

Relating species density to environmental variables in presence of spatial autocorrelation: a study case on soil nematodes distribution

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Rossi, J.-P. and Quénéhervé, P. 1998. Relating species density to environmental variables in presence of spatial autocorrelation: a study case on soil nematodes distribution. – *Ecography* 21: 117–123.

The relationships between soil nematodes and soil texture, carbon content and depth were assessed in both a cultivated and uncultivated plots. Simple correlation coefficient analyses indicated a negative linear correlation between the plant-parasitic species *Helicotylenchus retusus* Siddiqui and Brown and soil clay content in the uncultivated site. However, Mantel tests showed this correlation to be spurious and only due to the presence of a common spatial pattern in the variables distribution. Both *H. retusus* density and soil clay content appeared to be independently driven by a common, unknown cause. The use of suitable statistical methods to analyse spatially dependent variables proved to be particularly fruitful in that they prevent spurious correlations and allow us to test different causal models involving the set of variables at hand.

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Nematodes are important members of soil food webs that can have significant impact on soil processes and primary productivity. Free-living forms stimulate soil organic matter turn over and nutrient cycling by grazing on soil microfauna and microflora (Yeates 1979, Freckman 1988) and affect soil aggregation processes (Elliot et al. 1984, Elliot and Coleman 1988). On the other hand, plant-feeding species directly reduce plant growth and vigour. Assessing nematode effects on nutrient cycling and energy flows requires primarily to determine the size and distribution of populations. This task is complicated by the complex and multiscale spatial patterns of the populations. In pest management, the spatial pattern of parasitic nematode species is a key parameter if tailored inputs are to be applied.

Our knowledge of the factors (either biotic, abiotic or both) influencing soil fauna distribution across the

ecosystem, as well as the scale at which these factors act, is limited. Many studies have shown that soil properties like e.g. soil texture and carbon contents are frequently spatially structured at various scales (Webster 1985, Webster and Oliver 1990). Spatial patterns of soil invertebrate communities have been much less studied so far. Soil nematodes frequently display spatial autocorrelation at the field scale (i.e. < 100 m) (Robertson 1994, Wallace and Hawkins 1994, Robertson and Freckman 1995, Rossi et al. 1996). The spatial structure of populations at this scale is likely to be influenced by edaphic factors like e.g. soil texture, pH (Robertson and Freckman 1995, Koenning et al. 1996). At a very short scale, root patterning and row structure in cultivated soils may locally modify the soil pore volume distribution, and hence the water status, and so can determine micro-scale structures in nematode distribution

Accepted 23 July 1997

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ISSN 0906-7590

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(Delaville et al. 1996). At the finest scale, the size of solid particles and aggregates, as well as the type distribution and abundance of porosity, determine the ultimate micro-spatial distribution of nematodes inside and outside soil aggregates (Quénèhervé and Chotte 1996).

A variable is said to be autocorrelated if a measure made at one point brings information on another measure of that variable recorded at a point located a given distance apart. In that case the values are not independent in a statistical sense. Two situations can be encountered according the sign of autocorrelation. Positive autocorrelation at short distances indicates a contagious phenomenon whilst positive values at large distances reveal that structures are repeated through space. Negative autocorrelation indicates that neighbouring values are unlike. If present at small distances, negative autocorrelation may reveal a phenomenon of avoidance of organisms while at large distance, it might reveal the presence of a gradient in the spatial distribution (provided autocorrelation is positive at short scale, see Legendre and Fortin 1989). If spatial autocorrelation is present, assessing the relationships between variables is complicated by the ineffectiveness of most classical statistical tools like e.g. ANOVA or correlation analysis (Legendre and Fortin 1989, Legendre 1993). The presence of common patterns between two variables (e.g. nematode density and some soil parameters) may lead to spurious correlation, i.e. variables are apparently related whilst they only independently display a common spatial pattern. This situation may be encountered when two variables are independently driven by a common cause. In that case, it is necessary to examine the relationships between variables while controlling for the effect of the common spatial structure (Legendre and Troussellier 1988, Legendre and Fortin 1989).

This study aimed at assessing the possible relationships between several soil parameters and both plant-feeding and free-living nematodes in two adjacent situations: a plot submitted to intensive market gardening and a permanent pasture on a vertisol. On a single sample date, we analysed the spatial distribution of total carbon and nitrogen content, texture, depth down to the bedrock and the abundance of free-living and plant-feeding nematodes. Plant-feeding nematodes were further identified at the species taxonomic level. Specific statistical analyses were used to look for spatial autocorrelation in the data and segregate between true and spurious correlations. Spatial autocorrelation was assessed by the Moran's I coefficient (Moran 1950) and relationships between variables were tested with the product-moment correlation analysis and the matrix approach proposed by Mantel (1967).

Materials and methods

The study was carried out at the S.E.C.I. (Station d'Essais en Culture Irriguées) field station on a vertisol (black earth) developed on volcanic ash, located near Sainte-Anne in the south-east of Martinique (Lesser Antilles: 14°3'N, 62°34'W). In this tropical region, annual rainfall is 1300 mm with a dry season extending from March to June. Two plots were investigated. The first plot is a 10-yr-old permanent pasture (*Digitaria decumbens* Stent, cv. Pangola) with a dense and continuous root system. The second plot is a market gardening field cropped to tomatoes. In each plot, 60 points randomly distributed across the 60 × 25 m area were sampled for nematode counts and soil analysis.

Soil samples with adhering roots were removed from the 0–10 cm soil layer for nematode analysis. Nematodes were extracted from soil by the elutriation-sieving technique (Seinhorst 1962), and from the shredded roots in a mist chamber (Seinhorst 1950). Nematode population density was determined in a counting dish under a stereomicroscope and expressed either as the number of nematodes 100 cm⁻³ of soil or 1 g⁻¹ of dry weight of root (Southey 1986). Specific identification of plant-feeding nematodes was performed either on fresh material or on individuals killed by progressive heating, fixed in TAF and permanently mounted on aluminium slides according to the slow method of Goodey (1957).

Soil samples were removed from the 0–10 cm soil layer. Organic carbon and nitrogen contents were measured by dry way using a Nitrogen Carbon Sulfur Analyser NA 1500. Soil texture (clay, silt and sand contents) was determined by laser granulometry.

The analysis of Moran's I autocorrelation coefficient (Moran 1950, Legendre and Fortin 1989, Legendre 1993) was performed using the R-package (Legendre and Vaudor 1991) including coefficient testing for statistical significance following formulas given in Sokal and Oden (1978), Cliff and Ord (1981) and Legendre and Legendre (1984). The coefficient measures the autocorrelation between values recorded at sampling points a given distance apart. Fifteen inter-sample distance classes were formed with 3.9 m width. The positive values of the Moran's I coefficient indicate positive autocorrelation i.e. recorded values at points included in a given distance class are similar (Sokal and Oden 1978). The plot of the autocorrelation values against the distance classes is called the correlogram. The overall significance of the correlogram was tested with the Bonferroni method of correction for multiple comparison (Oden 1984). At a given overall significance level (here, 5%), a correlogram was taken as significant provided at least one of the autocorrelation values was significant at the statistical level, $\alpha' = \alpha/v$, with v the number of distance classes (here, 15).

Computation of the correlogram requires normally distributed data or at least data displaying a symmetrical frequency distribution. Before any computation, raw data were submitted to the Kolmogorov-Smirnov test of normality. Data sets that did not meet normality were submitted to the Box-Cox transformation (Sokal and Rohlf 1995) to reach normality or at least to decrease markedly their asymmetry.

The Mantel test (Mantel 1967) is based on distance matrices and its statistic is the sum of the cross-products of the corresponding values in two matrices, say A and B. It is denoted A.B. This statistic allows us to look for spatial trend in the data (Legendre and Troussellier 1988, Legendre and Fortin 1989). The spatial relationship among the sampling stations is represented by a matrix of geographic distances among all pairs of sampled localities. This test can be used to compare a distance matrix corresponding to the geographical distances among sampling points and a distance matrix describing the sample values for any variable.

Two variables may appear to be related whereas they are simply correlated to a common cause. In soil ecology, the spatial position of sampling points is likely to cause such spurious correlations. Determining whether there is a true or a spurious correlation can be achieved by computing a partial correlation between two matrices A and B while controlling for the effect of spatial position, say, a matrix C (Smouse et al. 1986, Legendre 1993). The partial Mantel statistic allows us to test for the correlation between matrices A and B while controlling for the matrix C (denoted (A.B).C).

The Mantel test can be normalised. In this case the statistic takes values ranging between -1 and $+1$. The significance of both simple and partial Mantel coefficients is checked by computing their associated probabilities by permutation (Legendre and Fortin 1989, Fortin and Gurevitch 1993). The correlation between two matrices (i.e. Mantel coefficient) is not equivalent to the correlation between the variables as it measures the extent to which the variation in the first matrix corresponds to that of the second. All the computations were carried out with the statistical package "Progiel R" (Legendre and Vaudor 1991).

Results

Nematode community composition

At the study sites, the plant-feeding nematode community comprised five different species, one migratory endoparasite *Pratylenchus zeae* Graham 1951, two sedentary endoparasites, *Meloidogyne incognita* (Kofoid and White 1919) Chitwood 1949 and *Rotylenchulus reniformis* Linford and Oliveira 1940 and two ectoparasitic species *Helicotylenchus retusus* Siddiqui and Brown

1964 and *Hemicriconemoides cocophyllus* (Loos 1949) Chitwood and Birchfield 1957.

Besides these plant-feeding nematodes (PFN), the other species were grouped as free-living species (FLN), comprising predaceous, fungivorous, bacterivorous and omnivorous nematodes. The density of these species varied depending on the site (i.e. permanent pasture and market gardening) (Table 1). Among the plant-feeding species, two were exclusive: *R. reniformis* and *H. cocophyllus* being respectively absent from the permanent pasture and the cultivated plot.

Descriptive statistics

Within-plot variability of nematode density was very high in both the permanent pasture and the cultivated plot as shown by high coefficients of variation (calculated as [standard deviation/mean]), respectively, ranging from 102 to 736% and 158 to 348% (Table 1) for each of the plant-feeding species. Considerably lower values were obtained with the group of free-living species, i.e. 63 and 67% respectively. In both plots, the frequency distribution of all the nematode species or groups was skewed to right with high positive values of the skewness. None of these distributions met normality (Kolmogorov-Smirnov test, $\alpha = 5\%$). The Box-Cox method (Sokal and Rohlf 1995) was used to estimate the best normalising transformations for all the nematode species and groups. Nematode species encountered at very low densities, i.e. *H. cocophyllus* and *M. incognita* in the pasture and *M. incognita* and *P. zeae* in the cultivated plot (Table 1), were not taken into account in further analyses.

Soil physico-chemical variables showed high coefficients of variation ranging from 10 to 30% and from 12 to 39% for the pasture and the cultivated plot respectively (Table 1). For most soil parameters the Box-Cox transformation was not necessary because the data were normally distributed.

Spatial structures

The correlograms were computed for all the variables except for the density of rare nematode taxa as indicated above. The overall significance of each of them was tested using the correction for multiple testing proposed by Oden (1984). As we used 15 distance classes, the statistical level of overall significance was $\alpha' = 0.05/15 = 3.33 \times 10^{-3}$. Table 2 shows variables that had a consistent spatial patterning across the studied plots. Correlograms computed for soil parameters showed that all the variables were significantly autocorrelated except silt content either in the pasture or in the culture plot. Figure 1 shows the correlogram obtained for clay content and density of the nematode species *H. retusus*

Table 1. Nematode species density (individuals 100 cm⁻³ dry soil) and soil parameters across a permanent pasture and a cultivated plot (market gardening) in south Martinique. PFN = plant-feeding nematodes. FLN = free-living species. SD = standard deviation. CV = coefficient of variation.

	Permanent pasture			Cultivated plot		
	Mean	SD	CV	Mean	SD	CV
<i>H. retusus</i>	111.83	396.66	354.7	107.9	170.9	158.4
<i>P. zeae</i>	100	101.77	101.8	0.27	0.94	348.1
<i>M. incognita</i>	0.07	0.52	742.9	12.07	25.69	212.8
<i>H. cocophyllus</i>	0.14	1.03	735.7	0	0	—
<i>R. reniformis</i>	0	0	—	74.73	148.16	198.3
PFN	212.05	423.67	199.8	194.97	259.98	133.3
FLN	2707.8	1709.8	63.1	380.73	254.37	66.8
Clay (%)	49.69	8.31	16.7	45.26	5.53	12.2
Silt (%)	22.74	2.19	9.6	19.94	2.88	14.4
Sand (%)	27.57	8.33	30.2	34.81	6.71	19.3
Carbon (‰)	32.09	6.25	19.5	11.05	1.87	16.9
Nitrogen (‰)	2.98	0.53	17.8	1.17	0.21	17.9
Depth (cm)	96.72	21.19	21.9	33.47	13.2	39.4

in the pasture. The pattern of the correlogram of clay content suggested the presence of a gradient while the correlogram computed for *H. retusus* density is somewhat different. The first autocorrelation values are positive and significant. From distance classes 5–8 the Moran's *I* coefficient is negative and significant. The difference between these correlograms is the positive value for distance class 11 and the increase in the autocorrelation for distance classes 9–11.

Relationships between variables

Relationships between normalised variables were first investigated by a product-moment correlation analysis. The soil variables included in the correlation analyses in each site were clay, carbon content and soil depth. Sand, silt and nitrogen were not used due to their high

correlation with respectively clay and carbon contents; their analysis would have produced redundant information. The significance of the correlation coefficient was corrected to take the multiple-testing into account (Bonferroni correction, see e.g. Legendre and Troussellier 1988). The results consisted in a correlation matrix for each site.

In the pasture plot, we found a significant correlation for the following pairs of variables: clay content and carbon-content ($r = 0.625$, $p = 0.0001$); clay content and *H. retusus* density ($r = -0.436$, $p = 0.0005$). The statistical level of overall significance after multiple-testing correction (7 simultaneous tests by site) was $\alpha' = 0.05/7 = 0.0007$.

In the cultivated plot, clay and carbon contents were positively related ($r = 0.603$, $p = 0.0001$) as well as carbon content and soil depth ($r = 0.467$, $p = 0.0002$). The statistical level after correction was the same as for the pasture. No relationship between clay content and *H. retusus* density was found at that site.

Table 2. Overall significance of the correlogram of nematode density and soil parameters. Correlograms are taken as significant if at least one of the Moran's *I* coefficient is significant at the Bonferroni-corrected probability level $\alpha = 3.33 \times 10^{-3}$. S = presence of a significant spatial autocorrelation. NC = not computed. NS = absence of significant autocorrelation. — Species absent from the plot, correlogram not computable. PFN = plant-feeding nematodes. FLN = free-living species.

	Pasture	Culture
<i>H. retusus</i>	S	S
<i>P. zeae</i>	NC	NC
<i>M. incognita</i>	NC	NC
<i>H. cocophyllus</i>	NC	—
<i>R. reniformis</i>	—	S
PFN	S	NS
FLN	NS	NS
Clay (%)	S	S
Silt (%)	NS	NS
Sand (%)	S	S
Carbon (‰)	S	S
Nitrogen (‰)	S	S
Depth (cm)	S	S

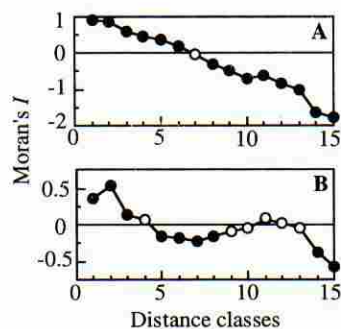


Fig. 1. Spatial correlogram of A) soil clay content and B) *Helicotylenchus retusus* density. Abscissa: distance classes; the width is 3.88 m. Ordinate: Moran's *I* coefficient. Black dots represent significant values at the statistical level $\alpha = 5\%$ before applying the Bonferroni correction to test the overall significance of the correlogram. White dots are non-significant values.

Table 3. Simple Mantel statistics (above the diagonal), partial Mantel statistics (below diagonal) and associated probabilities (tests of significance are one-tailed). The matrix held constant is indicated with the dot notation.

	HRET	CLAY	SPACE
HRET	—	0.13078 p = 0.00599†	0.16720 p = 0.0020†
CLAY	•SPACE = 0.02550 p = 0.19780, N.S.	—	0.67063 p = 0.00100†
SPACE	•CLAY = 0.10810 p = 0.00500‡	•HRET = 0.66373 p = 0.00100‡	—

† Simple Mantel test significant at the Bonferroni-corrected probability level of $(0.05/3 = 0.01667)$ for an overall significance level of 0.05 over three simultaneous tests. ‡ Partial Mantel test significant at the Bonferroni-corrected probability level of $(0.05/3 = 0.01667)$ for an overall significance level of 0.05 over three simultaneous tests. N.S. Not significant.

In a second step, the negative correlation between clay content and density of *H. retusus* in the uncultivated plot was investigated by taking into account the spatial pattern of the variables. The Mantel statistic was applied to three distance matrices formed as follow: 1) A distance matrix SPACE formed by taking the geographic distances among sampling stations. 2) A distance matrix HRET formed by taking the unsigned differences among values of *H. retusus* densities for all possible pairs of stations. 3) A distance matrix CLAY formed by taking the unsigned differences among values of the clay content for all possible pairs of stations.

The simple Mantel statistics (Table 3, above the diagonal) indicated the presence of a consistent spatial pattern for the variables *H. retusus* and clay content since simple Mantel statistics for HRET.SPACE and CLAY.SPACE were significant. These results are consistent with the information suggested by the shape of the correlograms (Fig. 1). The co-structure occurring between the variables *H. retusus* density and clay-content was also significant as indicated by the Mantel test computed for HRET and CLAY (Table 3, above the diagonal).

The last step was to determine whether the soil clay-content is a structuring factor of the *H. retusus* distribution or if the common pattern is independently determined by some unknown factor. The partial Mantel test was used to check for a relationship between *H. retusus* and clay content while correcting for space ((HRET.CLAY).SPACE) (Table 3, below the diagonal). The partial Mantel statistic for (HRET.CLAY).SPACE was not significant, which indicates the absence of a relationship between the matrices when the test is run by holding space constant. The relation between *H. retusus* density and clay content is thus simply due to a common spatial pattern leading to a spurious correlation.

Discussion

Cultivated and uncultivated sites differed markedly in the magnitude of soil carbon and nitrogen concentration and depth. These differences are consistent with the expected consequences of cultural practices in this

region. Carbon and nitrogen are lower in the cultivated site due to tillage and cultivation while soil depth is decreased by an important erosion and soil loss enhanced by the presence of slope. Composition of nematode community differed between sites, the differences in abundance of plant-feeding populations being likely to be due to host-plant specificity. As a consequence of cultural practices, free-living nematode densities were seven times higher in the uncultivated site. The within-site variability of nematode density was very high at both sites with frequency distributions skewed to the right. This is not surprising as frequency distributions displaying high asymmetry are frequent among soil biota that have clumped spatial distributions (Campbell and Noe 1985, Ferris et al. 1990).

Soil variables like clay or carbon contents were highly autocorrelated in both the cultivated plot and in the permanent pasture with significant positive values of autocorrelation at small distances. Certain plant-feeding nematodes were also spatially structured as indicated by correlogram analysis of Table 2 and simple Mantel test of Table 3 (above the diagonal). As positive autocorrelation values at small distance classes were significant, the degrees of freedom used in classical correlation testing are overestimated. The consequence is that a significant correlation may be in fact non-significant if true degrees of freedom were used. In contrast, nonsignificant correlation coefficients constitute valid results (Legendre 1993).

Correlation coefficient analyses showed no significant relations between nematodes and soil parameters in the investigated plots but for *H. retusus* density and clay content in the pasture. This significant negative linear correlation was confirmed by the simple Mantel test (Table 3). One might infer from the correlation coefficient that clay content is one ecological factor that affects the population of *H. retusus*. The absence of such a relation in the cultivated plot may be due to the difference in soil functioning, host-plant species and many other parameters. However, the partial Mantel statistic showed that when controlling for space, there was no relationship between clay-content and *H. retusus* density.

Legendre and Troussellier (1988) introduced the causal modelling in relation to simple and partial Man-

tel statistics. The same approach can be used here. Several causal relations can be made with the three variables under study (i.e. matrices HRET, CLAY and SPACE). We excluded the models where SPACE was a dependent variable and those where CLAY was dependent on HRET which do not make sense. Figure 2 shows the remaining four models.

The first model (Fig. 2-1) states that the nematode spatial distribution is independently caused by the spatial structure of the clay content and by other factors not explicitly mentioned in the model. If the model were supported by the data, we would expect the simple Mantel statistic $SPACE.CLAY$ not to be significantly different from zero which condition is not met in Table 3.

The second model (Fig. 2-2) claims that the spatial structure in the nematode population is partly caused by the spatial gradient in clay content and partly by other factors not explicitly identified in the model. If this model were supported by the data we would expect all the partial and simple Mantel statistics to be significant. These statements are not met in Table 3.

Model 3 (Fig. 2-3) states that nematode distribution is determined by the spatial pattern of clay content. In this case we would expect the partial Mantel statistic $(SPACE.HRET).CLAY$ not to be significantly different from zero condition, which again is not met in Table 3.

Finally, the fourth model (Fig. 2-4) states that both clay and nematode spatial patterns are independently controlled by unknown factors. If the model were supported by the data, we would expect the following predictions to be verified: 1) The simple Mantel test between the matrices SPACE and CLAY is significant: $SPACE.CLAY \neq 0$. 2) The simple Mantel test between the matrices SPACE and HRET is significant: $SPACE.HRET \neq 0$. 3) The partial Mantel test between

the matrices SPACE and CLAY when HRET is held constant is significant: $(SPACE.CLAY).HRET \neq 0$. 4) The partial Mantel test between the matrices SPACE and HRET when CLAY is held constant is significant: $(SPACE.HRET).CLAY \neq 0$. 5) The partial Mantel test between the matrices CLAY and HRET when SPACE is held constant is not significant: $(CLAY.HRET).SPACE = 0$. 6) The partial Mantel statistic between the matrices SPACE and HRET when CLAY is held constant is lower or equal to the simple Mantel statistic between the matrices SPACE and HRET: $(SPACE.HRET).CLAY \leq SPACE.HRET$. 7) The partial Mantel statistic between the matrices SPACE and CLAY when HRET is held constant is lower or equal to the simple Mantel statistic between the matrices SPACE and CLAY: $(SPACE.CLAY).HRET \leq SPACE.CLAY$. 8) The product of the simple Mantel statistics between SPACE and CLAY on one hand and SPACE and HRET on the other is approximately equal to the simple Mantel statistic between the matrices CLAY and HRET: $(SPACE.CLAY)(SPACE.HRET) \approx CLAY.HRET$. The seven first predictions are verified in Table 3 while the last one can easily be verified as: $0.67063 \times 0.16720 = 0.11212 \approx 0.13078$.

Our results clearly indicate the absence of a true effect of soil texture, organic matter content and soil depth on the distribution of soil nematodes at the scale of our investigation. According to Ferris et al. (1990), the spatial pattern of plant-parasitic nematode species has both macro- and micro-distributional components. The factors that mediate these structures may be different, for instance, soil texture is one of the factors that influence the nematodes macro-distribution. Soil texture influence has been reported in various soils and different nematode species (Starr et al. 1993, Wallace et al. 1993, Koening et al. 1996). No attempt, however, has ever been made to take into account the spatial patterns in relationship assessments and testing. Other sources of spatial variation are the micro-distributional components of the pattern which is assumed to be primarily mediated by food resource distribution (Ferris et al. 1990). Our sampling point number and spatial position did not allow good investigation of the nematode microscale pattern for which a very short inter-sample distance is required (Rossi et al. 1996). However, in the pasture plot, the distribution of the host-plant species was homogeneous enough throughout the sampled surface to assume the amount of food resource to be homogeneous. Nevertheless, such short-range potential source of variation in species pattern could not be appreciated in this study since the minimum inter-sample distance was 1 m. Considering the cultivated plot, the row-effect was a good candidate to affect the plant-feeding spatial patterning at a small scale because of the driving effect of row on root pattern and modification of soil porosity in and between rows (Delaville et al. 1996). Even if present in our study, that row-effect must have been masked by the strong large-scale pattern of the variables. It is likely that

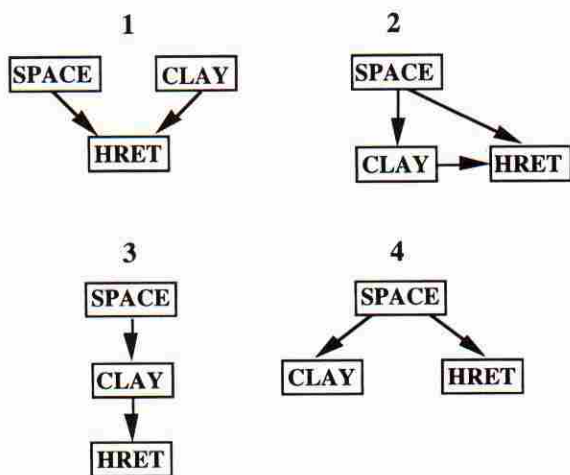


Fig. 2. Four models for causal relationships between the variables HRET, CLAY and SPACE (see text for details). Models 1–3 are not supported by the data.

nematode spatial pattern is influenced by many factors either biotic or abiotic that express themselves at a continuum of scales. Beyond the host plant major influence, soil environment directly affects nematode populations by physical and physiological impact on individuals and an indirect effect through host plant growth and health.

Because soil environmental variables and soil fauna are generally spatially dependent at the field scale, specific statistical analyses are required to segregate between true and false relations. Properly taking into account the spatial pattern of soil properties may significantly improve our understanding of the parameters affecting soil faunal communities composition and spatial distribution and their effects on ecosystem-level processes.

The potential appearance of spurious correlations and resulting errors in interpretations is, in our opinion, a very important issue for ecologists. Since spatial heterogeneity is a general aspect of ecological systems, caution is needed when relationships between factors are to be tested. Using specific statistical tools like Mantel tests prevents wrong conclusions and allows us to test different models of relationships between parameters.

Acknowledgements – We wish to thank P. Legendre who provided us with the Prociel-R package, P. Clochard and P. Topart for their technical assistance during the field and laboratory work, M. Mahieu (S.E.C.I.) for allowing access to the sites and providing help and advice at the experimental station. We are grateful to C. Kerdelhué, P. Lavelle, C. Lattaud and L. Rousseaux for helpful suggestions on the manuscript.

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