sp. (Pratylenchidae) in peatlands, which is usually restricted to flooded crops such as rice (Fortuner and Merny, 1973), was also previously observed by Scotto La Massese (1976) and Baujard et al. (1979b). In addition, the detection of species of the genera *Bitylenchus, Filenchus, Pratylenchus, Rotylenchus, Trichodorus* and *Xiphinema* in dry, mesophilous and wet conditions suggests that these nematodes support hydromorphic fluctuations. The potential impact of hydromorphicity on PPN is explained by the fact that the biological behaviour of PPN depends on the soil moisture and aeration status (Mateille et al., 2016).

The understorey plants played also an important role as it was shown in logged pine forests, since a high production of root biomass supports large populations of nematodes (Derouard and Lavelle, 1994). Indeed, we confirmed that *E. scoparia*, *U. minor* and *F. alnus, P. aquilinum*, and *C. vulgaris* are indicative of wet, mesophilous and dry lands, respectively, while *P. longifolium* is well adapted to bare and poor soils (Maizeret, 2005). Consequently, the hydromorphicity of the soils leads the structure of the plant communities which has repercussions on PPN communities.

Soil parameters are also structuring factors. Contrary to what was observed by Ait-Hamza et al. (2018), the *Rotylenchus* species were poorly adjusted to organic soils. Nevertheless, the MBPLS analysis pointed a texture gradient effect because fine textures favoured the development of *Helicotylenchus, Pratylenchus, Rotylenchus, Trichodorus* species, while coarse textures favoured others such as *Allotylenchus excretorius*. The sandy texture of the 'Landes of Gascogne' soils provides empty spaces between particles allowing nematode movement and water penetration and thus promoting their occurrence (Wallace, 1963) and spread (Wallace, 1971).

Climatic variations were also meaning drivers, because the MBPLS analysis pointed a high rainfall gradient influence on the PPN communities, and just a one-degree (C°) variation of the minimal temperature had a significant effect. However, as they contribute more on the second axis of the MBPLS analysis than on the first one, we can hypothesize that they drove less in the structuration of the PPN communities than the soil hydromorphicity.

Considering all these different factors, the soil hydromorphicity is the most important driver of PPN community structures in the 'Landes of Gascogne'. It affects both the PPN communities and the understorey plants composition. Therefore both components might be reciprocal indicators for the phytological communities or for moisture conditions.

Consequently, the afforestation activities in the 'Landes of Gascogne' did not alter the diversity of PPN species but significantly changed the structure of their communities. Similar observation was also reported by Carson et al. (2010) who demonstrated that the afforestation of three locations with *Eucalyptus globulus* or *Pinus pinaster* altered fungal community structures. In that way, Gunina et al. (2017) concluded that afforestation increased bacterial communities, and had stronger impacts on the development of fungal communities. Furthermore, a distinct structure of Archaea communities was highlighted between pinewood forest and moorland soils indicating that afforestation of moorland soils leads to community changes and subsequent potential impact on the ecosystem functions (Nicol et al., 2007).

Considering functional diversity indices, *cp*-4 (e.g., Trichodoridae) and *cp*-5 (e.g., Longidoridae) nematodes were in low abundance, suggesting that persistent species are not representative in the 'Landes de Gascogne'. As reported by Neher and Olson (1999) and Ou et al. (2005), this could confirm their low competition capacity with *cp*-2 and *cp*-3 groups that were dominant all over the different ecosystems. The wide proportion of *cp*-3 nematodes, especially in mesophilous conditions, indicated that opportunistic and colonizer species are able to occupy various wild habitats (Mateille et al., 2016). However, the high amount of *cp*-2 nematodes, as observed in logged pine forests, indicated 'stress' constraints, while those of *cp*-3 to *cp*-5 nematodes indicated natural succession mediated by increased environmental stability (Bongers and Ferris, 1999). The detection of high *Pratylenchus* populations (*cp*-3) in logged pine forests suggest that these species were either introduced into the region with the soil substrates of pine planting stocks and then enhanced by humid conditions as also observed by Baujard et al. (1979b), or they were enhanced by susceptible understorey vegetation associated to pine such as *M. caerulea* (Reid and Emery, 2017) and *E. scoparia* (Forge et al., 2012).

To conclude, although afforestation activities in the 'Landes of Gascogne' did not seem to considerably change the understorey plant community structure, the structure of PPN communities varied between ecosystems. In that way, a significant shift of community structure from old ecosystems - and from moorlands in particular - to logged pine forests was observed. The detection of some species such as *R. ouensensis* and *B. bryobius* in old and recent ecosystems suggests that they persisted throughout the history of the region. We expect that recent pine forests modified PPN communities with the relevance of high pathogenic nematodes such as *Pratylenchus* species. These new PPN structures reveal a potential PPN risk and should be (*i*) considered in pine-breeding programs (Raffin, 2014), and (*ii*) incurred by prospective programs for intensifying pine or replacing it with other tree species susceptible to PPN (Pastuszka et al., 2014).

Statement on data availability

The datasets analysed during the current study are available from the corresponding author on reasonable request.

Declaration of competing interest

None.

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