De l'extensif à l'intensif

L'étude extensive précédente nous a donné un premier aperçu des populations d'acariens vivant dans différentes grottes wallonnes, permettant de conclure que la composition des communautés cavernicoles est extrêmement variable (hypothèse 1). Cependant, au nombre élevé de cavernes visitées correspond assez logiquement un nombre réduit d'échantillons dans chacune des cavernes. Suivant deux critères pratiques, à savoir la possibilité de prendre un nombre élevé d'échantillons, et donc l'existence de plages de sédiments étendues, et la densité d'acariens présents, deux cavités ont été choisies. De nombreux échantillons ont été prélevés à trois périodes distinctes.

D'autre part, afin de réaliser la comparaison entre sols et cavernes, le milieu endogé surplombant les grottes a également été exploré, ainsi qu'un site endogé sur schiste.

Si nous avons montré que la structure spatiale des peuplements d'acariens cavernicoles au niveau du paysage est plutôt de type "insulaire", avec peu de similarité entre cavernes proches, il est naturel de s'intéresser maintenant à la structure spatiale *in situ*, à l'échelle locale (test de l'hypothèse 5 : les acariens cavernicoles sont plus agrégatifs que les acariens endogés). Afin de vérifier l'hypothèse selon laquelle cette répartition spatiale suit celle de la matière organique (hypothèse 4), nous avons également mesuré ce paramètre et comparé leur distribution spatiale respective, dans les sols et les cavernes.

Chapitre 2

Spatial microdistribution of mites and organic matter in soils and caves

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Abstract

Spatial variability is a key to understanding the structure and function of soil biodiversity. This research addressed the question of whether mite centimetric spatial pattern corresponds to that of organic matter in two caves and in the mineral horizon of three forest soils. Therefore, different statistical tools were used and compared: classical aggregation analysis through variance-to-mean ratio and Morisita's index, nested hierarchical ANOVA and Moran's I autocorrelation coefficient. The spatial pattern of organic matter was generally found to be of the gradient or patch type, influenced by slope and trees. Cave sediments far from the entrance contained smaller

organic carbon patches than deep soil and cave entrance. Mite density spatial patterns sometimes correspond to that of organic matter in soils but never in caves. Correlograms of mite species composition were significant in soils but not in caves. The difference of space available in caves compared to that in the tortuous pores of the soil is thought to be a major structuring factor for mites by influencing their mobility. Correlograms were the most dependable spatial analysis tools as they could be statistically tested and used to clarify the patterns detected by the nested hierarchical ANOVA method.

Résumé

La variabilité spatiale est une clé pour comprendre la structure et la fonction de la biodiversité du sol. Cette étude traite de la correspondance de la configuration spatiale des acariens à l'échelle centimétrique avec celle de la matière organique, dans deux cavernes et dans l'horizon minéral de trois sols forestiers. Pour ce faire, différents outils statistiques ont été utilisés et comparés : une analyse classique d'agrégation au travers du rapport moyenne/variance et de l'indice de Morisita, une ANOVA hiérarchisée et le coefficient I d'autocorrélation de Moran. La configuration spatiale de la matière organique est généralement de type gradient ou agrégat, sous l'influence de la pente ou des arbres. Dans les cavernes, les sédiments éloignés de l'entrée contiennent des agrégats de plus petite taille que le sol profond ou l'entrée des cavernes. La configuration spatiale de la densité d'acariens correspond parfois à celle de la matière organique dans les sols, mais jamais dans les cavernes. Les corrélogrammes de composition spécifique en acariens sont significatifs dans les sols mais pas dans les cavernes. La différence d'espace disponible dans les cavernes par rapport aux pores tortueux du sol est considérée comme un facteur majeur de

structuration pour les acariens de par son influence sur leur mobilité. Les corrélogrammes sont les outils d'analyse spatiale les plus fiables, vu qu'ils peuvent être testés statistiquement et utilisés pour clarifier les configurations détectées par la méthode d'ANOVA hiérarchisée.

Introduction

There is a general consensus today that our planet is facing a crisis of species diversity. This is why it has become even more urgent to understand the factors influencing biodiversity.

Among these factors, spatial variability is thought to be one of the main keys to understanding the structure and function of soil biodiversity (Giller 1996; Shorrocks et al. 1984; O'Connell & Bolger 1998; Ettema & Wardle 2002), as soil communities show only limited diet and habitat specialisation (Anderson 1975; Ghilarov 1977). Soil organisms have a space dependent pattern that sometimes ranges over hundreds of meters, and a patchy distribution at a scale ranging from centimeters to meters (Ettema & Wardle 2002).

The rare studies about mite microdistribution conclude that mites are lightly clumped (Pande 1973), show a patch size of 20 cm to a few meters (Usher & Booth 1986; Klironomos et al. 1999) and are affected by tree position (Torgersen et al. 1995) or not (Klironomos et al. 1999). Aggregation was frequently investigated using rough distribution of individuals in samples (e.g. Gérard 1970; Ekschmitt et al. 1997).

Data about the spatial structure of fauna in caves are even scarcer than those for soils. Christiansen (1970a) found that springtails restricted to the cave environment (= troglobites) had a lower aggregation than epigeic springtails or troglophiles (= organisms that can live their entire life in caves but are not

restricted to this ecosystem). Their aggregation around food was also found to be lower (Christiansen 1971).

Forest deep soils and caves differ in three major ways. On the one hand, caves are large-sized relatively to arthropods, a characteristic which enables them to walk on the surface of sediments and rocks, while they are forced to move in tortuous pores in deep soils. On the other hand, spatio-temporal distribution of organic matter is expected to differ between the two environments. In addition, caves are more frequently flooded than most soils. These two environments nonetheless share a number of environmental features: small temperature range, relative humidity close to saturation, darkness, low organic matter concentration.

Organic matter is certainly a major environmental factor affecting soil dwellers. For mites in particular, the highest densities have been recorded from thick forest litter (Petersen & Luxton 1982; André et al. 2002). In caves, densities were also found to be related to organic matter concentration (Christiansen et al. 1961).

In soils, Vieublé Gonod (2002) showed that soil carbon was organised in centimetric spots.

In caves, horizontal distribution of organic carbon depends on its origin. No production is made in situ, except for sulfur-based ecosystems (Sarbu et al. 1996). It comes from either active (animals, men) or passive (leaching, inundation) routes (Gers 1998). While flooding leaves a homogeneous substrate with some vegetal macro-fragments, other inputs lead to spots of carbon accumulation.

This research addressed the question of whether mite centimetric spatial pattern corresponds to that of organic matter in two caves and in the mineral horizon of three forest soils. Different statistical tools were used and

compared: classical aggregation analysis, nested hierarchical ANOVA and Moran's I autocorrelation coefficient.

Material and methods

Sites

The study was carried out in Rochefort, South Belgium (50°10' N, 5°13' E). The climate is temperate oceanic. Mean annual rainfall is 846 mm and mean annual temperature is 8.7°C (both values are means over the 30 last years; Institut Royal Météorologique, pers. comm.).

Five sites were sampled (Tables 2.1 and 2.2): two caves (HC for Han and NC for Nou Maulin), two calcareous forested soils situated above the caves (HS and NS), and one non-calcareous forest site equidistant from both caves (ES for Epraves).

Table 2.1. Characteristics of cave sampling sites.

	Han	Nou-Maulin
Abbreviation	HC	NC
Length (km)	12	1.6
Status	Touristic	Cavers only
Distance to nearest entrance (m)	350	65
Alluvium	silty	sandy
Flooded in winter	yes	yes

Sampling method

Period

Fifty samples were collected from each site in May and November 2000. The samples collected during this study constituted 10 distinct sets (five locations x two sampling periods). As our sampling method was

Table 2.2. Characteristics of deep soil sampling sites.

	Epraves (Bestin wood)	Han	Nou-Maulin
Abbreviation	ES	HS	NS
Subsoil	Schist	Loess on Limestone	Limestone
Soil type			
Belgian typology	fGbb	AbB	Gbbk
FAO typology	Umbric Leptosol	Eutric Cambisol	Rendzic Leptosol
Litter type	moder	moder	mull
Litter thickness (cm)	2-5	2-5	1-10
Vegetation	*Quercus petraea, Carpinus betulus.*	*Quercus petraea, Fagus sylvatica*	*Tilia cordata, Quercus robur, Carpinus betulus, Acer campestre, Acer pseudoplatanus, Fraxinus excelsior, Corylus avelana, Hedera helix, Rubus sp*

destructive, 3 to 4 meters separated November sampling plots from May plots. This is why we decided not to compare both seasons but rather to consider the autumn sampling as a replicate of May sampling.

Forest sites

Two perpendicular trenches with a common origin were dug in the soil (Fig. 2.1). Five-cm long samples were removed from the trench side at 5-cm intervals with a steel corer (∅ 3.5 cm), at a depth of 15-20 cm. The cutting side of the corer was a little narrower than the body in order to alleviate the compression of the samples. A hierarchical nested sampling (Oliver & Webster 1986) was used to test 3 distance classes: 5 cm, 20 cm and 1 m (Fig. 2.1).

Because of the presence of a lot of stones in NS, we were not able to push the corer into the side of the trenches. Therefore, we collected aggregates between rocks, for an equivalent apparent volume per sample as from the other sites. In May, a stump was present beside the Y axis in NS.

Cave sites

Five-cm long samples were taken vertically from a square of 1.5 m side chosen on the ground with the same corer as in forest sites (Fig. 2.1), thus allowing animals running on the surface to be collected. Sixteen samples were collected in a hierarchical way at fixed coordinates (the same as in forest sites on the medians of the square), and 34 more samples randomly within the square.

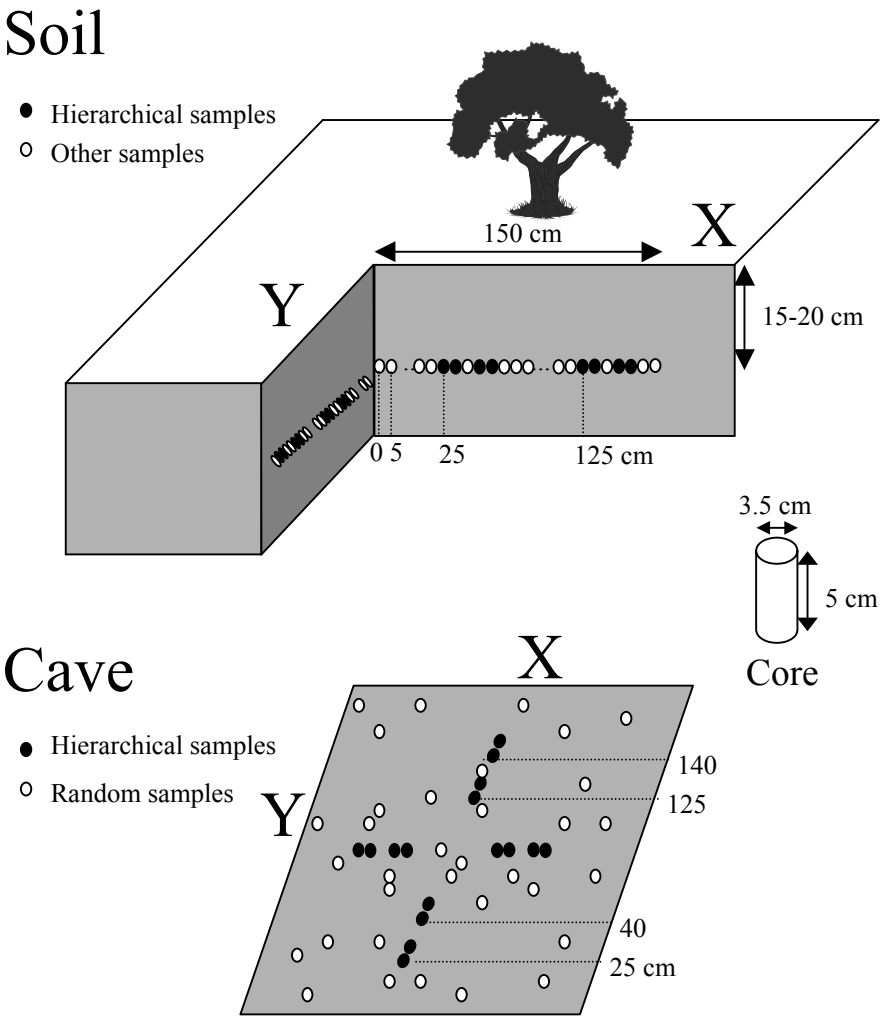

Figure 2.1. Sampling protocol.

Extraction of microarthropods

The samples were extracted, using Berlese-Tullgren funnels. Light bulbs (15 watts), 10 cm above the intact samples, were lit one week after the beginning of the extraction. Extraction lasted 3 weeks. The mean temperature in the extraction room was 20 °C.

Mites identification

All mites were mounted in lactic acid, or in Hoyer medium when necessary for identification. Contrary to common practice, most stases (developmental stages) were identified to the species level.

Physico-chemical characterisation

In each sampling set, organic carbon was estimated in the 16 cores from the hierarchical nested sampling (Fig. 2.1) through the Walkley and Black (1934) method, namely a wet oxidation of organic carbon in an acid dichromate solution followed by back titration of the remaining dichromate with ferrous ammonium sulfate. Total C and N were measured from the same samples through combustion followed by Gaseous Chromatography.

Data logger thermometers were placed in each site. The water content of samples was inferred by weighing before and after extraction of animals. Porosity was then calculated taking a particle density of 2.6 for all substrates. Granulometry, exchangeable cations (K, Mg, Na and Ca), water soluble P, pH-H_2O and pH-KCl were determined for one sample from each May sampling set.

Statistical tools

All basic statistics were computed using SAS 8 software (SAS Institute 1999).

CANOCO (ter Braak and Smilauer 1998) was used for Canonical Correspondence Analysis.

Coefficient of variation (CV) is defined as the square root of the variance divided by the mean, multiplied by 100. It is dimensionless and thus used to compare the dispersion of values around the mean in different populations.

The variance-to-mean ratio was traditionally used to measure the degree of aggregation of mites (e.g. Gérard 1970; Johnson & Petkau 1995). This ratio tends to 1 for a random distribution of animals (that is a Poisson distribution), is inferior for a uniform distribution and superior for an aggregative distribution. A χ^2 statistic on this ratio is used to test the departure from randomness of the distribution. Elliot (1971) indicated that the variance-to-mean ratio was affected by the total number of individuals in the sample. Therefore, Morisita (1971) developed an index of dispersion independent of the mean. It is defined as

$$I_\partial = \frac{n\left[\sum_{i=1}^{n}(Z_i^2) - \sum_{i=1}^{n} Z_i\right]}{\left(\sum_{i=1}^{n} Z_i\right)^2 - \sum_{i=1}^{n} Z_i}$$

where n is the number of sampling units and Z_i the count for the i^{th} sampling unit. It equals 1 for random distribution of individuals, is less than 1 for uniform distribution and greater than 1 for clumped distributions.

Indices of aggregation provide limited information on the spatial pattern since information on the actual location of samples with respect to each other is ignored. Therefore, we also used spatial data analysis tools. Spatial

dependence, also called autocorrelation, refers to the tendency of spatially-distributed phenomena to be more similar the closer they are to one another, and all the more dissimilar as the distance between them increases.

As already mentioned, nested hierarchical sampling (Oliver & Webster 1986) was used to characterise organic matter and mite spatial distribution. The mean squares of a nested hierarchical analysis of variance were used to calculate the component of the total variance that was contributed over different spatio-temporal scales: 5-cm, 20-cm, 1 m, the direction (that is the two perpendicular axes) and season factor. The advantage of such a sampling plan is the reduced number of samples needed compared to a classical homogeneous sampling strategy.

Correlograms of the organic carbon and mite density variables (see Legendre & Fortin 1989 for details) were plotted using the R statistical package (Legendre and Vaudor 1991). These graphs represent an autocorrelation coefficient (Moran's I) as a function of lag-distance. Lag-distance classes were chosen so as to keep a constant number of sample pairs within each of them. Moran's I coefficient has a huge advantage: it can be statistically tested by assuming a relaxed form of the stationarity hypothesis (Legendre & Legendre 1998) stating that a single autocorrelation function is adequate to describe the entire surface under study or, in other words, that the main large-scale structure is the same everywhere. We chose a α=5 % error level. To test correlograms globally, we used the Bonferroni correction (Cooper 1968). Indeed, several tests were done as each of the v points of the correlogram was tested at the same time for a given overall significance level α. The global test was made by checking to see whether the correlogram contains at least one value which is significant at the $\alpha'=\alpha/v$ significance level. In order to determine the extent of the correlation (i.e.

which distance class is reached by the autocorrelation), a progressive Bonferroni correction (Hewitt et al. 1997) was applied. In this method, the Moran's I of the first distance class is tested against the α significance level, the second at the $\alpha'=\alpha/2$ and so forth. The extent is the lag-distance before the first non-significant one.

Because variables could have different spatial properties in different directions (anisotropy), directional correlograms were computed. In soils, these were calculated, using data of only one of the two trenches. In caves, sample pairs aligned in the direction studied, with a tolerance of 45°, were used for computations.

Correlograms for the mite community composition were calculated using the Mantel method (see Legendre & Fortin 1989 for details) implemented in the R package (Legendre & Vaudor 1991). This method is based on a distance matrix built from the species composition of each sample. The distance was derived from Steinhaus similarity coefficient (Legendre & Legendre 1998). Each point of the correlograms was tested at the 5% significance level using Mantel's normal approximation. The Bonferroni test was also applied.

Results

Organic matter

In order to provide a good description of the sampled sites, general environmental variables are set out in Table 2.3.

Organic carbon contents (C_{org}) were found to be lower than the total carbon contents (C_{tot}) in NS and NC, identical in HS and ES and greater in HC. The latter is of course impossible, and we suspect that substances other than organic C were oxidised by dichromate during the Walkley and Black

Table 2.3. Environmental and biotic characteristics of sampled sites.

	ES	HS	NS	HC	NC
pH (water)	4.8	4.9	7.5	6.2	7.4
pH (KCl)	3.6	3.4	6.4	5.7	6.7
Mean temperature (°C)	9.8	9.5	9.6	8.6	7.7
Yearly temperature range (°C)	18.6	17.0	18.0	0.5	4.3
Daily temperature range (°C)	0.8	0.7	0.7	0.0	0.1
Water content in May (%)	24	25	35	104	34
Water content in November (%)	25	23	34	82	35
Porosity (%)	56	53	76	80	59
P soluble (mg/100g)	0.1	0.1	0.1	0.2	0.1
Exchange complex ($cmol_c\ kg^{-1}$)					
K	0.18	0.18	0.31	0.26	0.13
Mg	0.91	0.25	1.23	1.81	1.15
Na	0.04	0.09	0.09	0.09	0.09
Ca	0.90	0.80	48.40	15.32	16.92
Granulometry (%)					
clay	29	25	53	20	12
fine silt	39	32	21	51	14
coarse silt	10	38	19	28	15
fine sand	4	4	5	2	49
coarse sand	17	1	2	0	10
Ntot (%)	0.20	0.07	0.47	0.47	0.15
Ctot (%)	2.5	1.0	6.1	5.9	2.2
Corg (%)					
May	2.8	1.0	6.0	(6.9)	2.0
November	2.2	1.1	4.8	(6.6)	2.1
mean	2.5	1.0	5.4	(6.7)	2.1
Mite density (individuals/sample)					
May	5.7	2.4	16.2	0.4	3.6
November	8.9	4.6	9.5	0.4	1.3
mean	7.3	3.5	12.9	0.4	2.4
Variance-to-mean ratio of mite density					
May	4.1	1.8	21.4	1.1	5.2
November	6.1	6.4	4.7	1.1	1.6
Morisita index					
May	1.6	1.4	2.4	1.1	2.2
November	1.6	1.9	1.4	1.3	1.5

titration. Consequently, we will use the C_{tot} values instead of C_{org} values for HC in subsequent analyses.

There was little seasonal variation of C_{org} (Table 2.3).

In order to compare general variation of organic C, total C and total N (N_{tot}), the coefficient of variation (CV) was calculated for each site (Table 2.4). All values were around 20%, except those of the Han cave: about 4% only. There was no clear difference between seasons, except for NS where autumn CV was twice spring CV.

Table 2.4. Coefficient of variation of organic C (Corg), total C (Ctot) and N (Ntot) and mite density (d).

Site	Corg	Ctot	Ntot	d
ES	31	29	28	89
HS	25	24	24	111
NS	19	25	22	119
HC	5	5	4	159
NC	24	26	23	142

The distribution of variability within a 1-m range was explored through the percentage variance contributed at scales 4, 20 and 100 cm derived from a nested hierarchical ANOVA (Table 2.5). Overall, most of the variability in soils and HC was found in the first 5 cm, which means that no clear spatial pattern is expected. By contrast, in NC, most of the variability was found in the 1-m category. So, the spatial pattern of NC was more predictable. Two exceptions to these observations were found. On the one hand, in HC and HS, all organic determinants were more variable in the 20-cm category during autumn. On the other hand, in NS, C_{org} was more variable in the 20 and 100 cm categories during spring and autumn respectively.

Table 2.5. Percentage of variance contributed at each spatial scale to 1 meter for organic C (Corg), total C (Ctot) and N (Ntot) and mite density (d). Nov.=November; Tot.= both seasons. Bold figures are level of maximum variance.

	Corg			Ctot			Ntot			log (d+1)		
	May	Nov.	Tot.	May	Nov.	Tot.	May	Nov.	Tot.	May	Nov.	Tot.
ES												
100 cm	0	0	0	0	0	0	0	0	0	11	**52**	32
20 cm	19	50	31	0	40	17	8	**53**	29	16	3	9
5 cm	**81**	50	**69**	**100**	**60**	**83**	**92**	47	**71**	**73**	45	**59**
HS												
100 cm	7	3	7	0	8	3	19	5	11	6	**54**	32
20 cm	0	**66**	10	2	**65**	44	0	**61**	33	0	0	0
5 cm	**93**	31	**83**	**98**	27	**53**	**81**	34	**56**	**94**	46	**68**
NS												
100 cm	36	**54**	**47**	34	**50**	46	16	33	30	0	**72**	**48**
20 cm	**45**	33	37	23	2	8	29	0	0	**71**	2	21
5 cm	19	13	15	**44**	48	**47**	**55**	**67**	**70**	29	26	30
HC												
100 cm	**(58)**	(0)	(28)	30	0	0	29	0	0	20	0	0
20 cm	(24)	**(51)**	**(38)**	2	**70**	45	13	**86**	**63**	**54**	14	39
5 cm	(19)	(49)	(34)	**69**	30	**55**	**57**	14	37	25	**86**	**61**
NC												
100 cm	**89**	22	**67**	**89**	**50**	**78**	**91**	**40**	**75**	43	36	**54**
20 cm	0	**66**	22	0	18	5	0	37	12	1	0	0
5 cm	11	12	11	11	32	18	9	22	14	**56**	**64**	46

Correlograms were computed for each sampling set on C_{org} values (Fig. 2.2). Two main types of correlograms could be identified (Table 2.6). On the one hand, NC was typical of gradient data (Legendre and Fortin 1989). When a directional correlogram was calculated for axes X and Y, only Y was significant, which shows that the direction of the gradient was predominantly in that direction, that is parallel to the slope. On the other hand, in HS and NS, autocorrelation was positive at a distance of 4-cm, negative between 50 and 130-cm and positive again at 150-cm. HC had the same V-like

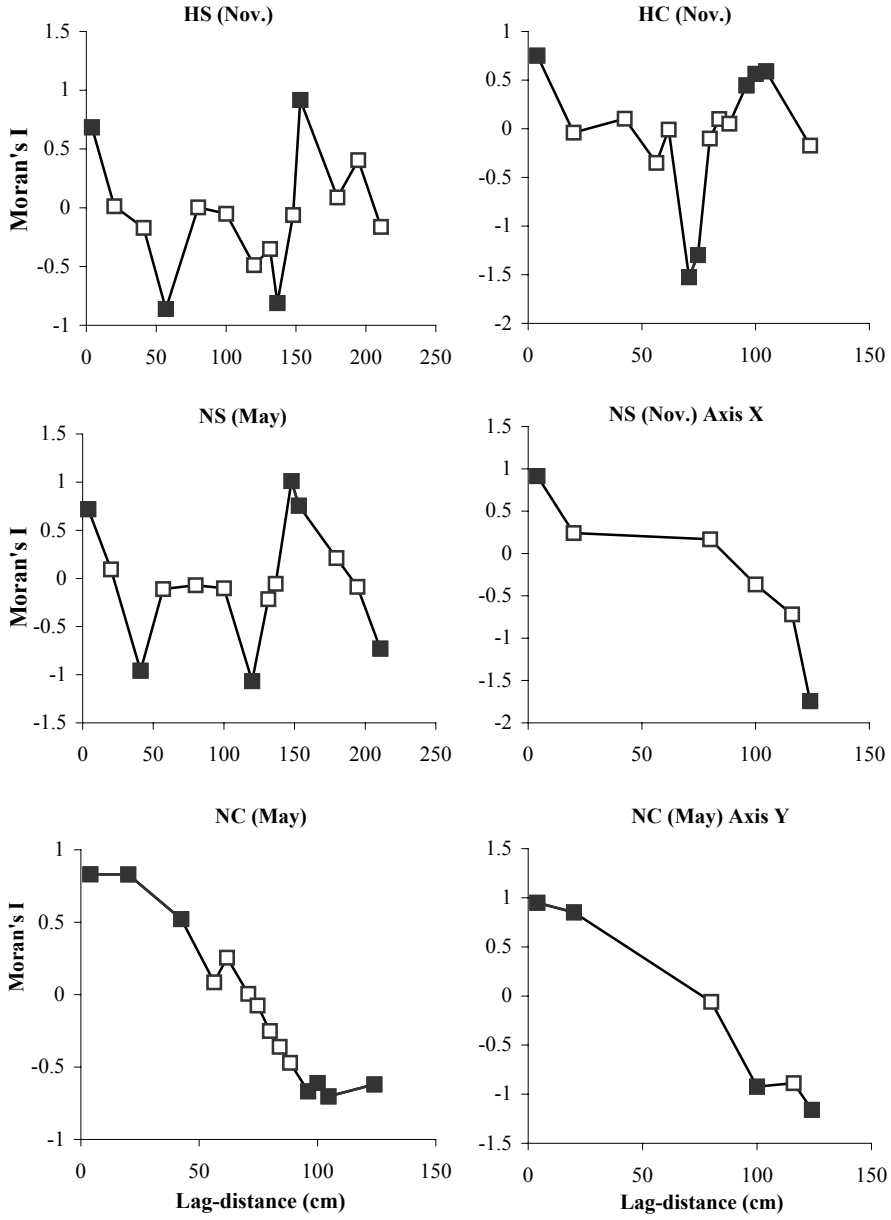

Figure 2.2. Significant correlograms of organic carbon (total carbon in the case of HC). Black squares represent significant values at the 5% level. Nov.=November

Table 2.6. Spatial structure of C_{org}, mite density and species arrangement in sampling sites as deduced from correlograms (GRA=gradient; PER=periodic; italic indication across axis X and axis Y columns denotes a structure in a non-identified direction)

	ORGANIC CARBON			MITE DENSITY			SPECIES COMPOSITION		
	Axis X	Axis Y	Global	Axis X	Axis Y	Global	Axis X	Axis Y	Global
ES	-	-	-	GRA	-	GRA	-	-	GRA
HS	*GRA/patch ?*		V-like	-	-	GRA ?	-	-	GRA
NS	GRA	patch ?	V-like	-	PER	PER	-	-	GRA
HC	*GRA/patch ?*		V-like	-	-	-	-	-	-
NC	-	GRA	GRA	GRA	-	GRA	-	-	-

correlogram, but the distances were different: negative at about 70-cm and positive at about 1-m. In order to interpret this V-like pattern, data were simulated (Fig. 2.3) to create a spatial structure showing a large patch in the X direction and a gradient in the Y direction. A correlogram was calculated (Fig. 2.4) from sixteen points of the simulation, chosen according to the schema used in our real sites (Fig. 2.3). It was V-shaped. Correlogram for simulated axis Y shows a gradient structure while the correlogram for simulated axis X was not significant. Similarly, NS axis Y correlogram shows a gradient directed towards the path. In HC and HS, directional correlograms were not significant.

The extent of the spatial relation, tested with the progressive Bonferroni method, was 20 cm in NC while it was restricted to 4 cm in HC, HS and NS.

Mite aggregation

Mites were significantly aggregative everywhere except in the Han cave as estimated by the variance-to-mean ratio (Table 2.3). The Morisita's index gave similar results (Table 2.3). The variance-to-mean ratio was linked to the

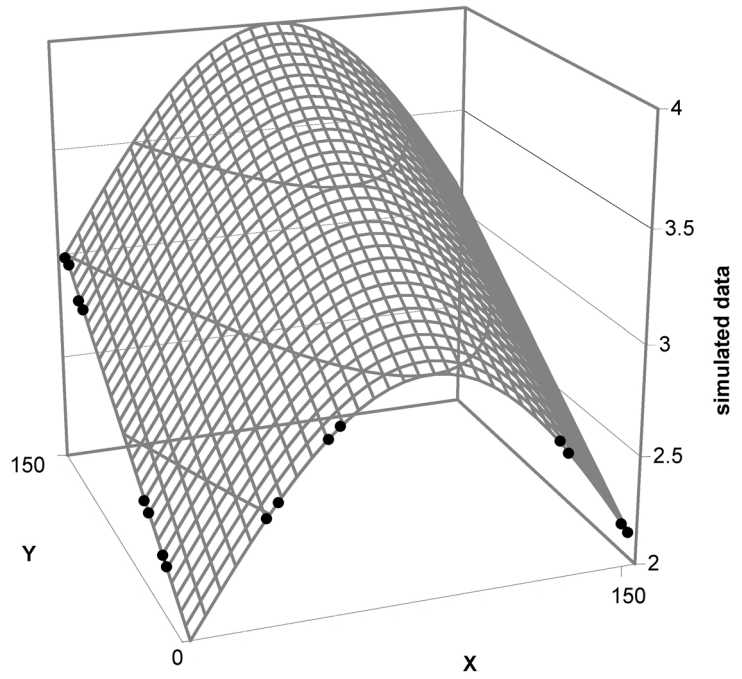

Figure 2.3 Data (Z) simulated such as axis X has a gradient structure and axis Y has a large patch structure (Z = 2 + (x/150) + sin (y/50)). Sampling points in black.

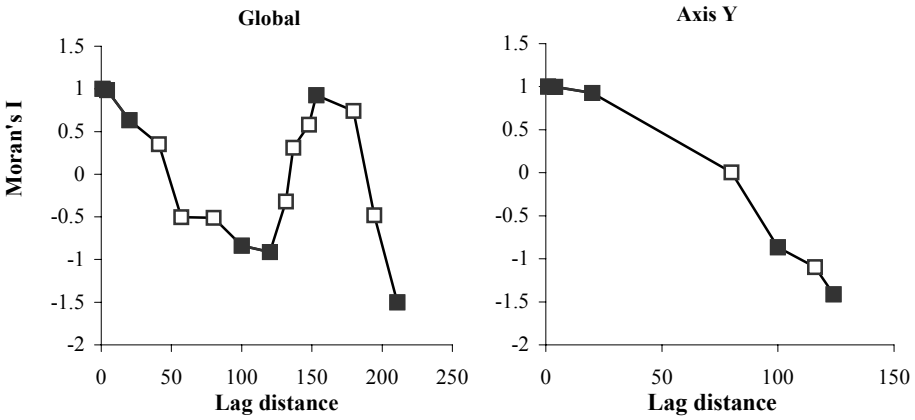

Figure 2.4. Significant correlograms for simulated data. Black squares represent significant values at the 5% level. See text for details.

mite density: the mite density variance in each sampling set fitted a variance predicted using a geometric function of the mean (r^2=0.8, n=10), as anticipated by Ekschmitt et al. (1997).

Mite density

Mite density was lower in caves than in soils (Table 2.3). In caves, HC had a very low density compared to NC. In the endogeous environment, NS hosted a large number of mites, while HS had only a mean of 3.5 mites per sample.

Mite density were log-transformed using the log(n+1) formula to normalise the distribution, as suggested by Gérard and Berthet (1966) and Legendre & Legendre (1998).

The relation of mite density to organic matter was evident in soils (Fig. 3.1a): the Spearman correlation with C_{org} amounted to 0.63 (P<0.001, n=96). The carbon contents in the two caves were characterised by extreme values with no intermediate points (Fig. 3.1b). It would thus have been spurious to calculate a general correlation coefficient. In addition, there was no significant correlation between mite density and organic C in any of the two caves (Spearman's r = $-0{,}26^{NS}$ and $-0{,}20^{NS}$ respectively in HC and NC, n=16). To sum up, there was a correlation of mite density with organic carbon in soils but not in caves. Correlations with total C and N gave similar results.

Mite density appeared much more variable than organic matter as expressed by the CV (Table 2.4). The CV were higher in caves than in soils.

No spatial pattern was detected by hierarchical nested ANOVA (Table 2.5), with a percentage of variance contributed at the smaller scale exceeding 50% in all sites, except in NS and NC. When data were decomposed per season,

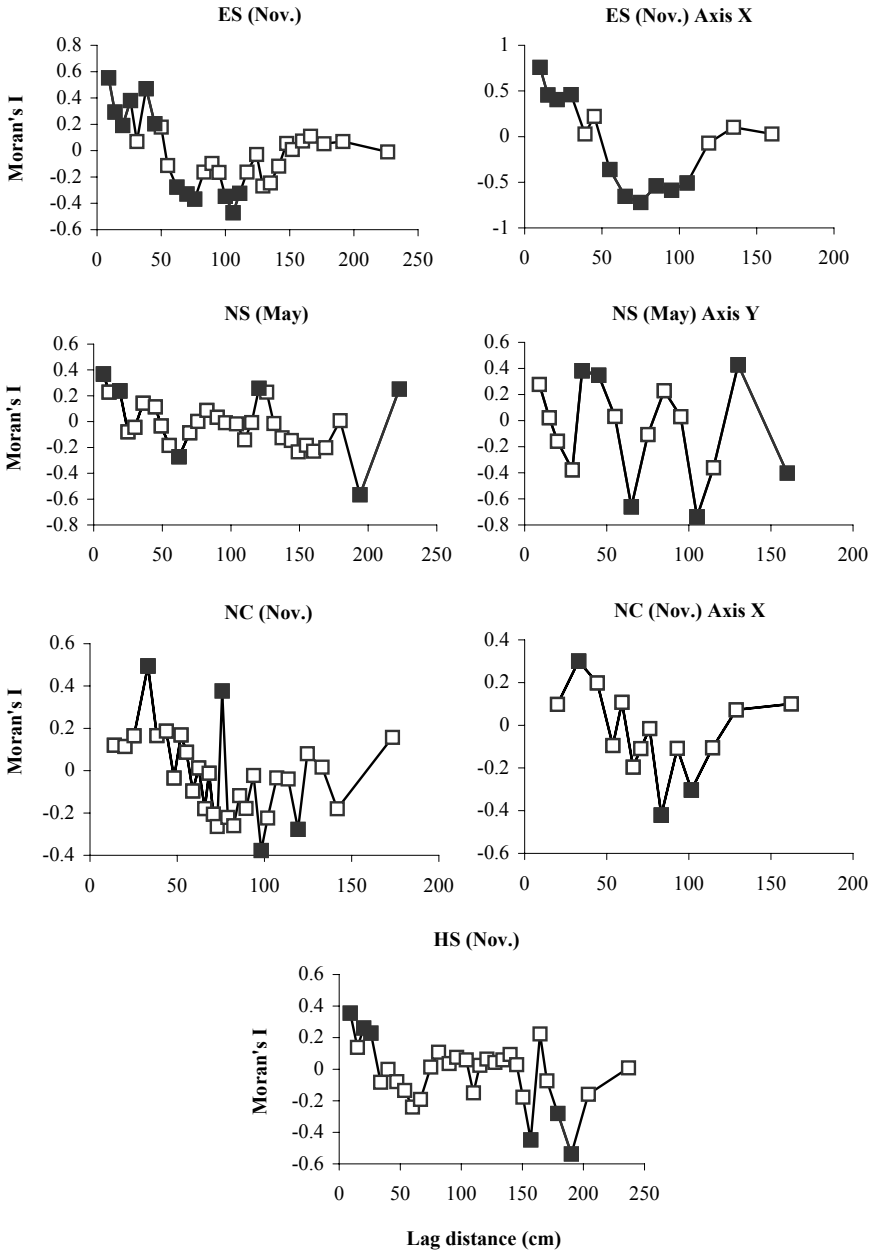

Figure 2.5. Significant correlograms for logarithmic mite density. Black squares represent significant values at the 5% level. Nov.=November

the variation was maximal in the 20 cm class in NS and HC in May and in the 1-meter class in ES, HS and NS in November.

Correlograms of mite logarithmic density were calculated for each sampling set (n=50). Four among them were significant: ES, HS and NC in November and NS in May (Fig. 2.5 and Table 2.6). ES correlogram suggested a gradient shape. This gradient structure was apparent in the X direction. The HS correlogram appeared to have a gradient shape, but directional correlograms were not significant. NS had an apparent periodic structure with a period of 120 cm or 40 cm when significant points only or all points were taken into account respectively. A directional correlogram suggested a periodic structure with a 40 cm period in Y direction. The NC correlogram is weird in that there was no spatial autocorrelation less than 32-cm. The general aspect suggested a gradient. Directional correlograms show that this gradient was predominantly in the X direction.

Species richness

To analyse the effect of organic matter on mite species richness at the local scale, a rank correlation analysis with organic matter was performed, which showed significant coefficients when grouped by habitat (Spearman's r = 0.61***, n=96 in soils and r = -0.37**, n=64 in caves). No coefficient was significant in any site (n=16). Partial correlations with mite density as a control variable were never significant, showing that at the scale studied, species richness was a mere consequence of the number of animals present in the sample.

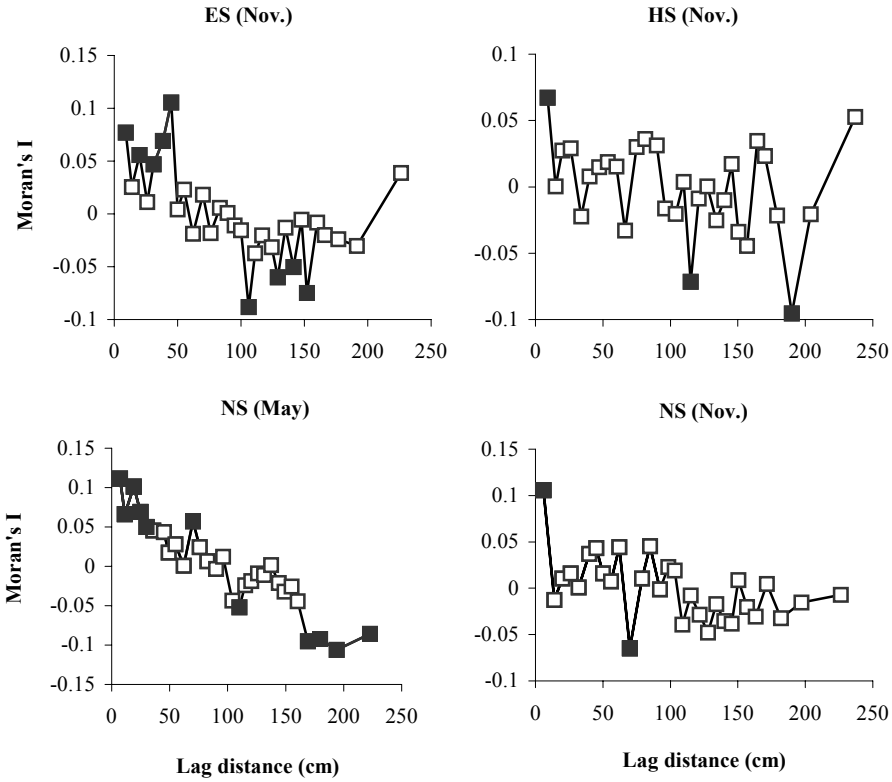

Figure 2.6. Significant mantel correlograms for mite species composition. Black squares represent significant values at the 5% level. Nov.=November

Mite species composition

A Canonical Correspondance Analysis was computed using C_{tot}, C_{org} and N_{tot} as environmental variables and the sites and seasons as covariables. The result was tested using Monte Carlo permutations as described in the CANOCO software manual (ter Braak and Smilauer 1998). It gave a non-significant canonical structure, showing that community assemblage at the sample scale was not influenced by organic matter. When the data were split

by habitat (soil or cave), the canonical structure appeared significant in caves but with only 5.8% of explained variation.

Mantel correlograms were significant in every soil site at least in one season, but never in caves (Fig. 2.6). They all had a gradient shape.

Discussion

Organic matter

The two chosen cave sites were obviously different: the sediment was spatially more homogeneous in HC than in NC, as expressed in the CV. This is probably due to the distance run by water during floods: near the cave entrance, larger organic debris are deposited and, as water enters deeper into the cave, debris size diminishes. The same phenomenon was observed for mineral particles: sand in NC, silt in HC.

The general concordance of C_{org}, C_{tot} and N_{tot} in most statistical analyses makes our results reliable as two different methods were used to estimate these variables.

Nested hierarchical ANOVA detected a spatial pattern mainly in NC and NS, and to a smaller extent in HC during autumn. This was further confirmed and clarified by the correlograms (Table 2.6): NC was characterised by a gradient following the slope, NS by a gradient perpendicular to the path and a big patch in the other direction. This patch corresponds to the stump observed beside the trench in May. In HC and HS, directional patterns could not be determined. This could be due to the restricted number of samples, and also to the choice of axes: if a gradient had been present in another direction, it could not have been detected.

We cannot give a simple comprehensive answer to the question of the difference in the spatial pattern of organic matter between deep soil and caves, as both caves were so different. We could hypothesise that sediment accumulations near the cave entrance induce a spatial pattern similar to that found in deep soil, with big vegetal debris analogous to tree roots, and then the size of organic matter patches would diminish the farther they were from the entrance. This was illustrated by the smaller autocorrelation extent in HC than in NC.

Mite density

Mite density CV were higher than organic matter CV. This has two probable explanations. The main factor is of course aggregation. But the mite extraction method, namely the Berlese-Tullgren funnels, is not 100% efficient. André et al. (2002) calculated that differences in extraction efficiency artificially raised the variance-to-mean aggregation index, and thus the CV. The higher CV in caves are probably mainly linked to the lower mean mite density in caves than in soils.

Nested hierarchical ANOVA detected more spatial patterns than correlograms: NS (November) and HC (May) did not produce a significant correlogram, probably because the data set was far larger for the correlograms (50 samples instead of 16 per sampling set). We cannot establish if these spatial patterns really existed, as the ANOVA method did not allow significance testing of the global spatial pattern.

Gradient in NC did not follow the slope. The absence of significant correlation in the smaller distance classes in NC could be explained by the random sampling design used in caves, making less frequent the number of samples separated by a small distance. Indeed, the first lag-distance class

superior limit is 16 cm instead of 6 for soil samplings. Directional correlogram in NS suggested a 40-cm wide periodic structure in the Y direction, which is the one near the stump. This periodic structure could be interpreted as patches of mites every 40 cm (Legendre and Fortin 1989).

Comparison of organic matter and mite spatial distribution

The most obvious way of testing a relation between mites and organic matter (o.m.) is a simple correlation. It proved to be significant in soils but not in caves. We could conclude that o.m. is a limiting factor in soils but not in caves.

If we take a closer look at spatial distribution patterns of mite density and o.m. (Table 2.6), we see that they sometimes match and sometimes do not. Maybe they match in HS (gradient type of unknown direction) and partially match in NS, axis Y (patchy distribution but the size of the patches seems to differ). They do not match in ES, where there is a very clear gradient of mite density but no o.m. spatial structure, in NS axis X (o.m. gradient but no mite density gradient), in NC (gradient in both cases but in different directions) and in HC (potential gradient and patchy structure for o.m. but no mite density structure).

At the beginning of this study, we expected to find a clear convergence of mite density and organic matter spatial patterns, not only because of the direct effects of o.m. as food or support of food for mites, but also because o.m. content is usually strongly correlated with other properties (pH, porosity, etc.), at least within soils. The convergence is not so strong in soil, and does not appear to exist in caves. Differences between both ecosystems hint at the mechanism that might be at work: the higher mobility of mites in caves could obscure spatial patterns. In soils, in addition to environmental

factors including o.m. content, biotic factors such as reproduction, predation or competition probably have an impact on the spatial distribution of mites.

Mite species composition

Canonical correspondence analysis revealed no clear relationship between species composition and organic matter content at the local scale.

Mantel correlograms were significant only in soils. This could arise in two ways. On the one hand, there could be an environmental gradient in soils and not in caves, and mites species could follow this gradient in any habitat. But we know that there is a gradient following the slope in NC, which invalidates this possibility. On the other hand, the reduced mobility of individuals in soils compared to caves, where mites could walk on the surface of sediments, may account for this.

Comparison of spatial analysis methods

Variance-to-mean coefficient proved to be useless: variance could be calculated roughly as a geometric transformation of the mean.

Nested hierarchical ANOVA showed low variance values for small distances when a clear spatial pattern was present and thus allowed identifying sites with autocorrelated data. However, correlograms have the great advantage of being statistically testable and can clarify the kind of spatial pattern: gradient, big or small patches. This is consequently the method that provides the most information among the three tested methods.

Conclusion

The testing of different methods already used in ecological studies to describe the spatial structure of animals showed that the variance-to-mean

aggregation coefficient is useless as it can be predicted from the mean density, and that the Moran's I correlograms provide more information than a hierarchical nested ANOVA method.

Organic carbon spatial distribution is not necessarily different in caves than in soils, as caves seem to be very diverse in this respect. However, the difference in the amount of space available in caves compared to that in the tortuous pores of soil is a major structuring factor for mites: the higher mobility in caves obscured spatial patterns. In soils, organic matter and/or correlated environmental variables influence the spatial distribution of mites, but other factors, such as reproduction, predation and competition, may also be part of the equation.