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Temporal evolution of soil nematode communities in *Pinus nigra* forests of Navarra, Spain [1]

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Summary – In this study the number of specimens and taxa belonging to the orders of Araeolaimida, Chromadorida, Rhabditida, Enoplida, Monhysterida, and some Dorylaimida (Mononchida) from *Pinus nigra* forests of varying age in Navarra (Northern Spain) are studied. The study considered two parameters : the differing geographical and climatic conditions (oceanic and mediterranean), and the age of the pineforests at the sampling sites. In both climatic areas the number of species, Margalef richness index, Shannon-Weaver diversity index, and maturity index of nematode communities were found to increase with the age of the pineforests. A regression analysis was carried out between pineforest age as independent variable and species number, richness, diversity and maturity index as dependent variable to confirm these results. The same indices were greater in those areas with an oceanic climate than in those with a mediterranean climate with the exception of the maturity index which remained constant. In order to characterise the taxa that were found, nine species categories were defined and compared with those previously established by other authors, thus allowing more precise values to to be assigned to the c-p categories of Bongers.

Résumé – ***Évolution dans le temps des communautés de nématodes du sol dans des pinèdes à* Pinus nigra *en Navarre, Espagne*** – Dans cette étude, ont été comparés les nombres d'individus et de taxons appartenant aux ordres Araeolaimida, Chromadorida, Rhabditida, Enoplida, Monhysterida, et certains de l'ordre des Dorylaimida (Mononchida) dans quelques pinèdes à *Pinus nigra* de différents âges situées en Navarre (nord de l'Espagne). L'étude a pris en compte deux paramètres : les conditions géographiques et climatiques des deux zones (océanique et méditerranéenne) et l'âge des pinèdes au lieu d'échantillonnage. Accompagnant le vieillissement des pinèdes, il est constaté une augmentation du nombre d'individus, de l'indice de Richesse de Margalef, de l'indice de diversité de Shannon-Weaver et de l'indice de maturité des communautés des nématodes. Pour confirmer ces résultats, il a été procédé à des analyses de régression concernant l'âge des pinèdes, pris comme variable indépendante, et le nombre d'individus, la richesse, la diversité et la maturité. Ces indices sont plus élevés dans les zones à climat océanique que dans celles à climat méditerranéen, à l'exception de l'indice de maturité qui reste constant. Pour caractériser les taxons trouvés, neuf classes d'abondance ont été définies et comparées avec des catégories établies antérieurement par d'autres auteurs, ce qui permet d'assigner des valeurs plus précises aux catégories c-p de Bongers.

Key-words : community, diversity, nematodes, *Pinus nigra,* population dynamics, reforestation, Spain, species categories.

Nematodes have characteristics that allow them to be used as biological indicators (Freckman, 1988; Wasilewska, 1989; Bongers & Van de Haar, 1990; Arpin, 1991; De Goede, 1993). Changes in the ecosystem, in this case reforestation, are reflected in the soil fauna through different changes; e.g., variation in the rate of reproduction, sex ratio, migration, quiescence, diapause, cryptobiosis, occupation of micro-habitats, use of different resources, displacement and elimination of species, etc. (Nicholas, 1984).

Nematodes can be allocated to different trophic groups (Yeates *et al.,* 1993) which reflect changes in environmental factors. Based on trophic groupings and other characteristics, different indices for measuring environmental changes have been proposed : the ratio of fungal feeders to bacterial feeders (Twinn, 1974), trophic diversity (Freckman & Ettema, 1993), the proportion of Rhabditida dauer larvae, (Sohlenius & Boström, 1984), the maturity index, the plant parasite index (Bongers, 1990), and an association of these last two indices (Yeates, 1994). The study of the trophic groupings in *Pinus nigra* Arnold forests in Navarra will be the topic of another paper.

As far as reforestation with *P. nigra* in the province of Navarra, Northern Spain (Fig. 1) is concerned, some studies have been reported. Jordana *et al.* (1987 *b*) studied the replacement of *Quercus ilex rotundifolia* Lamark by *P. nigra* in Sansoain (Southern Navarra) in relation to Nematoda, Oribatei, and Collembola. Hernández *et al.* (1987) studied the trophic groups of Nematoda in these same sites. Moreno (1991) studied Oribatei in the same areas as we report on. Other works have examined the

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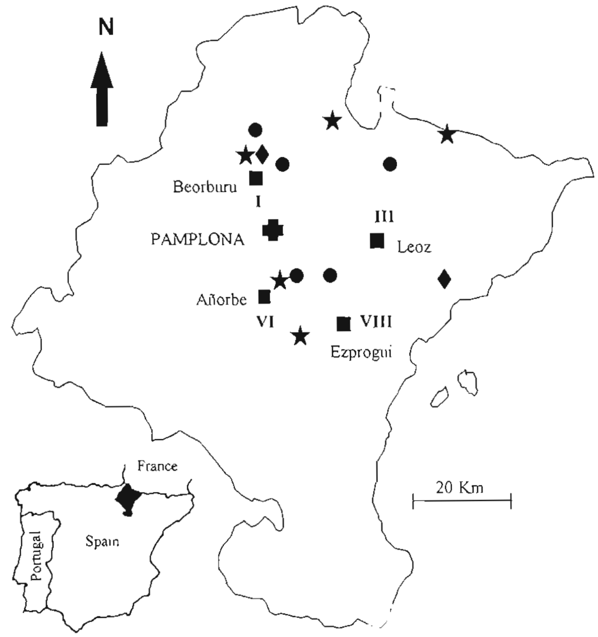

Fig. 1. *The province of Navarra showing samplings area of* ■ *present study,* ★ *Hernández & Jordana 1992, Hernández* et al. *1987, Jordana* et al. *1987* b; ● *Villanueva & Jordana 1988;* ◆ *Arbea & Jordana 1985, 1990.*

effects of conifer reforestation in natural forests on the changes in diversity and species substitution of soil fauna (Arbea & Jordana, 1985, 1990; Villanueva & Jordana, 1988; Hernández & Jordana, 1992).

In this paper, the frequency and proportion of nematode species, together with two diversity and maturity indices, were studied to elucidate the interactions between nematode fauna and the environment, the biology of some species with regard to the evolution and the maturity of the ecosystem, as well as the influence of climatic factors. The nematode species used in this paper belong to the orders of Araeolaimida, Chromadorida, Rhabditida, Enoplida, Monhysterida, and some Dorylaimida (Mononchida). Tylenchida, Aphelenchida, and the remaining Dorylaimida will be the object of a subsequent study.

Materials and methods

Elena-Rosello *et al.* (1985) make a territorial classification of Navarra as a basis for stratification sampling in ecological studies. The area under study was characterised by 184 physiographical, geological, lithological, climatic and anthropogenic variables. The classification method was the I.T.E. Land Classification System (Bunce *et al.,* 1975) using the Indicator Species analysis (Hill *et al.,* 1975). This method has been used previously to make a preliminary classification of the Iberian Peninsula, and its validity has been tested with the estimation of Spanish forestry productivity (Elena-Rosello & Bunce, 1984). Following this method Navarra is divided into 29 classes. Climatic information carries the main weight in the classification, with geological and physiographical information being of secondary importance.

Based on this data, four sampling areas were selected corresponding to the localities of Beorburu (I), Leoz (III), Añorbe (VI), and Ezprogui (VIII) (Fig. 1). The four pineforests *(P. nigra)* areas selected for this study (Tables 1, 2) are well characterised by Vernet (V) and Thornthwaite water indices (TH). In each area four pineforests of differing ages (B < 25 years old to E > 45 years old) were selected. The four sites at Añorbe (area VI) are isolated by their subhumid climate with an oceanic-mediterranean character. Ezprogui (area VIII) is isolated by its humid climate of an oceanic or pseudo-oceanic character. All the sites in areas I (Beorburu) and III (Leoz), except IC and IE, have a humid climate of an oceanic-mediterranean character; IC and IE have a perhumid climate and a pseudo-oceanic character (Elena-Rosello *et al.,* 1985).

The pedological factors (Table 1) were analysed by Spanish official analytical methods (Anon., 1994), phosphorus by the Olsen *et al.* (1954) method, and potassium, calcium, and magnesium by the Bower *et al.* (1952) method.

Sampling was carried out in spring and autumn of 1986. 64 samples (four areas, four sites in each area, two levels and two seasons) were taken within 20 m of specific trees. The sampling sites were close to sites used for Collembola, Acarina, superficial fauna (various invertebrates and small mammals taken with surface traps), mycorrhizae, and Oligochaeta (Arbea *et al.,* 1987; Moreno, 1991).

At each site, 500 g of organic layer (litter, F and H layers) and 1000 g of humidified organic-mineral layer of soil (A1H) were collected. After homogenisation, a subsample of 25 g w/w was extracted for nematodes using the centrifugal flotation method (Caveness & Jensen, 1955) as modified by Montenegro (*in* Jordana *et al.,* 1987 *a*). Subsequently they were fixed using the Seinhorst (1959) method and mounted in glycerol. The number of nematodes was estimated from three aliquots. From each sample 100 to 150 specimens were identified. Sample dry weight (10 g to 105 °C) was determined for comparisons between samples.

The frequency and proportion of each taxon and two diversity indices were calculated. Margalef's (1951) richness index relates the number of specimens (n) and taxa (s) in each sample according to the formula : $R = s - 1/ln\ n$. The Shannon and Weaver (1949) diversity index uses proportion (pi = proportion of each taxon in the sample) according to the formula : $H' = \Sigma\, pi{\cdot}ln\ pi$.

The association between frequency (number of samples in which a species is present) and abundance (num-

Table 1. *Geographical and pedological factors. SITES : areas I (Beorburu), III (Leoz), VI (Añorbe), VIII (Ezprogui) and age classes (B, C, D, E). AGE : years since planting. UTM : Universal Transversal Mercator coordinates. OM : Organic matter in %. pH (O) : pH (in water) of the organic layer. pH (S) : pH (in water) in soil. WRC : Water retention capacity (at pF = 0.3). N : N in organic layer %. C/N : C/N ratio in organic layer. AC : Active carbonates. * : ppm.*

Sites	Age	UTM	OM	pH (O)	pH (S)	WRC	N	C/N	AC	P*	K*	Ca*	Mg*
IB	21	30TXN05	3.80	8.2	7.9	317.4	.25	8.9	15.0	6	163	5537	85
IC	29	30TXN05	9.29	6.6	6.1	515.9	.39	13.8	4.6	7	150	3605	109
ID	41	30TXN05	5.59	8.3	8.1	340.9	.22	14.7	22.3	6	144	5592	55
IE	52	30TXN05	9.29	8.0	7.8	278.6	.44	11.0	9.2	5	138	5780	82
IIIB	22	30TXN33	2.41	8.0	8.1	419.0	.14	9.8	28.4	2	74	3504	68
IIIC	30	30TXN33	3.00	8.0	8.0	345.9	.40	4.3	25.6	1	125	3677	57
IIID	35	30TXN33	3.98	8.0	7.8	486.9	.22	10.1	27.8	2	116	4204	80
IIIE	47	30TXN33	2.75	7.9	7.7	319.6	.13	11.8	7.3	5	111	2914	58
VIB	15	30TXN02	4.13	8.2	8.1	296.8	.24	9.4	25.6	4	156	4381	96
VIC	33	30TXN02	2.59	8.3	8.1	282.9	.17	8.5	24.1	4	67	3609	76
VID	41	30TXN02	4.79	8.2	8.1	325.9	.27	10.2	20.0	2	150	4594	89
VIE	47	30TXN02	10.61	8.0	7.8	305.7	.35	16.5	20.7	4	104	4672	82
VIIIB	22	30TXN22	1.58	7.6	7.4	570.1	.11	8.4	5.6	5	124	4015	118
VIIIC	34	30TXN21	3.28	8.1	8.2	437.5	.16	11.8	16.9	6	130	4219	83
VIIID	39	30TXN21	1.65	7.6	7.7	248.8	.09	10.5	0.0	5	161	3894	121
VIIIE	50	30TXN21	4.25	8.3	8.3	249.0	.17	14.8	20.0	3	104	4732	59

Table 2. *Geographical and climatic factors. SITES : areas I (Beorburu), III (Leoz), VI (Añorbe), VIII (Ezprogui) and age classes (B, C, D, E). V : Vernet index. MED : Mediterranean climatic conditions. TH : Thornthwhaite hydric index. CLI : Climate. SSP : Slope sun potential. AMT : Annual mean temperature. RF : Rainfall. TEP : Thornthwhaite evapotranspiration potential. ALT : Altitude. SLP : Slope %. ORT : Orientation.*

Sites	V	MED	TH	CLI	SSP	AMT	RF	TEP	ALT	SLP	ORT
IB	– 2.29	Oceanic-Mediterranean	83.9	Humid	1.00	11.2	1160	668.0	630	38	E
IC	– 1.86	Pseudo-oceanic	121.1	Perhumid	1.16	9.9	1341	630.3	780	24	SW
ID	– 2.41	Oceanic-Mediterranean	77.2	Humid	0.99	11.4	1126	676.1	600	35	SE
IE	– 1.86	Pseudo-oceanic	121.1	Perhumid	0.99	9.9	1341	630.3	780	24	E
IIIB	– 2.50	Oceanic-Mediterranean	56.7	Humid	0.94	11.5	983	678.3	590	17	W
IIIC	– 2.36	Oceanic-Mediterranean	67.1	Humid	1.13	11.2	1043	667.6	630	12	SE
IIID	– 2.23	Oceanic-Mediterranean	75.6	Humid	1.11	10.8	1088	657.3	670	4	SE
IIIE	– 2.34	Oceanic-Mediterranean	67.1	Humid	0.79	11.1	1041	666.1	635	35	N
VIB	– 2.57	Oceanic-Mediterranean	5.6	Subhumid	0.96	12.0	626	693.7	530	30	N
VIC	– 2.08	Oceanic-Mediterranean	12.2	Subhumid	0.86	11.3	659	670.6	615	20	N
VID	– 2.50	Oceanic-Mediterranean	7.4	Subhumid	0.86	11.8	635	686.8	555	30	NW
VIE	– 2.01	Oceanic-Mediterranean	13.4	Subhumid	1.11	11.2	665	666.8	630	35	NW
VIIIB	– 0.95	Oceanic	45.3	Humid	1.09	8.4	798	585.8	960	5	SW
VIIIC	– 1.48	Pseudo-oceanic	24.0	Humid	0.97	10.2	713	636.4	750	8	S
VIIID	– 1.15	Pseudo-oceanic	35.7	Humid	1.06	9.2	762	607.5	870	20	SE
VIIIE	– 1.24	Pseudo-oceanic	31.2	Humid	0.76	9.6	744	618.7	825	35	N

ber of specimens in a sample) allows abundance classes to be defined and ranked. For this to be done, a threshold number of specimens per 10 g sample is necessary. Arpin (1979), in a framework restricted to Mononchida, considered 35 to be the limit between species with high and low abundance. In the present study, the limit has been set to 40 specimens/10 g. Cassagnau (1961) considered different abundance classes for Collembola communities, showing the adaptation of the species to the environment and their reproductive capacity. For the present study the following modified abundance classes are used :

Abundant species : more than 40 specimens/10 g in more than 25 % of the samples in which the species is present.

Extensive (ae), present in 32 to 64 samples.

Localised (al), present in 16 to 31 samples.

Very localised (av), present in less than 16 samples.

Low abundance species: more than 40 specimens/10 g in less than 25 % of the samples in which the species is present.

Diffuse (ld), present in 32 to 64 samples.

Disperse (lp), present in 16 or 31 samples.

Rare (lr), present in less than 16 samples.

Other categories have been defined that might allow the importance of species to be assessed based on their behaviour in the succession taking both the change in diversity with age and the geographic differences into account. Considering the age classes of pineforests, the following species categories are defined:

1 - Initial colonising (IC): species present in the younger pineforest and absent in the older stands.
2 - Decreasing (DC): species present in all the pineforest but which gradually decrease in number from the young to the old stands.
3 - Constant (C1): species present in similar numbers in all age classes.
4 - Final colonising (FC): species present only in old pineforests.
5 - Growing (GR): species present in all pineforests but more numerous in older stands.
6 - Unusual (UH): species present in one or two samples.
7 - Characteristic (CH): present in at least 50 % of the samples of an age class and with a proportion of more than 5 %.
8 - Exclusive (EX): species present only in one age class but in more than one sample.

Categories 7 and 8 are compatible with the former in that all species belonging of those categories are also included in another category. For example, *Acrobeloides nanus* is a constant species and is characteristic of autumn age class D.

In relation to the areas, the categories used are constant (C2), unusual (UH) and characteristic (CH) with the same definition as in the age categories. The exclusive species (EX) have a similar definition but referred to one or two areas (I and III in the north or VI and VIII in the south). However, in this case not all the exclusive species belong to another category. Furthermore, a new category must be added: non-spatial pattern (NP), species with a different behaviour.

The maturity index (MI) has been used according to the values proposed by Bongers (1990) and with the *c-p* values of each species set as a result of this work. $MI = \Sigma\, v(i) \cdot p(i)$, where $v(i)$ is the *c-p* value of taxon i and $p(i)$ is the proportion of that taxon in a sample.

Results

Nematodes identified

Seventy eight different taxa were identified in this study (Table 3). Some have been reported in previous papers (Armendáriz *et al.* 1991; Armendáriz & Hernández 1991, 1992). The number of nematodes found at different sites is quite variable and is shown in Table 4. Significantly, only one pineforest (Beorburu, 52 years old) has more than 50 % of the species collected (40/78). The high species substitution between sites can be seen in Tables 3 and 5.

There are seventeen taxa with a frequency of at least 25 %, 36 between 25 % and 5 %, and 25 below 5 % (Table 5). There are fifteen taxa whose proportion is greater than 2 %, 22 between 0.5 % and 2 % and 41 below 0.5 % (Table 5). Ten species represent more than 50 % of the specimens found in this work and there are 51 species with less than 1 %.

In the total number of nematodes found the proportion distribution according to taxonomic order is: Tylenchida plus Aphelenchida 35.48 %; Araeolaimida 22.86 %; Rhabditida 16.45 %; Dorylaimida 13.09 %; Chromadorida 4.95 %; Enoplida 4.33 % and Monhysterida 2.84 %.

According to the modified Cassagnau's (1961) classification, among the abundant species only four are extensive (*Anaplectus granulosus, Cephalobus persegnis, Plectus* sp. and *Tylocephalus andinus*), ten are localised and twenty are very localised. Among the low abundant species five are diffuse, nine are disperse and 30 are rare species. The fact that the very localised and rare species are the most abundant confirms the high species substitution at different sites.

These differences in species composition could be due to a maturation of the soil ecosystem with age or to geographical factors, and make it necessary to define other categories that might allow the importance of species to be regrouped depending on their behaviour in the succession. In this sense, two factors should be taken into consideration: the maturation dynamic from an initial situation to a more advanced phase with consequent colonisation stages, and the greater or lesser presence of a taxon in each geographical area.

Effects of geographical and climatic factors

The number of specimens at each area varies widely. It decreases towards the east and south (Table 4; Fig. 1). Thus, the largest number of specimens was found in Beorburu and the lowest in Ezprogui.

The number of species in each area decreases towards the south, being highest in Beorburu and lowest in Ezprogui.

The richness and diversity indices are greater in the northern than in the southern areas (Table 4). However these differences are very small as the maximum diversity index value is 5.87 and the minimum 5.40 and the maximum richness index value is 3.39 and the minimum 3.04.

The number of species from the modified Cassagnau's (1961) classification in geographical area is quite constant for the extensive, localised, diffuse and disperse species (Table 6). These species are the same in all areas. Only the very localised and rare species show a high variation, apparently without geographical influence.

According to the species categories defined in this paper (Table 7), 32 species are constant, twenty are exclusive, nineteen are unusual, fourteen are species with no spatial pattern, and fourteen are characteristic. Of the fourteen characteristic species thirteen are constant and only one is exclusive. There are more exclusive species in the northern (13) than in the southern areas (7). Of the thirteen exclusive species in the northern areas, only six are present in area I (Beorburu) and only one is present in area III (Leoz). The six remaining species are found in both areas. Of the seven species in the southern areas five are common to both areas and one is exclusive in each area.

The maturity index shows very little difference among the areas.

Effect of pineforest age

No trend in the number of specimens with regard to the age of the pineforest can be seen (Table 4). However, the number of species is higher in the older than in the younger forests as can be seen in Table 4. This is true for each area and the overall totals. The number of species increases with the age of the pineforest and the statistical significance of this trend was tested by regression analysis (Fig. 2). The indices of richness and diversity follow the same pattern in the different areas. This trend is illustrated by the regression analysis in the same figure, and is more significant for diversity than for richness. For both indices, there is a very important difference between age class B (pineforests less than 25 years old) and the rest of the age classes. When the pineforests of each locality are analysed, only Leoz does not follow this pattern. There is a reduction in both indices from age classes C to D in Beorburu, Añorbe, and Ezprogui and in the overall study. Some disturbance in silvicultural practices is suspected to be the cause for this. In general, both indices show the nematode communities to be more diverse as the age of the pineforest increases. This increase in the number of species is accompanied by a more balanced proportion distribution (that is, a greater number of taxa have a similar proportion).

According to the modified Cassagnau's (1961) classification, the only variation that can be seen in relation to the age classes correspond to the very localised and rare species, that increase its number with the pineforest age (Table 6).

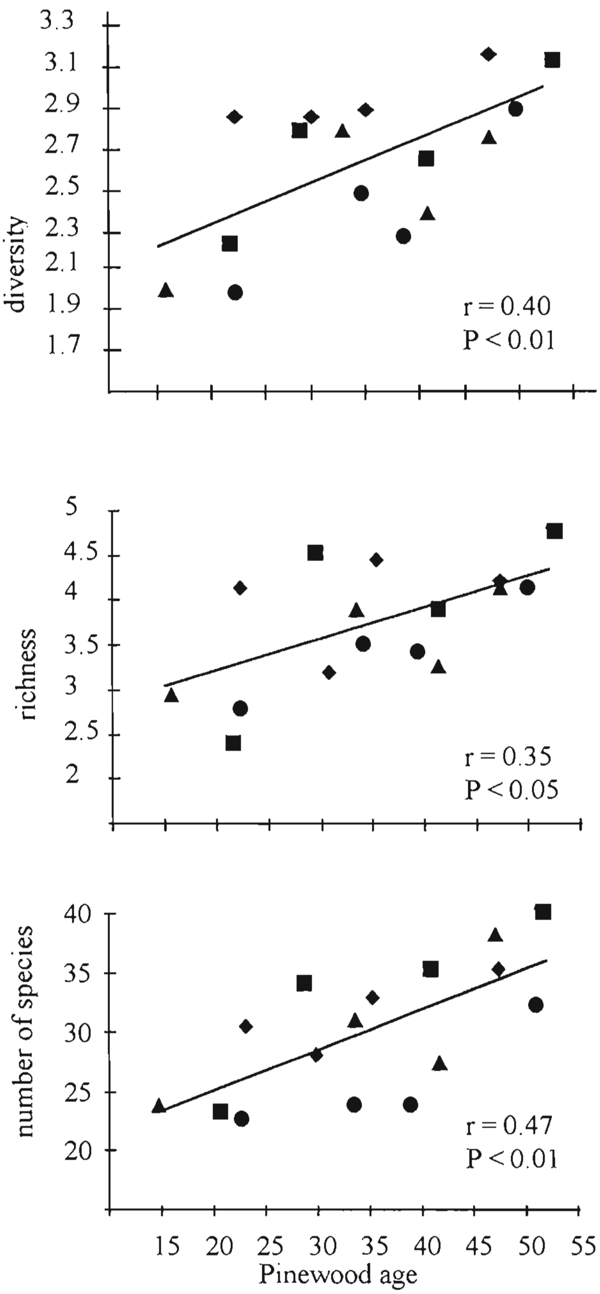

Fig. 2. *Regression analysis. Independent variable : pineforest age. Dependent variables : diversity (Shannon-Weaver), richness (Margalef), and number of species. ■ Beorburu samples, ♦ Leoz samples, ▲ Añorbe samples, ● Ezprogui samples.*

These differences in species composition could be due to a maturation of the soil ecosystem with age and, as species are grouped by their behaviour in the succession, it is possible to show the importance of species with the species categories defined in this paper (Table 7).

Table 3. *Number of specimens and frequency of each species in the areas (I, III, VI, VIII) and in the seasons (S : spring, A : autumn).*

			I (Beorburu)				III (Leoz)				VI (Añorbe)				VIII (Ezprogui)			
			S		A		S		A		S		A		S		A	
			N°/10 g	Freq.	N°/10 g	Freq.	N°/10 g	Freq.	N°/10 g	Freq.	N°/10 g	Freq.	N°/10 g	Freq.	N°/10 g	Freq.	N°/10 g	Freq.
1	*Achromadora ruricola*	(de Man, 1880) Micoletzky, 1925	1.77	25	72.76	50	28.10	63	7.77	13	2.24	13	100.42	25			0.24	13
2	*Achromadora* sp.		4.98	25			3.03	25										
3	*Acrobeles ciliatus*	Linstow, 1877									4.60	38	60.73	63	0.27	25	2.06	13
4	*Acrobeloides nanus*	(de Man, 1880) Anderson, 1968	6.38	63	25.59	88	4.89	50	35.43	88	8.61	38	10.31	50	1.43	38	39.99	50
5	*Alaimus meyli*	Andrássy, 1960							17.89	25					0.13	13	4.13	13
6	*Alaimus parvus*	Thorne, 1939	4.05	25	3.17	25			1.83	13								
7	*Alaimus* sp. 1		0.42	13					1.83	13	0.93	13	10.73	38				
8	*Alaimus* sp. 2																3.23	25
9	*Alaimus* sp. (immature)		0.87	13	7.78	38	1.46	13	5.40	38	0.44	13	1.08	13			0.21	13
10	Alirhabditidae g.n., sp. n.						0.95	13										
11	*Amphidelus lissus*	Thorne, 1939					1.13	13					0.83	13				
12	*Anaplectus granulosus*	(Bastian, 1865) De Coninck & S.S., 1933	24.51	75	37.49	50	33.41	75	29.99	50	11.21	63	205.77	100	23.38	63	97.63	75
13	*Anatonchus tridentatus*	(de Man, 1876) De Coninck, 1939	8.91	25	1.27	25												
14	*Aphanolaimus* sp. (imm.)						0.95	13										
15	*Autolaimus* sp.		1.23	25	0.14	13												
16	*Bastiania gracilis*	de Man, 1876									0.93	13			0.13	13	1.38	13
17	*Bunonema multipapillatum*	Stefansky, 1914	91.63	38	0.55	13	6.32	13	18.13	13	6.38	25	24.91	38	0.55	25	17.62	38
18	*Bunonema richtersi*	Jägerskjöld, 1905			16.23	38												
19	*Bunonema tuerkorum*	Sachs, 1949			0.91	13					3.35	13						
20	*Bunonema* sp. (immaturc)				5.91	25												
21	*Cephalobus persegnis*	Bastian, 1865	3.40	25	0.97	25	9.25	38	22.70	38	14.92	75	91.60	75	1.33	75	17.64	50
22	*Cephalobus* sp.						0.59	25										
23	*Ceratoplectus armatus*	(Bütschli, 1873) Andrássy, 1984	119.10	25	79.84	63	20.07	38	110.47	50	6.56	38	177.35	63	1.35	25	27.13	63
24	*Ceratoplectus assimilis*	(Bütschli, 1873) Andrássy, 1984	184.43	13	6.10	25			12.95	13	26.81	13	25.40	25				
25	*Ceratoplectus* sp. (immature)				4.42	25	0.04	13	2.59	13	1.39	13	1.26	25	0.18	13		
26	*Cervidellus serratus*	(Thorne, 1925) Thorne, 1937	0.57	13			2.26	13	3.41	25	12.14	63	71.36	88	0.90	25	20.01	25
27	*Chiloplacus minimus*	(Thorne, 1925) Andrássy, 1959											5.58	25			0.43	13
28	*Chiloplacus* sp.										1.39	13					0.93	13
29	*Clarkus papillatus*	(Bastian, 1865) Jairajpuri, 1970					5.62	50	16.28	63			2.74	38	0.12	13	4.59	25
30	*Cylindrolaimus bambus*	Andrássy, 1968	0.83	13			1.43	13	0.85	13							0.69	13
31	*Drilocephalobus coomansi*	Ali *et al.* 1973											1.67	13	0.06	13		
32	*Ereptonema arcticum*	Loof, 1971	0.10	13							8.13	38	8.17	38			7.45	13
33	*Eucephalobus mucronatus*	(Kozlowska & R. W., 1963) Andrássy, 1967											4.31	13				
34	*Eucephalobus oxyuroides*	(de Man, 1870) Steiner, 1936	126.45	50	23.22	25	5.42	25	40.37	38								
35	*Eucephalobus striatus*	(Bastian, 1865) Thorne, 1937					10.86	50	27.66	25			23.41	13			3.74	13
36	*Eucephalobus* sp. (immature)		0.83	13			1.49	25										
37	*Eumonhystera longicaudatula*	(Gerlach & Rienmann, 1973) Andrássy, 1981	0.83	13	14.10	13	7.25	25										
38	*Eumonhystera media*	Hernández & Jordana, 1988	6.66	13	3.87	25	17.05	25	6.30	25	1.82	38	78.05	100	0.23	13	2.78	13
39	*Eumonhystera multisetosa*	(Meyl, 1955) Andrássy, 1981			0.28	13	4.79	38	26.66	25			2.58	13			1.58	25
40	*Eumonhystera patiens*	Armendáriz & Hernández, 1992	27.98	38	32.90	13	0.95	13	5.94	25	0.99	13	4.17	13	4.01	38	19.32	25

Table 3 *(continued).*

41	*Eumonhystera vulgaris*	(De Man, 1880 Andrássy, 1981	1.58	13	4.04	25	19.60	38	5.56	13	0.25	13	3.94	25	0.24	25	8.14	25
42	*Eumonystera* sp. (immature)		0.57	13			2.31	25					0.83	13			1.87	13
43	*Geomonhystera villosa*	(Bütschli, 1873) Andrássy, 1981	21.06	25	2.33	25	5.94	13			1.83	25	5.00	13	0.63	25	4.65	25
44	*Heterocephalobus elongatus*	(de Man, 1880) Andrássy, 1967	10.97	38	17.22	13							2.25	25	0.18	13		
45	*Heterocephalobus loofi*	Andrássy, 1968													0.09	13		
46	*Heterocephalobus pseudolatus*	Hernández, 1990											1.17	13				
47	*Mesorhabditis spiculigera*	(Steiner, 1936) Dougherty, 1953			20.44	25			0.55	13	0.46	13	8.30	38			5.55	25
48	*Metateratocephalus crassidens*	(de Man, 1880) Eroshenko, 1973	3.33	13	7.59	25												
49	*Mylonchulus* sp.		1.13	13	0.55	13	1.46	13					1.96	25	0.18	13	0.69	13
50	*Panagrolaimus rigidus*	(Schneider, 1866) Thorne, 1937	23.19	25			1.13	13			47.81	25	12.10	25			5.75	38
51	*Paramphidelus dolichurus*	(de Man, 1876) Andrássy, 1977	1.82	25	2.78	25											2.06	13
52	*Paramphidelus* sp.								1.11	13	0.46	13						
53	*Plectus acuminatus*	Bastian, 1865	11.10	38	6.68	13	8.36	25	5.49	13	3.55	25					13.93	25
54	*Plectus cirratus*	Bastian, 1865	27.66	25	7.67	25	16.60	50	11.13	13	119.54	38	28.57	25	5.31	38	20.57	13
55	*Plectus geophilus*	de Man, 1880	38.39	50	21.85	38	11.35	25	29.56	38					1.32	38	61.01	38
56	*Plectus opisthoriculus*	Andrássy, 1952	13.05	38	2.23	13	21.86	50	54.63	38	55.12	38	35.55	50	0.18	13	7.45	13
57	*Plectus parvus*	Bastian, 1865	26.97	38	4.53	13	5.33	38			34.45	25	49.73	38	0.27	13		
58	*Plectus rhizophilus*	de Man, 1880	133.31	50	29.42	25			23.61	25	10.00	25	1.67	13	0.69	25		
59	*Plectus sambesii*	Micoletzky, 1915	11.08	13									2.35	13				
60	*Plectus* sp. (immature)		53.27	25	14.32	50	24.05	38	19.90	63	26.38	63	69.54	75	1.83	63	11.42	25
61	*Prionchulus muscorum*	(Dujardin, 1845) Wu & Hoeppli, 1927	12.69	50	2.72	13	18.30	38	28.37	38	4.36	25	7.65	25	2.00	38	6.66	38
62	*Prismatolaimus intermedius*	(Bütschli, 1873) de Man, 1880	3.33	13	9.40	13	17.69	38	10.74	25	0.93	25			0.22	13	0.73	13
63	*Prismatolaimus primitivus*	Loof, 1970			0.55	13									1.13	25	30.14	38
64	*Prismatolaimus* sp. (immature)										0.49	13	0.40	13				
65	*Prodesmodora arctica*	(Mulvey, 1865) Andrássy, 1984	107.74	38	149.53	50	33.83	50	30.20	38	1.98	25	117.21	63	18.94	50	47.30	50
66	*Protorhabditis tristis*	(Hirschmann, 1952) Dougerty, 1953	14.22	50	32.24	63	13.33	88	4.55	38	7.39	50	1.23	25	0.05	13	21.22	50
67	Rhabditida				0.14	13	2.20	13	40.73	50	2.94	25			0.18	13	60.02	63
68	*Rhabditis longicaudatula*	Bastian, 1865					1.62	25	27.43	25							7.48	13
69	*Rhabditis* sp.				2.72	13	2.44	25					3.14	25				
70	*Rhabditophanes* sp.						0.04	13										
71	*Rhodonema* sp.		0.42	13	0.91	13												
72	*Teratocephalus costatus*	Andrássy, 1958	16.64	13	27.12	38			16.31	25					0.15	25	22.36	13
73	*Teratocephalus terrestris*	(Bütschli, 1873) de Man, 1876			45.35	63	3.16	13			2.81	25	11.76	38	2.91	25	2.67	13
74	*Teratocephalus sp.* (immature)						0.37	13					2.35	13				
75	*Tripyla filicaudata*	de Man, 1880	1.67	13	0.50	13	3.27	38	11.13	13								
76	*Tripyla filipjevi*	(Filipjev, 1929) Tsalolichin, 1983	3.40	25	11.31	50	13.30	38	6.17	25	0.44	13	3.15	25	7.17	25		
77	*Tripyla* sp. (immature)				2.42	13							11.71	13				
78	*Tylocephalus andinus*	Zell, 1985	221.90	38	82.53	50	29.87	50	96.83	50	28.69	38	143.37	75	20.70	50	83.77	63

For example, *Tylocephalus andinus* has a proportion of 11.48 % and a frequency of 51.56 %. It is an abundant-expansive (ae), and constant species (C1 and C2); it is present in all age classes and areas and is characteristic (CH) of some of them. On the other hand, *Alaimus parvus* has a proportion of 0.15 % and a frequency of 7.81 %. It is a low-rare (lr), and constant (C1) species, exclusive (EX) to the northern areas (Beorburu and Leoz).

According to these species categories, 31 species are constant; five are initial colonising; four are decreasing; seventeen are final colonising species; eleven are growing species, ten are unusual species, six are exclusive species, and eight are characteristic species (Table 7). In relation to the proportion of each species category it is interesting to point out that constant species are the most numerous (78.71 %), followed by growing species (11.85 %), final colonising (4.59 %), decreasing species

Table 4. *Age (years since planting). Number of specimens, number of species, richness (Margalef index), diversity (Shannon-Weaver), MI (maturity index) and MI′ (recalculated maturity index) according to areas (I, III, VI, VIII) and age classes (B, C, D, E).*

Sites	Age	Specimens in 40 g/dw	Species	Richness	Diversity	MI	MI′
I B (Beorburu)	21	7098	23	2.48	2.21	1.96	2.98
I C (Beorburu)	29	1451	34	4.53	2.82	2.21	2.79
I D (Beorburu)	41	5942	35	3.91	2.65	2.33	3.18
I E (Beorburu)	52	3292	40	4.82	3.15	1.98	3.26
III B (Leoz)	22	1316	31	4.18	2.88	2.27	2.82
III C (Leoz)	30	3953	28	3.26	2.86	2.15	2.91
III D (Leoz)	35	1215	33	4.51	2.92	2.16	3.23
III E (Leoz)	47	3462	35	4.17	3.19	2.05	3.13
VI B (Añorbe)	15	2125	24	3.00	2.01	2.00	2.99
VI C (Añorbe)	33	2262	31	3.88	2.77	1.95	3.06
VI D (Añorbe)	41	2810	27	3.27	2.38	2.23	3.30
VI E (Añorbe)	47	7979	38	4.12	2.76	2.03	3.15
VIII B (Ezprogui)	22	2299	23	2.84	1.98	1.96	2.91
VIII C (Ezprogui)	34	750	24	3.47	2.52	2.07	2.94
VIII D (Ezprogui)	39	974	24	3.34	2.26	1.89	3.09
VIII E (Ezprogui)	50	2376	33	4.12	2.95	2.14	3.29
		Totals B to E					
I (Beorburu)		17783	57	5.72	3.11	2.10	3.14
III (Leoz)		9946	55	5.87	3.39	2.13	3.08
VI (Añorbe)		15176	53	5.40	3.06	2.05	3.21
VIII (Ezprogui)		6399	50	5.59	3.04	2.03	3.12
		Totals I to VIII					
B	< 25	12838	48	4.97	2.76	2.00	2.95
C	25-34	8416	59	6.42	3.40	2.11	2.96
D	35-45	10941	57	6.02	3.09	2.25	3.21
E	> 45	17109	65	6.57	3.45	2.04	3.19

(3.96), initial colonising (0.53 %) and unusual species (0.36 %).

Of the 31 constant species in the age classes, twenty are also constant in the geographical areas, seven have no spatial pattern, and four are exclusive species. Twelve species are constant in the geographical areas and they are not constant in the age classes; nine of them are growing species and one is a final colonising species; only two belong to the decreasing species category.

The number of exclusive species grows with the age of the pineforest: nil in pineforests less than 25 years old, one species in pineforests between 25-34 years old, two species in 35-45 year-old pineforests and three in pineforests over 45 years old. By definition, initial colonising species decrease in number with the age and final colonising species increase in number with the pineforest age.

To calculate the maturity index (MI), the *c-p* category values proposed by Bongers (1990) are related to the family level rather than the species level. Species of the same family can show different behaviour patterns, as is the case with the Monhysteridae which are considered by Bongers as coloniser species with a value of *c-p* = 1. However, *Geomonhystera villosa* is a decreasing species, *Eumonhystera media* and *E. patiens* are constant species. *E. multisetosa* and *E. vulgaris* are growing species, and *E. longicaudatula* is a final colonising species. Bongers suggests a refinement of his system and for this reason the following *c-p* values are proposed for the categories used in this paper:

initial colonising	1
decreasing	2
constant	3
growing	4
final colonising	5

The remaining categories have been left with the family *c-p* values assigned to them by Bongers until their role in the index can be confirmed (Table 8). In the last two columns of this Table, the *c-p* Bongers' values and the new values used in this paper are given for each species.

With those values the maturity index has been calculated (Table 4) with the species identified in this work. There are two columns : MI, maturity index calculated with Bongers' values, and MI' which was calculate with the modified values. Both show a different evolution with pineforest age. MI' is greater than MI in every site and age. In relation to age classes, both maturity index values increase with pineforest age until class D (35-45 years old); in age E (> 45 years old) MI decreases almost to values of the youngest pineforests (B class) whereas MI' is quite stable between D and E age classes. When a regression analysis was applied to the two MI values against the pineforest age as an independant variable, only the correlation with MI' was significant (Fig. 3). Furthermore, this correlation was more significant than those obtained from richness, diversity, and species number correlations.

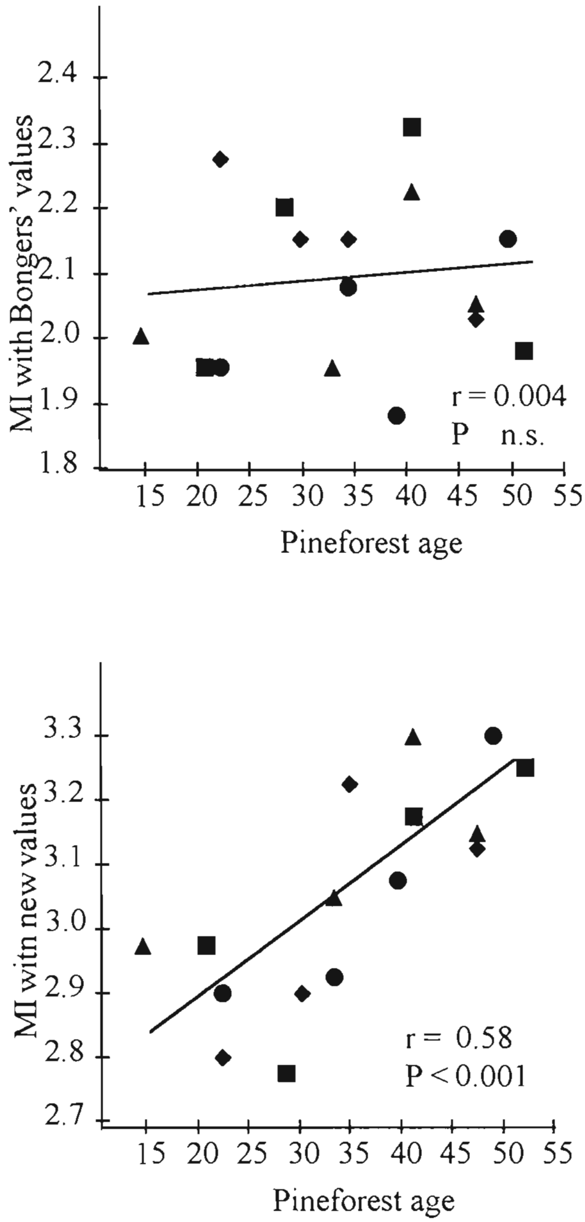

Fig. 3. *Regression analysis. Independent variable pineforest age. Dependent variables : maturity index with Bongers' values and maturity index with new values. ■ Beorburu samples, ♦ Leoz samples, ▲ Añorbe samples, ● Ezprogui samples.*

Discussion

Freckman and Ettema (1993) discussed the reliability of various ecological indices to predict the degree of human intervention in agricultural and successional systems, concluding that the most representative are the multivariate analysis and the Maturity Index (MI). The latter is applicable to this study with the qualification that not all nematodes were identified. Yeates and Bird (1994) proposed the use of richness and diversity to show the fauna composition in cultured soils.

The diversity values obtained in this study are similar to those given by Sohlenius (1993) (H' = 3.37) in 130-140 year-old stands of *P. sylvestris* and to those by Sohlenius and Wasilewska (1984) (H' = 2.94 for all layers but 3.20 for irrigated plots in a 20-25 year-old pineforest).

De Goede (1993), in a plant dune succession on sandy soils reforested with *Pinus sylvestris,* reported an increase in diversity and abundance in connection with the development of an organic soil profile. In a study of agroecosystems Freckman and Ettema (1993) found an increase in trophic diversity, Shannon and Maturity indices in connection with a decrease in human intervention, while Wasilewska (1989) found lowered stability and richness as a result of high levels of fertilisation or drainage in cultivated natural grassland.

These observations on the decrease in ecosystem maturity as a result of human action can be applied to the pineforests studied. After a high level of human intervention caused by the substitution of the original biotope with a monospecific culture, the former is left to evolve by itself over long periods with only small adjustments (replanting in the early years, thinning, cleaning). The strong litter production helps create a humus layer and better structured soil populations (more species with a similar proportion). In this disturbed habitat colonisation process, nematode species with a different colonising capability intervene (Bongers, 1990), resulting in a higher ecosystem maturity ranking (Ettema & Bongers, 1993).

However, Jordana *et al.* (1987 *b*) reported a rupture in the structure and dynamics of soil fauna populations in reforestation with conifers. The pineforests became poorer both numerically and specifically than adjacent

Table 5. *Cassagnau's (1961) abundance classes, proportion and frequency of each species. Number of specimens and frequency of each species in the age classes (B, C, D, E).*

		Cassagnau's Ab. Class	%	Freq.	B (< 25 y.)				C (25-35 y.)				D (35-45 y.)				E (> 45 y.)			
					S		A		S		A		S		A		S		A	
					N°/10 g	Freq.	N°/10 g	Freq.	N°/10 g	Freq.	N°/10 g	Freq.	N°/10 g	Freq.	N°/10 g	Freq.	N°/10 g	Freq.	N°/10 g	Freq.
1	*A. ruricola**	al	3.46	25.00			9.54	25	12.10	38			3.37	25	161.51	38	16.64	38	10.13	38
2	*Achromadora* sp.	lr	0.13	6.25									6.43	38			1.58	13		
3	*A. ciliatus*	av	1.10	17.19					2.20	25	15.29	25	2.12	13	23.16	25	0.55	25	24.35	25
4	*A. nanus*	lp	2.15	57.81	1.71	38	12.20	63	10.08	63	15.71	75	3.77	38	55.00	75	5.74	50	28.40	63
5	*A. meyli*	av	0.36	6.25			17.89	25									0.13	13	4.13	13
6	*A. parvus*	lr	0.15	7.81			1.83	13	2.92	13	2.48	13	1.13	13					0.69	13
7	*Alaimus* sp. 1	lp	0.23	9.38			4.36	25	0.42	13							0.93	13	8.20	25
8	*Alaimus* sp. 2	lr	0.05	3.13							1.85	13							1.38	13
9	*Alaimus* sp. (imm.)	lr	0.28	17.19			2.91	25	1.31	25	0.91	13			2.63	25	1.46	13	8.03	38
10	Alirhabditidae g. n. sp. n.	lr	0.02	1.56									0.95	13						
11	*A. lissus*	lr	0.03	3.13							0.83	13	1.13	13						
12	*A. granulosus*	ae	7.52	68.75	21.82	63	70.44	63	24.68	75	8.28	50	27.99	88	59.19	100	18.02	50	232.96	63
13	*A. tridentatus*	av	0.17	6.25					0.42	13	0.99	13	8.50	13					0.28	13
14	*Aphanolaimus* sp. (imm.)	lr	0.02	1.56									0.95	13						
15	*Aulolaimus* sp.	lr	0.02	4.69									1.13	13			0.10	13	0.14	13
16	*B. gracilis*	lr	0.04	4.69													1.05	25	1.38	13
17	*B. multipapillatum*	al	2.69	25.00	82.43	25	2.42	25	0.44	13	5.00	13	9.36	38	12.02	13	12.66	25	41.76	50
18	*B. richtersi*	ld	0.26	4.69							0.50	13							15.73	25
19	*B. tuerkorum*	lr	0.07	3.13							0.91	13					3.35	13		
20	*Bunonema* sp. (imm.)	lr	0.10	3.13											5.91	25				
21	*C. persegnis*	ae	2.63	50.00	6.85	75	8.69	38	12.08	38	78.69	50	3.76	63	5.44	50	6.20	38	40.10	50
22	*Cephalobus* sp.	lr	0.01	3.13	0.14	13			0.45	13										
23	*C. armatus*	al	8.79	45.31	106.72	38	132.52	63	1.76	25	95.21	38	22.43	38	102.52	50	16.16	25	64.54	88
24	*C. assimilis*	av	4.15	10.94	184.43	13	1.64	13			25.40	25					26.81	13	17.41	25
25	*Ceratoplectus* sp. (imm.)	ld	0.16	12.50			2.61	25	0.04	13	0.83	13	0.18	13			1.39	13	4.82	25
26	*C. serratus*	al	1.80	31.25	1.00	13	10.73	25	5.01	38	26.79	25	5.06	38	18.23	38	4.79	25	39.02	50
27	*C. minimus*	lr	0.10	4.69			5.58	25			0.43	13	3.77	38	55.00	75	5.74	50	28.40	63
28	*Chiloplacus* sp.	lr	0.04	3.13							0.93	13					1.39	13		
29	*C. papillatus*	lr	0.48	23.44	2.63	25	2.90	38	1.69	25	8.13	38	1.43	13	8.86	38			3.73	13
30	*C. bambus*	lr	0.06	6.25					0.83	13	0.85	13	1.43	13					0.69	13
31	*D. coomansi*	lr	0.03	3.13							1.67	13					0.06	13		
32	*E. arcticum*	av	0.39	12.50					0.51	13	5.40	25			2.77	13	7.73	38	7.45	13
33	*E. mucronatus*	lr	0.07	1.56			4.31	13												
34	*E. oxyuroides*	av	3.17	17.19	112.99	25	9.85	13	8.71	13	16.69	13	2.26	13			7.91	25	37.05	38
35	*E. striatus*	ld	1.07	12.50	4.92	25	14.71	25			16.69	13	5.94	25					23.41	13
36	*Eucephalobus* sp. (imm.)	lr	0.04	4.69					0.83	13			1.13	13			0.37	13		
37	*E. longicaudatula*	av	0.36	6.25					0.83	13			7.25	25	14.10	13				
38	*E. media*	al	1.89	31.25	0.23	13	15.10	50	3.33	25	17.98	38	7.97	38	29.94	38	14.23	13	27.99	38
39	*E. multisetosa*	lp	0.58	14.06			0.24	13			11.13	13	3.21	25	3.91	25	1.58	13	15.81	25
40	*E. patiens*	av	1.56	21.88	10.36	25			3.55	13	9.73	25	8.60	38	33.28	25	11.43	25	19.32	25
41	*E. vulgaris*	lp	0.70	21.88	0.42	25	0.42	13	0.25	13	7.38	25	1.90	13			19.10	38	13.89	50
42	*Eumonhystera* sp. (imm.)	lr	0.09	7.81			1.87	13			0.83	13	0.57	13			2.31	25		
43	*G. villosa*	av	0.67	18.75	27.00	38	2.33	25	0.72	25	5.93	25	0.36	13			1.39	13	3.73	13
44	*H. elongatus*	av	0.50	10.94			1.08	13	7.80	25	17.22	13					3.34	25	1.17	13
45	*H. loofi*	lr	0.00	1.56													0.09	13		
46	*H. pseudolatus*	lr	0.02	1.56															1.17	13
47	*M. spiculigera*	lp	0.57	14.06			5.80	50							24.35	38	0.46	13	4.69	13
48	*M. crassidens*	av	0.18	4.69							0.91	13	3.33	13					6.68	13
49	*Mylonchulus* sp.	lr	0.10	10.94									1.31	25	0.79	13	1.46	13	2.41	38

***Table 5** (continued).*

50	*P. rigidus*	lp	1.46	15.63					3.50	25			1.13	13	1.73	25	67.50	25	16.12	38
51	*P. dolichurus*	lr	0.11	7.81					1.25	13	0.99	13	0.57	13					3.85	25
52	*Paramphidelus* sp.	lr	0.03	3.13			1.11	13									0.46	13		
53	*P. acuminatus*	lp	0.80	17.19	0.20	13	5.49	13	4.77	25			6.77	13			11.26	38	20.62	38
54	*P. cirratus*	al	3.85	28.13	34.89	63	20.57	13	10.50	38	16.56	25	0.81	13	5.15	13	122.89	38	25.64	25
55	*P. geophilus*	al	2.65	28.13	25.94	38	35.31	25	8.33	25	13.70	25	7.20	25	26.36	38	9.59	25	37.04	25
56	*P. opisthocirculus*	al	3.08	31.25	0.02	13	24.43	38	10.75	38	31.98	25	6.82	50			72.61	38	43.46	50
57	*P. parvus*	av	1.97	20.31	10.99	13			1.11	25	5.56	25	20.02	25	7.73	13	34.91	50	40.98	13
58	*P. rhizphilus*	av	3.22	20.31	31.32	25	5.49	13	30.03	38	28.86	25	69.99	25			12.66	13	20.36	25
59	*P. sambesii*	av	0.22	3.13													11.08	13	2.35	13
60	*Plectus* sp. (imm.)	ae	3.58	50.00	2.23	25	5.02	63	9.62	50	23.58	50	6.61	50	38.18	25	87.07	63	48.41	75
61	*P. muscorum*	lp	1.34	32.81	0.46	13	3.66	13	18.27	63	32.11	50	5.59	25	8.94	38	13.04	50	0.69	13
62	*P. intermedius*	av	0.70	17.19			0.73	13	0.22	13	5.56	13	12.00	50	9.40	13	9.95	25	5.18	13
63	*P. primitivus*	ld	0.52	9.38			0.55	13							0.21	13	1.13	25	29.93	25
64	*Prismatolaimus* sp. (imm.)	lr	0.01	3.13									0.49	13	0.40	13				
65	*P. arctica*	al	8.22	45.31	71.71	38	28.82	63	16.73	50	41.93	50	40.11	25	138.86	25	33.93	50	134.64	63
66	*P. tristis*	lp	1.53	46.88	2.95	38	9.20	50	1.41	38	15.96	50	7.75	75	6.43	38	22.89	50	27.65	38
67	Rhabditida	av	1.72	21.88	2.20	13	23.95	50	0.18	13	40.67	38	2.47	13			0.46	13	36.27	38
68	*R. longicaudatula*	av	0.59	7.81	0.04	13	7.48	13			22.25	13					1.58	13	5.18	13
69	*Rhabditis* sp.	lr	0.13	7.81	0.06	13	1.08	13			4.78	25	2.38	13						
70	*Rhabditophanes* sp.	lr	0.00	1.56	0.04	13														
71	*Rhodonema* sp.	lr	0.02	3.13					0.42	13	0.91	13								
72	*T. costatus*	av	1.34	14.06							11.13	13	16.64	13	4.70	13	0.15	25	49.96	50
73	*T. terrestris*	av	1.11	21.88			1.09	13	4.15	25	10.59	25	1.57	25	28.74	38	3.16	13	19.36	38
74	*Teratocephalus* sp. (imm.)	lr	0.04	3.13													0.37	13	2.35	13
75	*T. filicaudata*	lp	0.27	9.38	1.84	25			1.67	13	11.62	25	1.43	13						
76	*T. filipjevi*	al	0.73	25.00	0.57	13	4.67	25	0.44	13	5.44	13	6.48	38	1.21	13	12.80	38	13.33	50
77	*Tripyla* sp. (imm.)	av	0.23	3.13											2.42	13			11.71	13
78	*T. andinus*	ae	11.48	51.56	210.88	38	124.17	75	8.58	50	91.37	50	38.81	50	122.92	50	42.89	38	68.04	63

For generic names see Table 3.

***Table 6.** Number of species belonging to the modified Cassagnau's (1961) classification in the different geographical areas I (Beorburu), III (Leoz), VI (Añorbe), VIII (Ezprogui), age classes B (< 25 y.), C (25 – 34 y.), D (35 – 45 y.), E (> 45 y.) and total number.*

	Abundant species			Low abundance species		
	Expansive (ae)	Localised (al)	Very localised (av)	Diffuse (ld)	Disperse (lp)	Rare (lr)
I	4	10	17	4	9	13
III	4	10	13	3	9	16
VI	4	9	13	3	8	16
VIII	4	10	13	4	7	12
B	4	10	12	4	8	10
C	4	10	17	4	8	16
D	4	10	15	4	8	16
E	4	10	19	5	8	19
Total	4	10	20	5	9	30

***Table** 7. Abundance categories defined in this paper for each species. C1 and C2 (constant), CH (characteristic), DC (decreasing), EX (exclusive), FC (final colonizing), GR (growing), IC (initial colonizing), NP (no spatial pattern), UH (unusual). For the EX and CH columns : Age classes (B < 25 y., C 25-34 y.$_{-1}$, D 34-45 y., E > 45 y.), areas (I Beorburu, III Leoz, VI Añorbe, VIII Ezprogui), seasons (S spring, A autumn).*

	Areas						Age classes								
	C2	UH	EX	NP	CH		IC	DC	C1	FC	GR	UH	EX	CH
Alaimus (imm.)	*					*A. ruricola*			*					
*A. ruricola**	*				IA, IIIS	*A. nanus*			*					DA
A. nanus	*				VIIIA	*Alaimus* (imm.)			*					
A. granulosus	*				IIIS, VIA, VIIIS A	*A. meyli*			*					
B. multipapillatum	*					*A. parvus*			*					
Ceratoplectus (imm.)	*					*A. granulosus*			*					BA, CS, DS, EA
C. persegnis	*				VIA	*A. tridentatus*			*					
C. armatus	*				IA, IIIA, VIA	*B. multipapillatum*			*					
C. serratus	*				VIA	*C. persegnis*			*					BS, CA
E. media	*				VIA	*Ceratoplectus* (imm.)					*			
E. multisetosa	*					*C. armatus*			*					BA, DA
E. patiens	*					*C. assimilis*			*					
Eumonhystera (imm.)	*					*C. serratus*			*					
E. vulgaris	*					*C. papillatus*			*					
G. villosa	*					*C. bambus*			*					
P. cirratus	*					*Eumonhystera* (imm.)			*					
P. opisthocirculus	*					*E. media*			*					
P. rhizophilus	*				IA	*E. patiens*			*					
Plectus (imm.)	*				VIS	*Eucephalobus* (imm.)			*					
P. intermedius	*					*E. oxyuroides*			*					
P. arctica	*				IA, IIIS, VIA, VIIIS A	*P. dolichurus*			*					
P. tristis	*					*P. cirratus*			*					
Rhabditida	*				VIIIA	*P. geophilus*			*					
T. filipjevi	*					*P. opisthocirculus*			*					
T. terrestris	*				IA	*P. rhizophilus*			*					
T. andinus	*				IA, IIIS A, VIA, VIIIS	*P. muscorum*			*					CS
M. spiculigera	*					*P. arctica*			*					CS A, EA
Mylonchulus sp.	*					*P. tristis*			*					
P. parvus	*					*R. longicaudata*			*					
P. rigidus	*					*T. terrestris*			*					
P. acuminatus	*					*T. andinus*			*					BA, CS A, DS A, EA
P. muscorum	*					*Cephalobus* sp.	*							
A. parvus			I III			*C. minimus*	*							
Achromadora sp.			I III			*Rhabditis* sp.	*							
Alaimus sp. 2		*	VIII			*Rhodonema* sp.	*						C	
A. ciliatus			VI VIII			*T. filicaudata*	*							
A. tridentatus			I			*E. striatus*		*						
Aulolaimus sp.			I			*G. villosa*		*						
B. richtersi			I			*H. elongatus*		*						
Bunonema (imm.)		*	I			*Rhabditida*		*						
B. gracilis			VI VIII			*Alaimus* sp. 1					*			
Cephalobus sp.		*	III			*E. multisetosa*					*			
Chiloplacus sp.		*	VI VIII			*E. vulgaris*					*			
C. minimus			VI VIII			*M. spiculigera*					*			
D. coomansi		*	VI VIII			*P. rigidus*					*			
E. oxyuroides			I III		IS	*Plectus* (imm.)					*		D	ES
Eucephalobus (imm.)			I III			*P. acuminatus*					*			
E. longicaudatula			I III			*P. parvus*					*			
M. crassidens			I			*P. intermedius*					*			

***Table** 7 (continued).*

Prismatolaimus (imm.)	*	VI		*P. primitivus*		*		
Rhodonema sp.	*	I		*T. filipjevi*		*		
T. filicaudata		I III		*Achromadora* sp.	*			
Alirhabditidae g. n., sp. n.	*			*A. ciliatus*	*			
Aphanolaimus (imm.)	*			*Aulolaimus* sp.	*			
B. tuerkorum	*			*B. gracilis*	*			E
E. mucronatus	*			*B. richtersi*	*			
H. loofi	*			*B. tuerkorum*	*			
H. pseudolatus	*			*Chiloplacus* sp.	*			
P. sambesii	*			*D. coomansi*	*			
Paramphidelus sp.	*			*E. articum*	*			
Rhabditis sp.	*			*E. longicaudatula*	*			
Rhabditophanes sp.	*			*M. crassidens*	*			
Teratocephalus (imm.)	*			*Mylonchulus* sp.	*			
Tripyla (imm.)	*			*P. sambesii*	*			E
A. meyli			*	*Prismatolaimus* (imm.)	*			
Alaimus sp. 1			*	*T. costatus*	*			
A. lissus			*	*Teratocephalus* (imm.)	*			E
C. assimilis			*	*Tripyla* (imm.)	*			
C. papillatus			*	*Alaimus* sp. 2			*	
C. bambus			*	Alirhabditidae g. n., sp. n.			*	
E. articum			*	*A. lissus*			*	
E. striatus			*	*Aphanolaimus* (imm.)			*	
H. elongatus			*	*Bunonema* (imm.)			*	D
P. dolichurus			*	*E. mucronatus*			*	
P. geophilus			*	*H. loofi*			*	
P. primitivus			*	*H. pseudolatus*			*	
R. longicaudata			*	*Paramphidelus* sp. 1			*	
T. costatus			*	*Rhabditophanes* sp.			*	

* For generic names see Table 3.

natural areas. The critical conditions of these reforestations (minimal rainfall, high evaporation, and absence of others vegetables species) halts their evolution. The organic material builds up and there is no soil genesis.

Nevertheless, our reforestations are in better condition and there is a further evolution. The organic material is transformed into soil and humus is produced. Historicaly, most of the reforestation of theses areas was carried out in old pastures once the cattle farming had stopped. Trees prevent erosion and the created and sustained soil allows natural regeneration to occur (for example *Fagus silvatica* L. in Beorburu 52 year-old pineforest).

If geographical distribution is considered, there is a notable geographic axis in Navarra, ranging from an alpine climate in the north-east (Pyrenees) to a semiarid climate in the south-west (Bardenas). If the geographical location of the *P. nigra* forests studied is considered, it becomes apparent that those in the southern areas are in a worse state (they are not in their natural distribution area). Further evolution has not been stopped, but is slower and less structured communities are found in the oldest stands. These results coincide with those of Moreno (1991) on the Acari fauna.

In this study some species categories are given. From the study of this classification it can be concluded that pineforest reforestation provides good conditions for the growth of the soil fauna and that these categories may be useful in the characterisation of the nematode fauna. Their validity lies in the fact that they can describe taxa behaviours in the different situations established by the reforestation. Bongers (1990) established five different categories ranging from colonisers (r-strategists) to persisters (K-strategists) and assigned a value to different nematode families. However, the species categories used in present work show that nematode species belonging to a family may have different colonisation capabilities and the *c-p* value should thus be defined at the species level. This observation is supported by Ruess (1995) who found no correlation between MI and tree damage in spruce forest in Germany.

Both calculations of the maturity index show a different predominance in the geographical areas. With de *c-p* values proposed by Bongers, it is the northern areas that

Table 8. *Comparison of different categories for each species.*

	This paper		Cassagnau 1961	Wasilewska 1991	Hodda & Wanless, 1994		Bongers' values	
	Temporal categories	Spatial categories			Temporal categories	Spatial categories	1990	This paper
*A. ruricola**	C1	C2 CH	al	Subdominant	No temp. pat	Generalist	3	3
A. nanus	C1 CH	C2 CH	lp	Accidental	No temp. pat	Generalist	2	3
Alaimus (imm.)	C1	C2	lr	Accidental	No temp. pat	Generalist	4	4
A. granulosus	C1 CH	C2 CH	ae	Subdominant	No temp. pat	Generalist	2	3
B. multipapillatum	C1	C2	al	Subdominant	No temp. pat	Generalist	1	3
C. persegnis	C1 CH	C2 CH	ae	Subdominant	No temp. pat	Generalist	2	3
Ceratoplectus (imm.)	C1	C2	ld	Accidental	No temp. pat	Generalist	2	2
C. armatus	C1 CH	C2 CH	al	Subdominant	No temp. pat	Generalist	2	3
C. serratus	C1	C2 CH	al	Accidental	No temp. pat	Generalist	2	3
Eumonhystera (imm.)	C1	C2	lr	Accidental	No temp. pat	Generalist	1	1
E. media	C1	C2 CH	al	Accidental	No temp. pat	Generalist	1	3
E. patiens	C1	C2	av	Accidental	No temp. pat	Generalist	1	3
P. cirratus	C1	C2	al	Subdominant	No temp. pat	Generalist	2	3
P. opisthocirculus	C1	C2	al	Subdominant	No temp. pat	Generalist	2	3
P. rhizophilus	C1	C2 CH	av	Subdominant	No temp. pat	Generalist	2	3
P. muscorum	C1 CH	C2	lp	Accidental	No temp. pat	Generalist	4	3
P. arctica	C1 CH	C2 CH	al	Subdominant	No temp. pat	Generalist	3	3
P. tristis	C1	C2	lp	Accidental	No temp. pat	Generalist	1	3
T. terrestris	C1	C2 CH	av	Accidental	No temp. pat	Generalist	3	3
T. andinus	C1 CH	C2 CH	ae	Dominant	No temp. pat	Generalist	2	3
A. meyli	C1	NP	av	Accidental	No temp. pat		4	3
C. assimilis	C1	NP	av	Subdominant	No temp. pat		2	3
C. papillatus	C1	NP	lr	Accidental	No temp. pat		4	3
C. bambus	C1	NP	lr	Accidental	No temp. pat		2	3
P. dolichurus	C1	NP	lr	Accidental	No temp. pat		4	3
P. geophilus	C1	NP	al	Subdominant	No temp. pat		2	3
R. longicaudata	C1	NP	av	Accidental	No temp. pat		1	3
A. parvus	C1	EX	lr	Accidental	Other pat.	Specialist	4	3
A. tridentatus	C1	EX	av	Accidental	No temp. pat	Specialist	4	3
Eucephalobus (imm.)	C1	EX	lr	Accidental	No temp. pat	Specialist	2	2
E. oxyuroides	C1	EX CH	av	Subdominant	No temp. pat	Specialist	2	3
E. multisetosa	GR	C2	lp	accidental	Increas. abun.	Generalist	1	4
E. vulgaris	GR	C2	lp	Accidental	Increas. abun.	Generalist	1	4
M. spiculigera	GR	C2	lp	Accidental	Increas. abun.	Generalist	1	4
P. rigidus	GR	C2	lp	Accidental	Increas. abun.	Generalist	1	4
Plectus (imm.)	GR EX	C2 CH	ae	Subdominant	Increas. abun.	Generalist	2	4
P. acuminatus	GR	C2	ld	Accidental	Increas. abun.	Generalist	2	4
P. parvus	GR	C2	av	Accidental	Increas. abun.	Generalist	2	4
P. intermedius	GR	C2	av	Accidental	Increas. abun.	Generalist	3	4
T. filipjevi	GR	C2	al	Accidental	Increas. abun.	Generalist	3	4
Mylonchulus sp.	FC	C2	lr	Accidental	Other pat.	Generalist	4	5
G. villosa	DC	C2	av	Accidental	Decreas. abund.	Generalist	1	2
Rhabditida	DC	C2 CH	av	Accidental	Decreas. abund.	Generalist	1	2
Cephalobus sp.	IC	EX UH	lr	Accidental	Other pat.	Specialist	2	1
C. minimus	IC	EX	lr	Accidental	Other pat.	Specialist	2	1
Rhabditis sp.	IC	UH	lr	Accidental	Other pat.	Specialist	1	1
Rhodonema sp.	IC EX	EX UH	lr	Accidental	Other pat.	Specialist	1	1
T. filicaudata	IC	EX	lp	Accidental	Other pat.	Specialist	3	1
E. striatus	DC	NP	ld	Accidental	Decreas. abund.		2	2
H. elongatus	DC	NP	av	Accidental	Decreas. abund.		2	2
Alaimus sp. 1	GR	NP	lp	Accidental	Increas. abun.	Specialist	4	4
P. primitivus	GR	NP	ld	Accidental	Increas. abun.		3	4

***Table 8** (continued).*

Achromadora sp.	FC	EX	lr	Accidental	Other pat.	Specialist	3	5
A. ciliatus	FC	EX	av	Accidental	Other pat.	Specialist	2	5
Aulolaimus sp.	FC	EX	lr	Accidental	Other pat.	Specialist	3	5
B. gracilis	FC EX	EX	lr	Accidental	Other pat.	Specialist	3	5
B. richtersi	FC	EX	ld	Accidental	Other pat.	Specialist	1	5
B. tuerkorum	FC	UH	lr	Accidental	Other pat.	Specialist	1	5
Chiloplacus sp.	FC	EX UH	lr	Accidental	Other pat.	Specialist	2	5
D. coomansi	FC	EX UH	lr	Accidental	Other pat.	Specialist	2	5
E. articum	FC	NP	av	Accidental	Other pat.		2	5
E. longicaudatula	FC	EX	av	Accidental	Other pat.	Specialist	1	5
M. crassidens	FC	EX	av	Accidental	Other pat.	Specialist	3	5
P. sambesii	FC EX	UH	av	Accidental	Other pat.	Specialist	2	5
Prismatolaimus (imm.)	FC	EX UH	lr	Accidental	Other pat.	Specialist	3	3
Teratocephalus (imm.)	FC EX	UH	lr	Accidental	Other pat.	Specialist	3	3
T. costatus	FC	NP	av	Accidental	Other pat.		3	5
Tripyla (imm.)	FC	UH	av	Accidental	Other pat.	Specialist	3	3
Alaimus sp. 2	UH	EX UH	lr	Accidental			4	4
Alirhabditidae g. n., sp. n.	UH	UH	lr	Accidental		Specialist	1	1
A. lissus	UH	NP	lr	Accidental			4	4
Aphanolaimus (imm.)	UH	UH	lr	Accidental		Specialist	3	3
Bunonema (imm.)	UH EX	EX UH	lr	Accidental		Specialist	1	1
E. mucronatus	UH	UH	lr	Accidental		Specialist	2	2
H. loofi	UH	UH	lr	Accidental		Specialist	2	2
H. pseudolatus	UH	UH	lr	Accidental		Specialist	2	2
Paramphidelus sp.	UH	UH	lr	Accidental		Specialist	4	4
Rhabditophanes sp.	UH	UH	lr	Accidental		Specialist	1	1

* For generic names see Table 3.

are more mature. With the modified *c-p* values, the southern areas are more mature. Nevertheless, this variation is minimal because comparisons were made between areas of similar age. As for age classes, MI increases with pineforest age with both computation formulae. When the *c-p* values are used at the family level, the results are similar to those of Bongers (1990) in a *Fago-quercetum* and of Ruess (1995) in a spruce forest, but lower than in a beech French forest (Armendáriz & Arpin, pers. comm.). The MI based on the new *c-p* values is always higher than that calculated at the family level.

Other categories have been proposed in the literature. Wasilewska (1991), using a restrictive criterion of dominance, referred to superdominant, dominant, subdominant and accidental species (with a proportion of 30 %, 10-30 %, 2.5-9 % and lower than 2.5 % respectively). Hodda and Wanless (1994) set up other categories based on spatial distribution and temporal distribution criteria. The equivalence between these categories and those proposed in this study can be seen in Table 8.

Conclusions

Our results lead to the establishment of a nematode community structuring process in the reforestation with *P. nigra*. The initial situation created by the reforestation process is characterised by a small number of species with a high proportion of specimens. The final stage is a community with a greater number of specimens and taxa and furthermore, a greater number of taxa have a similar proportion. Richness, diversity and maturity indices, calculated with new values, are greater in this final stage. This general maturation process is common to both climatic zones, but is more pronounced in the northern area (oceanic climate) where more structured communities develop eventually. In the southern area, with mediterranean climate, reforestation is in a worse state as far as nematode communities are concerned.

Moreover, the different species involved in this study are classified into nine abundance classes which allows the importance they play in the process to be described. Species are associated with a particular stage in the reforestation (temporal categories) or with a particular climate (spatial categories).

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