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Spatial Distribution of Dorylaimid and Mononchid Nematodes from the Southeast Iberian Peninsula: Environmental Characterization of Chorotypes

G. Liébanas,[1] P. Guerrero,[1] J.-M. Martín-García,[2] and R. Peña-Santiago[1]

Abstract: The aim of this study was to determine the incidence of 18 environmental variables in the spatial distribution of 30 chorotypes (species groups with significantly similar distribution patterns) of dorylaimid and mononchid nematodes by means of logistic regression in a natural area in the southeastern Iberian Peninsula. Six variables (elevation, color chroma, clay content, nitrogen content, $CaCO_3$, and plant community associated) were the most important environmental factors that helped explain the distribution of chorotypes. The distribution of most chorotypes was characterized by some (one to three) environmental variables; only two chorotypes were characterized by five or more variables, and four have not been characterized.

Key words: biogeography, chorotypes, Dorylaimida, environmental characterization, Iberian Peninsula, Mononchida, spatial distribution.

In a previous contribution (Liébanas et al., 2002) the chorological relationships among dorylaimid and mononchid species collected in the Sierra Mágina Natural Park (Southeast Iberian Peninsula) were established. Fourteen collective and 16 individual chorotypes, i.e., isolate species or assemblages of species displaying a particular distribution pattern (Baroni-Urbani, 1978; Birks, 1987), were identified in that paper. A subsequent step in the study of spatial distribution of these biotic elements is to infer the environmental factors that may explain the patterns observed. With this aim, the approach of Real et al. (1992) (see also Márquez et al., 1997) is followed.

Material and Methods

Identification of chorotypes: The distribution of 138 species of dorylaims and mononchs in 203 Operational Geographic Units (OGU) of 1 km^2, corresponding to the Universal Tranversal Mercator (UTM) 1 × 1-km grid, was compiled in a "sample × species" matrix. Then a chorological classification protocol was followed to establish relationships among species and identify chorotypes. Additional information concerning site description, sampling, nematode species, and chorotypes identified may be obtained from Liébanas et al. (2002).

Spatial distribution of chorotypes: The distribution pattern of each chorotype was projected on a map of the area. The presence of the respective chorotype in the corresponding OGU was indicated in black circles. Collective chorotypes were labeled with Roman numerals; individual chorotypes were identified by species name. Relative proportion (percentage) of species that, forming part of a chorotype, were found in a particular was illustrated graphically by enlarging the diameter of circles, proportionally.

Environmental factors: Data concerning elevation (m), orientation (°), slope (%), and plant community associated with each of the 203 soil samples collected were taken in situ. In addition, a portion of every soil sample was used for physico-chemical and edaphic analysis, with the following values or parameters determined: color, gravel (%), sand (%), silt (%), clay (%), organic carbon (%), nitrogen (%), C/N ratio, pH, $CaCO_3$ (%), and electric conductivity. Such soil properties were obtained according to methods recommended by the U.S. Soil Conservation Service (1972), and the color of aggregates was determined using the Munsell Color System (Munsell Color Company, 1990).

Analytical procedures: A logistic regression was used to analyze the relationships among the environmental variables considered and the distribution of chorotypes. The protocol proposed by Márquez et al. (1997) was used to implement this task. The analytical procedures were performed by SPSS 8.0 (SPSS Inc., Chicago, IL) as follows.

(i) To analyze statistically the influence of the environmental variables on the presence and absence of each chorotype in the 203 OGU of the area, the following logistic regression model was used:

$$p = \frac{e^y}{1 + e^y} \qquad (1)$$

in which p represents the likelihood of the chorotype being present, e is the base of the Napierian natural logarithms, and y is an equation of regression of the following type:

$$y = a + bx_1 + cx_2 + \ldots + nx_n \qquad (2)$$

where x_n are those environmental variables that may explain the presence/absence of each chorotype in the 203 OGU of the area.

(ii) A forward stepwise method to select the variables to be included in the model was used. This method

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[1] Departamento de Bilogía Animal, Biología Vegetal y Ecología, Universidad de Jaén. Campus "Las Lagunillas" s/n, Edificio B3, 23071-Jaén, Spain.
[2] Departamento de Geología, Universidad de Jaén. Campus "Las Lagunillas" s/n, Edificio B3, 23071-Jaén, Spain.
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E-mail: gtorres@ujaen.es
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incorporates successively only the significant variables and rejects those having no influence on the dependent variable. To select these variables the Wald test (Wald, 1943) was used. First, a score statistic was calculated for each variable ($P < 0.05$) not in the model to determine whether the variable should enter the model. Second, the Wald statistic was calculated ($P < 0.10$) for the variables in the model to determine whether a variable should be removed.

(iii) The estimation of the parameters *a, b, . . . n* in equation (2) was by maximum likelihood.

(iv) The logistic model was tested by a chi-square test of goodness-of-fit.

(v) The odds that favor the presence of a chorotype in an OGU were determined by the formula:

$$pr = \frac{p}{1-p} \quad (3)$$

Odds exceeding 80% ($P > 0.8$) were interpreted as an OGU very favorable for the chorotype, and probabilities less than 20% ($P < 0.2$) were interpreted as an OGU very unfavorable to a chorotype.

This procedure shows which environmental variables best indicate the presence of a chorotype, which potential OGU the chorotype may occupy, and which of the OGU occupied do not provide ideal environmental conditions for the species belonging to this chorotype.

Results

The distribution maps of 30 chorotypes identified, of which 14 are collective and 16 are individual, are illustrated (Figs. 1 and 2). These maps reveal distinct distribution patterns that can be characterized and explained.

The environmental ranges of each chorotype with respect to 15 quantitative variables or factors, together with the ranges calculated for the whole studied area, are summarized (Table 1). Data are presented as follows: mean ± standard deviation (range). For example, values of Chorotype I in relation to elevation are: 1470 ± 285 (800 to 2100), in which 1470 is the mean of the

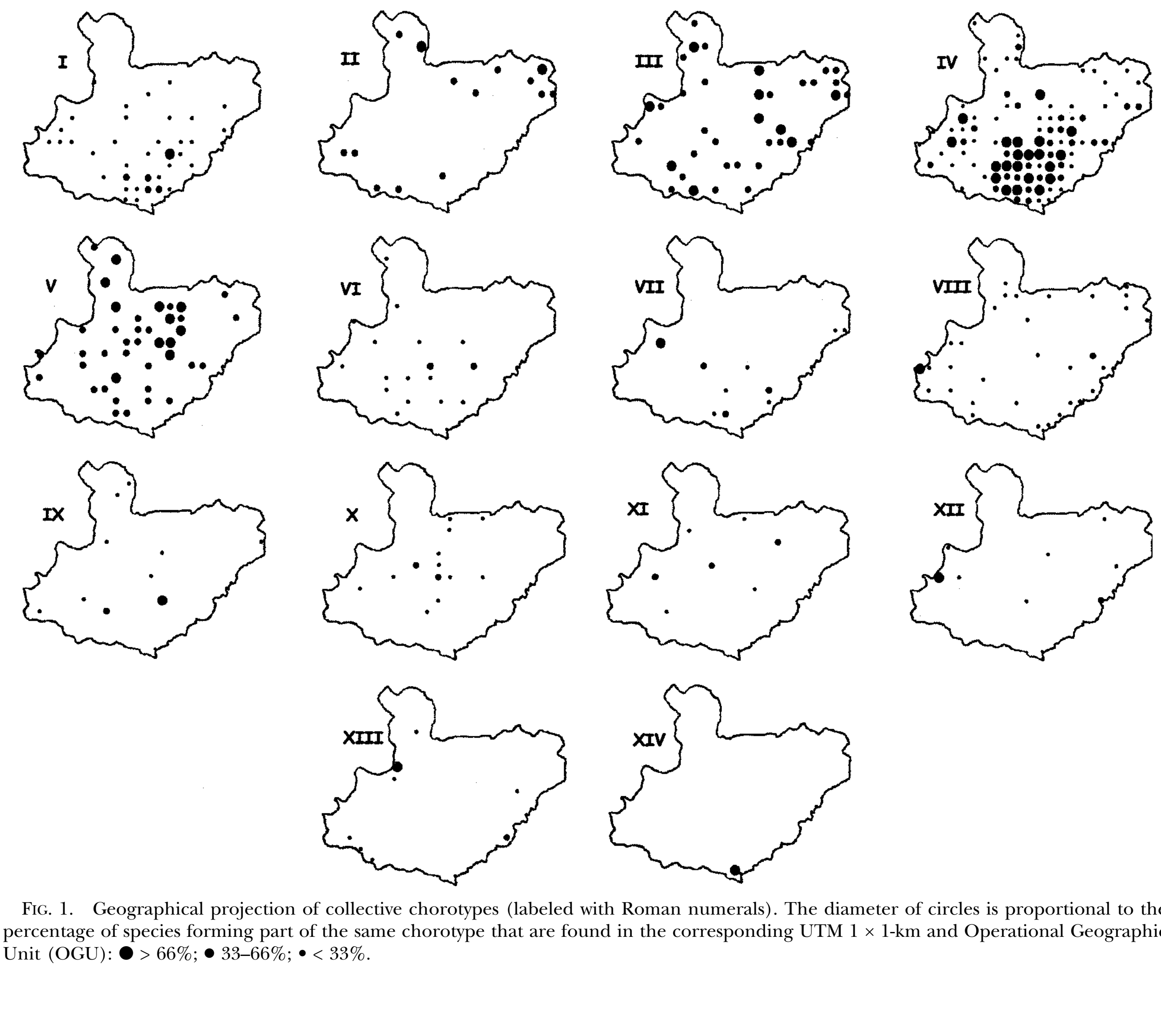

Fig. 1. Geographical projection of collective chorotypes (labeled with Roman numerals). The diameter of circles is proportional to the percentage of species forming part of the same chorotype that are found in the corresponding UTM 1 × 1-km and Operational Geographic Unit (OGU): ● > 66%; ● 33–66%; • < 33%.

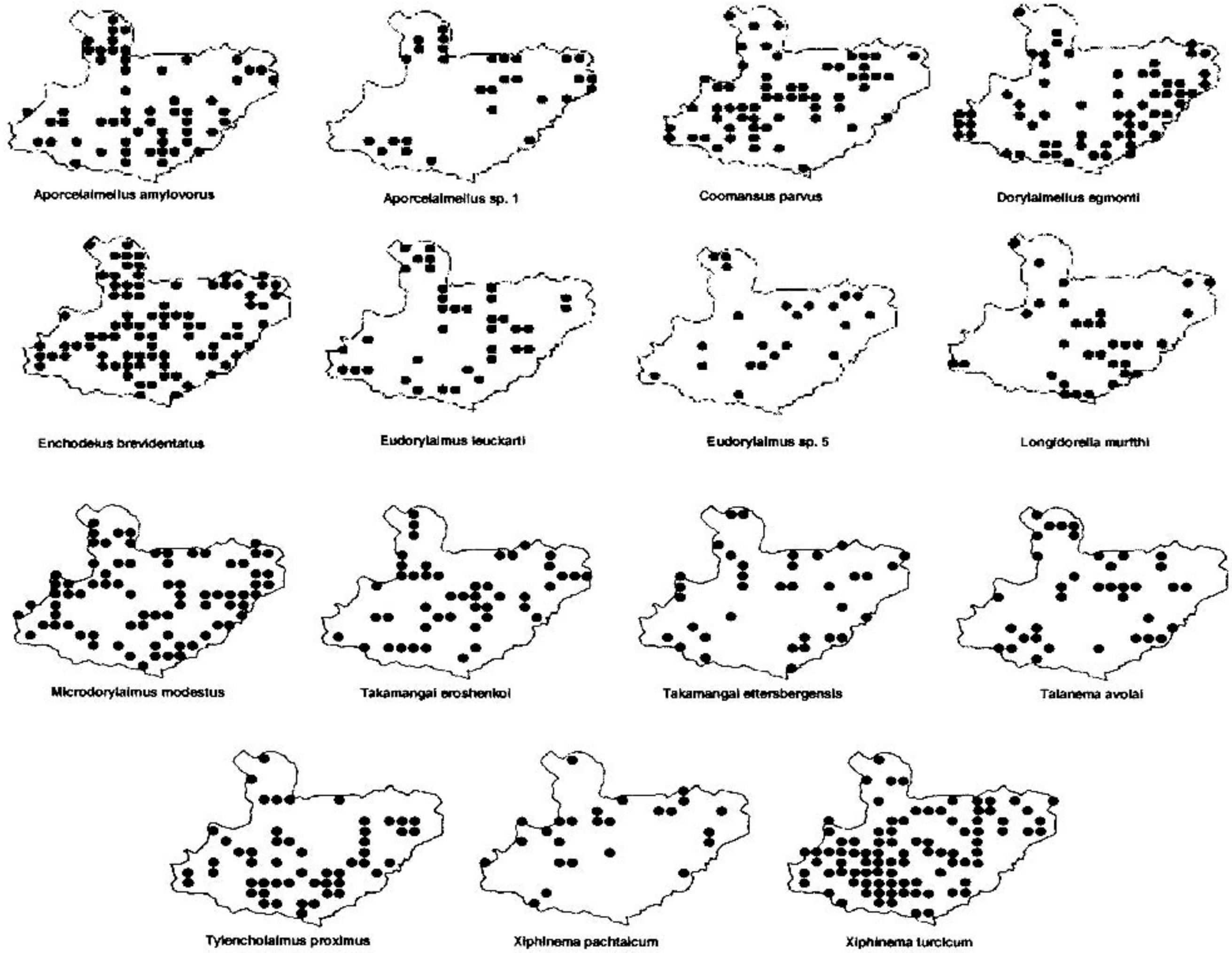

FIG. 2. Geographical projection of individual chorotypes, labeled with the corresponding species name.

elevation of the 38 localities where the species forming part of the chorotype are present, 285 is the standard deviation of the distribution, 800 is the minimum elevation in which the chorotype is found, and 1960 the maximum elevation in which the chorotype is found. Figure 3 provides data corresponding to the three discrete variables: plant community (Fig. 3A), soil texture (Fig. 3B), and orientation (Fig. 3C).

According to the logistic regression, four chorotypes (XII, XIV, *Eudorylaimus leuckarti*, and *Prionchulus muscorum*) do not show a relationship between their distributions and the tested environmental factors. In these cases, logistic regression offers no explanation for the distribution of the respective chorotypes. In the cases of the remaining chorotypes, logistic regression provides predictive equations (Table 2), determining the environmental variables that best indicate the distribution of each chorotype. In the case that equations include discrete variables, for example, plant community (PC), a corresponding value depends on the type of plant community and can be found in the respective appendix.

As mentioned above, this analytical procedure predicts the theoretical presence/absence of a chorotype in an OGU and makes possible its comparison with the actual presence/absence. For example, an equation obtained for Chorotyope I predicts the absence of this chorotype in 95.12% of the number of OGU in which it was not actually found, the presence in 62.16% of the number of OGU in which it was actually found, and 89.05% of the total number of OGU. Note that the model predicts a high percentage (i.e., always >60%, very often >80%) of the total OGU for all chorotypes. All equations obtained were significant at $P \leq 0.001$.

DISCUSSION

The distribution patterns of chorotypes differ in several features. Some of them are distributed widely, e.g., Chorotype IV and *Xiphinema turcicum* are present in 93 and 89 soil samples, respectively. In contrast, other chorotypes have a rather restricted distribution (Chorotypes XI, XII, and XIII are present in 7, 8, and 8 soil samples, respectively); and one of them has been found in just one soil sample, as in Chorotype XIV. Although

TABLE 1. Mean ± Standard deviation (range) of environmental properties defining the habitat of chorotypes.

	n	Elevation (m)	Slope (%)	Color hue	Color value	Color chroma	Gravel (%)	Sand (%)
Total of samples	203	1293 ± 316 (660–2100)	43.8 ± 19.5 (0–100)	19.7 ± 1.37 (12.5–22.5)	4.79 ± 1.24 (2.5–8)	3.80 ± 1.35 (2–8)	42.6 ± 18.1 (2–84)	19.1 ± 12.4 (0.08–59.1)
CHOROTYPE								
I	38	1470 ± 285 (800–1960)	43.0 ± 20.8 (0–83)	20.2 ± 0.90 (17.5–22.5)	4.45 ± 0.98 (3–7)	3.18 ± 1.11 (2–6)	53.6 ± 15.3 (17–84)	25.6 ± 13.0 (2.6–55.7)
II	14	1172 ± 284 (770–1650)	44.3 ± 16.2 (7–62)	19.4 ± 1.06 (17.5–20)	4.25 ± 1.01 (3–7)	4.50 ± 1.44 (2–7)	38.2 ± 19.0 (4–65)	14.4 ± 8.96 (3.03–30.4)
III	37	1282 ± 303 (770–1900)	40.7 ± 18.7 (0–71)	19.7 ± 0.98 (17.5–22.5)	4.39 ± 1.06 (2.5–7)	3.76 ± 1.37 (2–6)	44.6 ± 19.9 (2–77)	18.8 ± 12.5 (0.08–55.7)
IV	93	1442 ± 317 (810–2100)	45.6 ± 18.8 (0–100)	19.7 ± 1.20 (12.5–22.5)	4.39 ± 1.18 (2.5–7)	3.54 ± 1.35 (2–7)	44.6 ± 17.2 (5–80)	21.5 ± 14.0 (1.83–59.1)
V	40	1392 ± 282 (860–1980)	50.3 ± 16.3 (17–71)	19.8 ± 1.53 (12.5–22.5)	4.28 ± 1.09 (2.5–7)	3.54 ± 1.12 (2–6)	46.2 ± 18.5 (8–84)	13.8 ± 11.7 (0.08–55.7)
VI	17	1500 ± 279 (1060–2060)	45.3 ± 19.7 (7–71)	20.1 ± 0.60 (20–22.5)	4.24 ± 0.79 (3–6)	3.21 ± 1.36 (2–6)	50.6 ± 18.9 (19–84)	22.2 ± 14.7 (4.91–59.1)
VII	10	1404 ± 337 (900–1950)	54.5 ± 20.8 (31–100)	20.2 ± 0.79 (20–22.5)	4.60 ± 0.84 (4–6)	3.05 ± 0.76 (2–4)	55.2 ± 6.22 (45–65)	29.7 ± 14.4 (6.95–55.7)
VIII	32	1162 ± 276 (770–1840)	39.4 ± 21.6 (0–72)	20.0 ± 1.41 (17.5–22.5)	5.31 ± 1.37 (2.5–8)	3.66 ± 1.17 (2–6)	37.7 ± 19.1 (3–72)	23.8 ± 11.3 (5.87–50.6)
IX	10	1345 ± 361 (770–1840)	48.2 ± 22.4 (2.0–83)	19.7 ± 0.79 (17.5–20)	4.25 ± 1.29 (2.5–7)	3.8 ± 1.68 (2–6)	32.7 ± 15.1 (3–54)	12.2 ± 6.39 (5.64–28.0)
X	13	1485 ± 386 (850–2060)	49.8 ± 20.5 (15–83.3)	20.3 ± 0.93 (20–22.5)	4.61 ± 1.34 (2.5–7)	3.42 ± 1.05 (2–6)	40.5 ± 19.8 (3–65)	17.3 ± 11.1 (7.02–43.3)
XI	7	1400 ± 391 (950–1950)	49.7 ± 27.6 (0–83)	19.6 ± 0.94 (17.5–20)	4.07 ± 1.01 (2.5–5)	4.21 ± 1.82 (2–6)	52.3 ± 18.6 (26–84)	15.5 ± 16.1 (2.03–50.6)
XII	8	1298 ± 405 (900–2060)	39.1 ± 23.1 (2–71)	20.3 ± 0.88 (20–22.5)	5.18 ± 0.99 (4–7)	3.97 ± 1.56 (2–6)	39.6 ± 18.7 (16–63)	19.2 ± 12.2 (6.60–42.1)
XIII	8	1138 ± 154 (975–1400)	30.3 ± 13.2 (9–55)	19.0 ± 1.29 (17.5–20)	5.50 ± 0.92 (4–7)	5.12 ± 2.11 (2.5–8)	33.9 ± 14.7 (16–54)	21.6 ± 12.7 (4.91–42.7)
XIV	1	1150	57.1	17.5	6	4	22	44
Aporcelaimellus amylovorus	61	1254 ± 285 (800–1950)	42.9 ± 20.6 (0–100)	20.0 ± 0.91 (17.5–22.5)	4.86 ± 1.22 (2.5–7)	3.67 ± 1.20 (2–6)	45.1 ± 18.8 (3–80)	23.2 ± 11.4 (0.08–47.6)
Aporcelaimellus sp. 1	59	1344 ± 293 (810–1960)	47.4 ± 17.7 (0–83)	19.5 ± 1.32 (12.5–22.5)	4.72 ± 1.17 (2.5–7)	4.08 ± 1.34 (2–8)	38.7 ± 19.1 (2–84)	14.9 ± 10.4 (1.83–44.0)
Coomansus parvus	29	1087 ± 197 (770–1650)	46.5 ± 21.5 (0–83)	19.4 ± 1.03 (17.5–20)	4.65 ± 1.34 (3–7)	4.29 ± 1.13 (2–6)	44.6 ± 17.4 (3–77)	18.5 ± 10.7 (2.03–48.4)
Dorylaimellus egmonti	57	1390 ± 345 (770–2060)	44.6 ± 19.7 (0–100)	19.7 ± 0.97 (17.5–22.5)	4.42 ± 1.19 (2.5–8)	3.96 ± 1.54 (2–8)	43.3 ± 18.9 (2–74)	19.2 ± 11.7 (1.83–44.5)
Enchodelus brevidentatus	33	1321 ± 288 (850–1950)	46.2 ± 22.2 (0–100)	20 ± 0.62 (17.5–22.5)	4.71 ± 1.11 (2.5–7)	3.60 ± 1.05 (2–6)	46.6 ± 16.6 (2–77)	24.1 ± 14.1 (3.56–55.7)
Eudorylaimus leuckarti	22	1371 ± 360 (860–2100)	49.5 ± 15.8 (16–83)	19.7 ± 0.73 (17.5–20)	4.38 ± 0.96 (2.5–6)	3.70 ± 1.34 (2–6)	35.9 ± 18.5 (10–70)	16.3 ± 11.2 (0.08–47.6)
Eudorylaimus sp. 5	37	1303 ± 248 (890–1950)	43.8 ± 18.8 (7–83)	19.8 ± 0.90 (17.5–22.5)	4.24 ± 0.97 (2.5–6)	3.74 ± 1.61 (2–8)	46.8 ± 18.0 (8–84)	19.5 ± 13.2 (3.77–55.7)
Longidorella murithi	87	1332 ± 331 (660–2100)	43.0 ± 19.7 (0–83)	19.8 ± 1.31 (12.5–22.5)	4.65 ± 1.11 (2.5–7)	3.81 ± 1.29 (2–7)	43.2 ± 17.5 (8–84)	19.3 ± 13.3 (1.83–59.2)
Microdorylaimus modestus	77	1270 ± 327 (800–2100)	40.3 ± 19.9 (0–83)	19.8 ± 1.14 (17.5–22.5)	4.75 ± 1.28 (3–8)	3.79 ± 1.30 (2–7)	44.6 ± 16.8 (14–84)	21.1 ± 13.1 (2.03–59.2)
Prionchulus muscorum	25	1272 ± 301 (850–1980)	46.8 ± 13.4 (14–62)	19.0 ± 1.13 (17.5–22.5)	4.58 ± 1.18 (2.5–7)	3.7 ± 1.21 (2–6)	41.0 ± 19.5 (3–70)	19.5 ± 13.1 (3.56–46.3)
Takamangai eroshenkoi	47	1343 ± 354 (660–1970)	41.5 ± 20.9 (0–83)	19.7 ± 1.45 (12.5–22.5)	4.72 ± 1.42 (2.5–8)	3.85 ± 1.35 (2–8)	41.3 ± 18.3 (2–80)	18.5 ± 13.4 (2.48–59.1)
Takamangai ettersbergensis	35	1219 ± 284 (660–1790)	38.0 ± 20.0 (0–71)	19.2 ± 1.55 (12.5–20)	5.17 ± 1.19 (3–8)	4 ± 1.59 (2–8)	38.2 ± 18.0 (4–68)	16.0 ± 10.3 (1.83–50.6)
Talanema avolai	38	1203 ± 214 (850–1725)	46.9 ± 20.3 (0–100)	19.7 ± 1.27 (17.5–22.5)	4.56 ± 1.22 (3–8)	4.21 ± 1.40 (2–8)	42.0 ± 19.1 (8–77)	16.3 ± 10.7 (0.08–47.6)
Tylencholaimus proximus	54	1416 ± 263 (920–2060)	47.3 ± 17.7 (0–72)	20.1 ± 0.68 (17.5–22.5)	4.53 ± 1.17 (2.5–8)	3.27 ± 1.21 (2–6)	46.9 ± 19.5 (3–84)	19.9 ± 11.0 (1.83–46.3)
Xiphinema pachtaicum	25	1101 ± 271 (660–1660)	34.2 ± 17.3 (9–71)	19.3 ± 2.84 (12.5–22.5)	5.96 ± 1.30 (4–8)	3.5 ± 1.13 (2–6)	31.7 ± 16.5 (8–68)	18.2 ± 9.86 (5.04–42.1)
Xiphinema turcicum	89	1361 ± 296 (825–1960)	47.8 ± 17.2 (0–100)	19.8 ± 0.83 (17.5–22.5)	4.57 ± 1.17 (2.5–7)	3.73 ± 1.42 (2–8)	41.6 ± 18.2 (2–77)	17.1 ± 11.5 (0.08–47.6)

TABLE 1. *Continued*

	Silt (%)	Clay (%)	Organic carbon (%)	Nitrogen (%)	C/N	pH	$CaCO_3$ (%)	Electrical conductivity
Total of samples	48.1 ± 11.4	32.7 ± 14.4	5.09 ± 3.40	0.45 ± 0.28	11.6 ± 4.50	7.86 ± 0.34	24.4 ± 21.1	0.41 ± 0.28
	(25.3–78.9)	(5.15–63.8)	(0.67–20.0)	(0.07–1.58)	(2.05–30.3)	(6.48–8.59)	(0–85.7)	(0.15–2.06)
CHOROTYPE								
I	51.6 ± 11.0	22.6 ± 12.8	5.89 ± 3.11	0.50 ± 0.26	12.6 ± 5.31	7.9 ± 0.21	34.7 ± 19.8	0.36 ± 0.15
	(29.1–71.4)	(6.8–57.4)	(1.4–14.8)	(0.12–1.12)	(7.27–26.8)	(7.34–8.32)	(0.24–69.3)	(0.16–0.75)
II	49.1 ± 12.0	36.4 ± 14.2	5.83 ± 4.06	0.51 ± 0.34	11.3 ± 3.75	7.87 ± 0.35	19.2 ± 17.3	0.45 ± 0.48
	(30.6–72.7)	(13.9–63.5)	(1.01–16.1)	(0.14–1.35)	(6.52–20.3)	(7.03–8.38)	(0–49.8)	(0.19–2.06)
III	50.1 ± 11.6	31.1 ± 15.1	6.95 ± 3.76	0.56 ± 0.24	12.2 ± 4.29	7.73 ± 0.36	21.8 ± 18.8	0.55 ± 0.41
	(30.4–76.8)	(6.85–63.8)	(1.01–16.3)	(0.14–1.35)	(5.75–24.5)	(6.48–8.15)	(0.02–67.0)	(0.15–2.06)
IV	49.7 ± 11.8	28.7 ± 15.4	6.09 ± 3.88	0.54 ± 0.31	11.6 ± 3.99	7.83 ± 0.37	25.4 ± 23.2	0.4 ± 0.23
	(29.1–76.8)	(5.15–63.8)	(0.67–20.6)	(0.10–1.58)	(2.05–24.5)	(6.48–8.48)	(0–85.7)	(0.15–1.44)
V	50.1 ± 11.7	35.9 ± 15.3	7.04 ± 4.11	0.63 ± 0.34	11.3 ± 3.88	7.79 ± 0.29	14.7 ± 17.9	0.47 ± 0.34
	(31.3–76.8)	(7.5–61.3)	(1.94–16.8)	(0.14–1.58)	(4.33–27.1)	7.03–8.36)	(0.21–67.3)	(0.15–2.06)
VI	53.9 ± 10.3	24.0 ± 15.2	7.85 ± 3.17	0.74 ± 0.34	11.7 ± 4.35	7.76 ± 0.25	27.6 ± 21.0	0.52 ± 0.28
	(35.6–71.8)	(5.15–55.7)	(2.86–14.8)	(0.29–1.46)	(3.78–23.2)	(7.26–8.13)	(0.45–64.9)	(0.25–1.36)
VII	49.5 ± 9.59	20.7 ± 7.46	6.12 ± 1.92	0.50 ± 0.20	12.9 ± 4.19	7.96 ± 0.28	34.8 ± 14.1	0.34 ± 0.13
	(33.9–61.1)	(9.85–33.6)	(3.60–9.72)	(0.28–0.92)	(9.48–23.6)	(7.34–8.44)	(2.02–55.9)	(0.19–0.68)
VIII	45.3 ± 10.6	30.7 ± 12.7	3.53 ± 2.02	0.31 ± 0.16	12.0 ± 5.04	8.02 ± 0.32	35.5 ± 21.1	0.29 ± 0.12
	(30.4–71.8)	(5.55–63.5)	(0.71–8.19)	(0.07–0.71)	(5.77–26.2)	(6.65–8.58)	(0–85.7)	(0.18–0.75)
IX	54.5 ± 12.0	33.2 ± 15.3	5.76 ± 4.54	0.59 ± 0.40	9.62 ± 3.71	7.59 ± 0.52	13.5 ± 19.8	0.52 ± 0.42
	(42.5–76.8)	(5.55–49.5)	(1.01–16.8)	(0.13–1.58)	4.83–17.6)	(6.65–8.15)	(0–57.1)	(0.21–1.37)
X	46.1 ± 9.7	36.6 ± 12.3	4.34 ± 1.87	0.49 ± 0.21	9.51 ± 3.76	7.72 ± 0.36	14.5 ± 14.8	0.30 ± 0.10
	(33.8–67.8)	(14.7–52.2)	(1.75–8.17)	(0.18–0.86)	(4.33–20.4)	(6.65–7.98)	(0–46.1)	(0.17–0.53)
XI	53.4 ± 16.2	30.5 ± 17.8	8.42 ± 5.20	0.67 ± 0.41	12.4 ± 4.76	7.66 ± 0.30	14.5 ± 12.3	0.69 ± 0.61
	(31.2–72.7)	(12.6–59.9)	(2.74–16.1)	(0.29–1.35)	(7.25–20.0)	(7.03–7.96)	(0.21–34.6)	(0.34–2.06)
XII	45.4 ± 6.19	35.2 ± 15.4	3.56 ± 2.06	0.32 ± 0.16	11.6 ± 4.93	7.90 ± 0.24	27.9 ± 22.5	0.39 ± 0.15
	(37.7–56.2)	(14.7–55.7)	(1.70–8.17)	(0.11–0.67)	(4.83–21.1)	(7.69–8.31)	(1.94–51.3)	(0.22–0.73)
XIII	46.0 ± 13.8	32.3 ± 14.7	3.25 ± 2.34	0.27 ± 0.18	12.1 ± 6.29	7.95 ± 0.35	33.9 ± 31.1	0.43 ± 0.28
	(30.4–77.2)	(8.45–52.2)	(0.79–8.06)	(0.12–0.63)	(5.97–26.4)	(7.29–8.35)	(2.42–85.7)	(0.16–0.92)
XIV	30.5	25.4	2.87	0.16	17.9	8.22	5.5	0.18
Aporcelaimellus amylovorus	48.3 ± 11.0	28.4 ± 12.7	5.08 ± 3.18	0.41 ± 0.22	12.5 ± 4.66	7.97 ± 0.26	33.1 ± 21.5	0.35 ± 0.19
	(25.3–71.8)	(5.4–57.3)	(0.99–14.8)	(0.10–0.94)	(5.97–30.3)	(7.16–8.59)	(0.16–85.7)	(0.15–1.37)
Aporcelaimellus sp. 1	44.8 ± 10.0	40.2 ± 10.9	5.01 ± 3.69	0.46 ± 0.30	11.0 ± 4.43	7.80 ± 0.35	16.1 ± 18.4	0.39 ± 0.24
	(30.4–76.8)	(13.4–61.3)	(0.67–16.8)	(0.11–1.58)	(2.05–27.1)	(6.48–8.37)	(0–85.7)	(0.16–1.37)
Coomansus parvus	48.0 ± 11.7	33.3 ± 12.2	5.59 ± 3.74	0.50 ± 0.32	11.5 ± 4.63	7.88 ± 0.41	22.4 ± 18.6	0.49 ± 0.39
	(31.0–75.1)	(9.5–59.9)	(1.04–16.1)	(0.11–1.35)	(3.69–23.6)	(6.63–8.59)	(0–67.3)	(0.18–2.06)
Dorylaimellus egmonti	48.9 ± 11.7	31.7 ± 14.4	5.62 ± 3.13	0.49 ± 1.11	11.7 ± 4.18	7.83 ± 0.38	23.1 ± 21.2	0.40 ± 0.25
	(30.4–78.9)	(8.10–63.5)	(1.01–14.8)	(0.10–1.11)	(5.97–24.5)	(6.48–8.37)	(0–85.7)	(0.16–1.37)
Enchodelus brevidentatus	49.5 ± 11.2	26.3 ± 13.7	4.29 ± 2.55	0.40 ± 0.18	10.6 ± 4.80	7.91 ± 0.31	30.5 ± 22.9	0.34 ± 0.17
	(30.5–70.9)	(5.55–53.3)	(0.67–12.3)	(0.12–0.77)	(2.05–24.5)	(6.48–8.31)	(0.02–69.3)	(0.17–0.89)
Eudorylaimus leuckarti	49.4 ± 11.1	34.2 ± 15.8	6.22 ± 3.08	0.52 ± 0.26	12.4 ± 4.36	7.74 ± 0.35	16.9 ± 19.0	0.37 ± 0.16
	(34.7–73.5)	(5.55–59.9)	(3.18–13.2)	(0.23–1.17)	(7.91–27.1)	(6.86–8.36)	(0–67.4)	(0.15–0.82)
Eudorylaimus sp. 5	49.3 ± 13.4	31.1 ± 16.7	6.01 ± 3.07	0.52 ± 0.27	11.8 ± 3.62	7.85 ± 0.32	21.9 ± 18.0	0.45 ± 0.31
	(29.2–78.9)	(5.55–63.5)	(1.4–14.8)	(0.13–1.34)	(3.69–21.6)	(7.16–8.46)	(0.16–67.4)	(0.15–1.37)
Longidorella murithi	48.9 ± 11.9	31.6 ± 14.8	5.25 ± 3.65	0.50 ± 0.33	10.8 ± 3.68	7.84 ± 0.31	22.7 ± 19.8	0.41 ± 0.26
	(31.2–78.9)	(5.15–61.3)	(0.67–20.6)	(0.08–1.58)	(2.05–26.2)	(6.63–8.59)	(0–69.3)	(0.16–1.44)
Microdorylaimus modestus	47.5 ± 10.7	31.3 ± 15.1	5.40 ± 3.41	0.48 ± 0.30	11.7 ± 4.59	7.85 ± 0.34	26.6 ± 21.6	0.45 ± 0.28
	(25.3–76.8)	(5.15–63.8)	(0.79–16.3)	(0.07–1.46)	(3.69–30.3)	(6.63–8.59)	(0–71.5)	(0.18–1.37)
Prionchulus muscorum	48.7 ± 11.8	31.8 ± 15.1	5.56 ± 3.88	0.46 ± 0.28	12.5 ± 5.52	7.79 ± 0.42	22.5 ± 21.4	0.44 ± 0.37
	(25.3–72.7)	(5.55–57.3)	(0.67–16.3)	(0.19–1.35)	(2.05–30.3)	(6.65–8.31)	(0–59.6)	(0.20–2.06)
Takamangai eroshenkoi	48.0 ± 10.7	33.2 ± 12.9	5.42 ± 3.78	0.53 ± 0.33	11.5 ± 4.42	7.79 ± 0.35	22.0 ± 21.3	0.41 ± 0.21
	(31.0–77.2)	(5.15–59.9)	(0.67–16.3)	(0.08–1.46)	(2.05–26.2)	(6.48–8.44)	(0–64.9)	(0.17–1.15)
Takamangai ettersbergensis	48.3 ± 12.2	35.4 ± 14.4	4.37 ± 2.58	0.35 ± 0.17	12.7 ± 5.40	7.91 ± 0.25	21.0 ± 19.2	0.39 ± 0.20
	(31.2–78.9)	8.10–61.3)	(1.01–10.7)	(0.07–0.76)	(4.83–26.4)	(7.50–8.58)	(0.21–67.0)	(0.16–1.18)
Talanema avolai	48.4 ± 10.8	35.2 ± 13.8	5.42 ± 3.55	0.48 ± 0.27	11.5 ± 4.35	7.88 ± 0.23	20.0 ± 18.0	0.38 ± 0.15
	(31.0–77.2)	(8.15–61.3)	(1.04–14.8)	(0.07–1.34)	(3.69–26.4)	(7.36–8.58)	(0–63.9)	(0.17–0.75)
Tylencholaimus proximus	53.0 ± 11.6	27.0 ± 14.6	6.14 ± 3.59	0.52 ± 0.29	12.1 ± 3.80	7.84 ± 0.29	27.6 ± 21.2	0.41 ± 0.25
	(33.8–76.8)	(5.55–61.1)	(1.50–20.6)	(0.11–1.58)	(6.12–24.5)	(7.01–8.36)	(0–69.9)	(0.17–1.44)
Xiphinema pachtaicum	42.3 ± 5.27	39.3 ± 12.2	3.02 ± 1.79	0.25 ± 0.14	12.1 ± 4.94	7.99 ± 0.28	34.3 ± 23.4	0.33 ± 0.16
	(30.6–51.2)	(15.1–63.5)	(0.71–7.78)	(0.07–0.64)	(7.03–27.1)	(7.38–8.58)	(0.16–71.5)	(0.20–0.89)
Xiphinema turcicum	49.1 ± 11.5	33.7 ± 15.2	5.72 ± 3.61	0.49 ± 0.28	11.9 ± 4.44	7.81 ± 0.36	20.0 ± 19.9	0.40 ± 0.26
	(25.3–77.2)	(5.40–63.5)	(0.67–20.6)	(0.10–1.58)	(2.05–30.3)	(6.48–8.48)	(0–80.1)	(0.17–1.44)

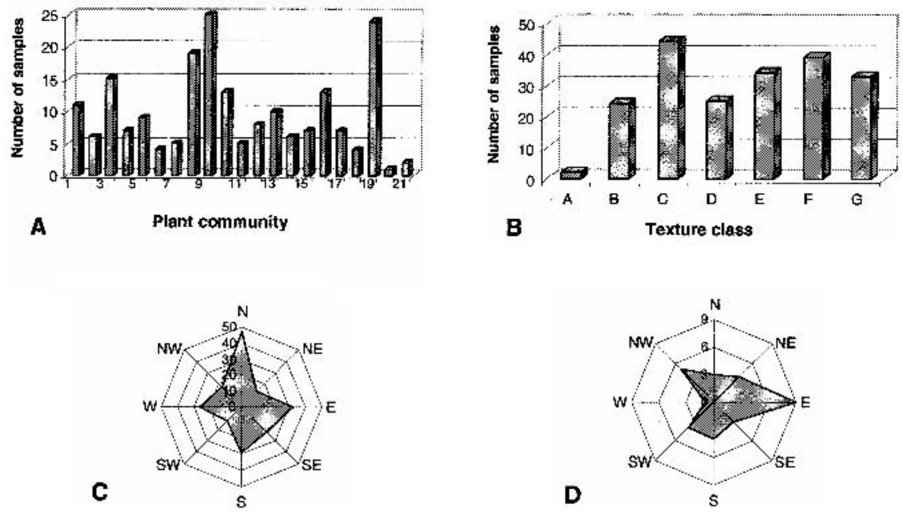

FIG. 3. Distribution of discrete variables. A) Plant community (for identification of plant communities, see the corresponding appendix in Table 2). B) Soil texture (for identification texture classes, see the corresponding appendix in Table 2. C) Orientation, whole area. D) Orientation, Chorotype *Enchodelus brevidentatus.*

TABLE 2. Chorotypes explained by logistic regressions according to the environmental factors[a] analyzed. 'Explained percentages' show the percentage of 'matches' (coincidences in theoretical and actual results) in presence, absence, and total, respectively.

		Explained percentage		
Chorotype	Equation	Absence	Presence	Total
I	y = 0.0082 EL *** + 0.4566 C/N *** −0.4541 OC ** + PC * (•) + 0.0808 GRA *** −0.0438 SL ** + TEX *(♦) − 18.7053	95.12	62.16	89.05
II	y = 0.37 Cc ** −4.1138	100	0	93.03
III	y = 0.1176 OC *** −2.5338	98.79	8.33	82.59
IV	y = 0.0034 EL *** + 0.0642 SA *** − 0.4672 Cv *** −3.4759	75.00	67.74	71.64
V	y = 0.0343 CL ** +2.3899 N *** −3.8172	96.91	12.82	80.60
VI	y = 0.0329 $CaCO_3$ ** + 3.5337 N *** −5.201	98.91	5.88	91.04
VII	y = TEX * (♦ ♦) − 4.7158	99.48	10.00	95.02
VIII	y = 0.0171 $CaCO_3$ ** −2.7750 N ** −1.0964	100	0	84.08
IX	y = −1.8513 pH ** + 11.4061	100	0	95.02
X	y = PC * (••) − 7.8946	99.47	7.69	93.53
XI	y = 1.8912 EC ** −4.2902	100	0	96.52
XIII	y = 1.1147 Cc *** + PC * (•••) + 14.0010	99.48	37.50	97.01
Aporcelaimellus amylovorus	y = 0.0280 $CaCO_3$ *** − 1.5766	92.86	13.11	68.66
Aporcelaimellus sp. 1	y = 0.0011 EL ** + 0.0592 CL *** −4.3643	88.03	23.73	69.15
Coomansus parvus	y = −0.005 EL *** + 3.1307 N *** + 2.7421	98.26	6.90	85.07
Dorylaimellus egmonti	y = 0.0014 EL *** −2.7189	99.31	1.75	71.64
Enchodelus brevidentatus	y = −0.0424 CL *** + OR * (■) − 0.3787	97.62	9.09	83.08
Eudorylaimus sp. 5	y = −0.5317 Cv *** + TEX * (♦ ♦ ♦) + 1.9450	100	5.41	82.59
Longidorella murithi	y = −0.0733 C/N ** + 0.5775	87.72	12.64	55.22
Microdorylaimus modestus	y = −0.0152 SL ** + 0.1778	95.97	7.79	62.19
Takamangai eroshenkoi	y = 1.1201 N ** − 1.7252	99.35	0.00	76.12
Takamangai ettersbergensis	y = −0.0459 SA ** −2.7557 N *** + 0.3853	100	0	82.59
Talanema avolai	y = 0.2606 Cc ** − 2.4868	100	0	81.09
Tylencholaimus proximus	y = 0.0875 C/N ** − 0.4673 Cc ** + 0.6379 C h ** + 0.0604 SI *** + PC * (••••) − 18.3524	90.48	53.70	80.60
Xiphinema pachtaicum	y = 0.0931 CL *** + 0.7370 Cv *** + 0.0374 $CaCO_3$ ** − 10.3163	98.86	24.00	89.55
Xiphinema turcicum	y = 0.0009 EL * + 0.0158 SL ** −0.0143 $CaCO_3$ ** − 1.7985	75.89	48.31	63.68

[a] Abbreviations: EL = elevation; SL = slope; OR = orientation; Ch = color hue; Cv = color value; Cc = color chroma; GRA = gravel; SA = sand; SI = silt; CL = clay; TEX = texture class; OC = organic carbon; N = nitrogen; C/N = carbon/nitrogen ratio; $CaCO_3$ = calcium carbonate; EC = electric conductivity; PC = plant community.

(•), (••), (•••), (••••) See appendix 1, Table of plant community.

(♦), (♦ ♦), (♦ ♦ ♦) See appendix 2, Table of texture.

(■) See appendix 3, Table of orientation.

Significance level: *($P < 0.1$); **($P < 0.05$); ***($P < 0.01$).

the area studied is relatively small (203 km^2), it is also possible to detect geographical trends of distribution. For example, Chorotype II and *Coomansus parvus* display a bipolar (southwestern-northeastern) distribution, Chorotype VII is distributed in the southern half of the area, and Chorotype XIII is mostly peripheral.

In general, environmental ranges of distribution of chorotypes are broad and follow those of the entire study area (see Table 1), certainly indicating that nematodes have high tolerance to the spatial variations of mechanical and physico-chemical properties of soils in this natural region. Nevertheless, logistic regression equations identify a (usually) low number of environmental variables determining the distribution of a particular chorotype.

Table 3 shows a compendium of the relationships among such chorotypes and environmental variables. Obviously, not all variables have the same incidence on chorotype distribution patterns. Six of them (elevation, color chroma, clay content, nitrogen content, $CaCO_3$, and plant community associated) characterize totally or partially four to six chorotypes, with these being the most important among those considered in this study. On the contrary, six other variables (orientation, color hue, gravel, silt, pH, and electric conductivity) characterize only one chorotype totally or partially. Unfortunately, available nematological literature does not provide information to verify the results obtained. Several contributions suggest that elevation (Háněl, 1996; Norton, 1989), clay content (McSorley and Frederick, 2002; Norton et al., 1971), nitrogen content (Kimpinski and Welch, 1971), calcium (Kandji et al., 2001; Trevathan et al., 1985), and plant community associated (Háněl 1993) are important factors for nematode distribution. This is confirmed by our data. Other studies (Büttner, 1989; Norton, 1978; Norton et al., 1971) emphasize the role of soil pH on nematode distribution, which is not confirmed by this study. Finally, some chorotypes are rather "enigmatic" in their distribution; e.g., *Enchodelus brevidentatus* is characterized by orientation (see Fig. 3C,D for a comparison with the entire study area) and clay content.

The distribution of most chorotypes is characterized by some (one to three) environmental variables (12 chorotypes by only one variable), whereas Chorotype I is characterized by seven variables, and *Tylencholaimus*

TABLE 3. Relationships between environmental factors and a chlorotype's distributions ("+" indicates a positive relationship and "–" indicates a negative relationship. ● In the orientation, the texture class and the plant community.

Chlorotype	EL[a]	SL	OR	Ch	Cv	Cc	GRA	SA	SI	CL	TEX	OC	N	C/N	pH	$CaCO_3$	EC	PC	
I	+	–					+				●	–		+				●	7
II						+													1
III												+							1
IV	+				–			+											3
V										+			+						2
VI													+			+			2
VII											●								1
VIII													–			+			2
IX															–				1
X																		●	1
XI																	+		1
XII																			0
XIII						+												●	2
XIV																			0
Aporcelaimellus amylovorus																+			1
Aporcelaimellus sp. 1	+									+									2
Coomansus parvus	–												+						2
Dorylaimellus egmonti	+																		1
Enchodelus brevidentatus			●							–									2
Eudorylaimus leuckarti																			0
Eudorylaimus sp. 5					–						●								2
Longidorella murithi														–					1
Microdorylaimus modestus		–																	1
Prionchulus muscorum																			0
Takamangai eroshenkoi													+						1
Takamangai ettersbergensis								–					–						2
Talanema avolai						+													1
Tylencholaimus proximus				+		–			+					+				●	5
Xiphinema pachtaicum					+					+						+			3
Xiphinema turcicum	+	+														–			3
	6	3	1	1	3	4	1	2	1	4	3	2	6	3	1	5	1	4	

[a] Abbreviations: EL = elevation; SL = slope; OR = orientation; Ch = color hue; Cv = color value; Cc = color chroma; GRA = gravel; SA = sand; SI = silt; CL = clay; TEX = texture class; OC = organic carbon; N = nitrogen; C/N = carbon/nitrogen ratio; $CaCO_3$ = calcium carbonate; EC = electric conductivity; PC = plant community.

proximus is characterized by five variables. These results suggest that nematode distribution at local or regional scales could be determined by a limited number of abiotic and(or) biotic factors. Concerning the distribution of particular chorotypes, our findings agree generally (and disagree in several respects) with the scarce information available from literature. Our data confirm those provided for *Trichodorus giennensis* by López and Arias (1997) and for *Iotonchus rotundicaudatus* by Jiménez-Guirado et al. (1995), both species forming part of Chorotype I; for *Xiphinema pachtaicum* by Arias et al. (1986) and Jiménez-Guirado et al. (1995); for *Coomansus parvus* by Popovici and Ciobanu (2000) but not data by Arpin (1979) and Jiménez-Guirado et al. (1995); for *Longidorella parva*, a member of chorotype II, by Vinciguerra et al. (1995); for *Microdorylaimus longicollis*, a member of Chorotype III, by Vinciguerra et al. (1995); for *Eudorylaimus* species, forming part of Chorotype XI, by Powers et al. (1998) but not for data provided for *Paratrichodorus teres*, a member of Chorotype XIV, by López and Arias (1997); and for *Prionchulus muscorum* by Vinciguerra and Giannetto (1987).

Our current knowledge of the spatial distribution of dorylaims and other nematode taxa is still incomplete, with the proposal of any general pattern being only tentative. Nevertheless, studies at local and regional scale provide fundamental information about their general trends and about the environmental factors that determine them. Available analytical methods provide useful tools to address this question.

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Appendix 1.

Plant community	(●)	(●●)	(●●●)	(●●●●)
1: Pine-juniper wood	−2.5036	6.49	2.1229	1.7495
2: Hawthorn scrubland	−1.61897	7.2015	−3.0651	2.6513
3: Mediterranean garigue: *Erinacea anthyllis*	1.3590	6.8830	−2.9304	2.2658
4: Meadow of *Helicototrichum filifolium* and *Festuca scariosa*	1.2568	−3.3082	5.6309	−6.2955
5: Supramediterranean evergreen-oak wood	3.2043	−3.3082	7.6124	2.7807
6: *Genista cinerea* community	8.1690	−3.3082	−3.6706	2.2490
7: Maple—wood	3.8280	−3.3082	−2.1045	−6.1526
8: Lavender—field	1.6619	−3.3082	6.5013	2.1812
9: Reforested pine wood	1.1824	5.4523	−3.3107	3.0922
10: Pine-juniper-scrubland	1.1388	−3.3082	−1.5527	2.5851
11: Perennial pasture	4.7478	−3.3082	−3.5289	2.9898
12: Mesomediterranean evergreen-oak wood	−21.4125	−3.3082	−3.6618	2.5913
13: *Pistacia terebinthus* community	9.0136	5.6974	−3.4725	−5.9288
14: Broom community	−7.3687	−3.3082	−3.4248	−6.8296
15: Thyme fields	2.1879	−3.3082	−3.9909	1.7614
16: Holly-oak-lentise scrubland	−2.2902	−3.3082	−4.4119	3.0522
17: Esparto grass community	−6.8028	−3.3082	−3.6618	1.8785
18: Annual pasture	6.7516	6.7960	−2.3211	4.6334
19: Olive grove	−0.1167	−3.3082	6.4589	0.3153
20: Olive + fruit tree grove	−4.7802	−7.8946	10.0996	−5.5993
21: River bank vegetation	6.9633	−3.3082	10.9356	−5.9709

Appendix 2.

Texture	(♦)	(♦♦)	(♦♦♦)
A: Sandy loam	13.8472	4.7158	6.9129
B: Loam	−0.5203	3.1063	−1.0547
C: Silt loam	0.2305	1.6712	0.8616
D: Clay loam	0.0716	1.5377	−1.4869
E: Silt clay loam	−1.1167	1.9432	−1.3067
F: Silt clay	−5.8042	−6.4871	−1.8123
G: Clay	−6.2471	−6.4871	−0.3907

Appendix 3.

Orientation	(■)
N: 337.5°–22.5°	−0.9448
NE: 22.5°–67.5°	0.9256
E: 67.5°–112.5°	0.7459
SE: 112.5°–157.5°	−0.0736
S: 157.5°–202.5°	−0.3953
SW: 202.5°–247.5°	0.7058
W: 247.5°–292.5°	−1.7217
NW: 292.5°–337.5°	0.7581