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Local variations of ecosystem functions in Mediterranean evergreen oak woodland

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Summary — The spatial variation of ecosystem function was studied in a *Quercus ilex* coppice growing on hard limestone with low soil water availability. Spatial structures obtained from data on i) leaf area index, ii) leaf litterfall, and iii) leaf litter decay rate were compared. All these variables were sampled on 26 points located within a 30 x 30 m plot. Mean average leaf litterfall over 10 years (1984–1993) was 254 $g.m^{-2}$. For each year, the semivariograms of leaf litterfall have been fitted using a spherical model. The values of the range parameter (indicating the limit of the spatial dependence) ranged from 6.4 to 10.3 m, very close to the value (9.2 m) of the range parameter obtained when fitting the semivariogram of mean leaf litterfall over 10 years. This result indicates the temporal persistence of the spatial pattern of leaf litterfall. The leaf area index (LAI) was estimated at the same points with a plant canopy analyzer. The mean value was 2.96 ± 0.30. The limit of spatial dependence for LAI was very close to that obtained for leaf litterfall (range = 8.5 m). The litter decomposition pattern was obtained through analysis of litter samples taken at the same points. The percentage of ash-free litter mass remaining (LMR) estimated using near-infrared reflectance spectroscopy indicates the stage of decomposition. It decreased strongly between the surface (mean value 85.6%) and the subsurface layers (mean value 63.4%). The two semivariograms can be described by spherical models, the sill being reached at a range of 21.4 and 18.7 m for the surface and subsurface layers, respectively. The two variables directly related to the structure of the canopy (LAI and leaf litterfall) exhibited close spatial dependence and differed from the soil process-related variables (stage of decomposition) whose ranges were approximately double. These geostatistical analyses show promise for use in developing hypotheses concerning the spatial scale of process–pattern interactions.

***Quercus ilex* / geostatistics / decomposition / leaf area index / litterfall / local variation**

Résumé — Variations locales du fonctionnement d'un taillis de chêne vert. *Les variations locales de paramètres structuraux et fonctionnels ont été estimées pour un taillis de* Quercus ilex *se développant sur karst en climat méditerranéen. Les structures spatiales de i) l'indice foliaire, ii) la chute de litière des feuilles, et iii) les taux de décomposition des litières ont été identifiées par une analyse géostatistique. Ces paramètres ont été mesurées sur 26 points d'échantillonnage répartis dans une placette de 30 x 30 m. Les chutes de litière ont été collectées pendant 10 années (1984–1993) autorisant la comparaison des structures spatiales obtenues pour chaque année. L'ajustement annuel des chutes de litières de* *feuilles à un modèle sphérique donne des valeurs de la portée du semi-variogramme (indiquant la limite de dépendance spatiale) comprises entre 6,4 et 10,3 m. Ces valeurs sont très proches de celle (9,2 m) calculée à partir de la moyenne des chutes de litières pour la période 1984–1993. Ce résultat montre la persistance du patron spatial de chute de litières. L'indice foliaire moyen de la parcelle était de 2,96 (± 0,3). La limite de dépendance spatiale de cette variable est de 8,5 m, très proche de celle obtenue pour la chute de litière. Les taux de décomposition des litières sur les mêmes points d'échantillonnage, exprimés en pourcentage restant de la matière organique initiale, ont été estimés par spectroscopie proche infrarouge. Ces taux décroissent fortement entre l'horizon de surface (valeur moyenne 85,6%) et l'horizon immédiatement sous-jacent (valeur moyenne 63,4 %). Les portées des semi-variogrammes obtenus sont de 21,4 m et 18,7 m pour ces deux horizons. Les deux paramètres directement reliés à la structure du taillis (indice foliaire et chute de litière) présentent des structures spatiales très proches. Elles diffèrent fortement de celles des paramètres décrivant des processus édaphiques. L'approche géostatistique employée permet ainsi de développer des hypothèses relatives à l'analyse spatiale des interactions entre patrons et processus écologiques.*

tailis /* Quercus ilex */ géostatistique / décomposition / indice foliaire / litière / variabilité locale

INTRODUCTION

As emphasized by Robertson et al (1993), spatial heterogeneity of soil resources at local scale can have important consequences for both community structure and ecosystem processes. Undestanding how litter decomposition patterns are related to other functional processes in a given ecosystem can help determine the appropriate scale to study spatial dependence of ecological processes. The local variability of soil resources and biological parameters can be comprehensively quantified using the geostatistical approach (Journel and Huijbregts, 1978; Webster, 1985; Rossi et al, 1992) based on the theory of regionalized variables (Matheron, 1965).

This approach has been widely developed for the study of soil properties in agricultural sites (Trangmaar et al, 1985; Webster, 1985; Webster and Oliver, 1990), in old-field and disturbed sites (Robertson et al, 1988, 1993), in very discontinuous ecosystems (Jackson and Caldwell, 1993) and to a lesser extent in forest ecosystems (Grier and McColl, 1971; van Waesemel and Veer, 1992). Most of these studies concerned physical and chemical properties (mineralogy, pH, nutrient content, etc) more than biological ones. Van Waesemel and Veer (1992) studied local variation of biological process-related variables such as organic matter accumulation and litter decomposition in six Mediterranean-type forests in Tuscany. They showed that the spatial variation in the amount of organic matter at the field scale (< 50 m) was considerable, and related to the type of vegetation. Nevertheless, for each plot, they did not consider the associated variability of canopy parameters (height, leaf area index, etc) and therefore can make no conclusions about the similarity of spatial patterns of vegetation and soil variables.

No studies have been conducted at local scales in forest ecosystems to address this question and very few attempts have been made to a simultaneous study of spatial variability of structural parameters of the canopy. The purpose of this paper is to compare the spatial patterns of leaf area index, leaf litterfall and litter decomposition stage in a holm oak (*Quercus ilex* L) coppice stand.

MATERIALS AND METHODS

Study area

The study site is located 35 km NW of Montpellier (southern France) in the Puéchabon State

Forest (3°35'50"E, 43°44'30"N). This forest is located on hard Jurassic limestone. Because of the large amount of rocks and stones in the soil profile, available soil water, cumulated over a 5 m depth, does not exceed 150 mm. Mean annual rainfall and mean annual air temperature over the 1984–1992 period were 778 mm and 13.4 °C, respectively. The Puéchabon State Forest has been managed as a coppice for many centuries and the last clearcut was performed in 1942 (see detailed description of the vegetation in Floret et al, 1989). The coppice stand was thus 41 years old at the beginning of the study in 1983. Mean tree height of *Q ilex* was about 4.5 m, stem density was 977 ± 71 ha^{-1} (diameter at breast height [DBH] > 7.5 cm) and 10 316 ± 616 ha^{-1} (DBH > 1 cm) (Cartan-Son et al, 1992).

Litter production

Litter was collected at 26 points (area of each collector 0.141 m^2) located within a 30 x 30 m plot since 1984 (fig 2). The frequency of collection was variable according to the phenology of the trees (approximately every month during spring and summer, and every second month during autumn and winter). The collected litter was sorted into leaves, flowers, twigs and acorns, oven-dried at 70 °C for 72 h, and weighed. Only leaf litter is considered in this paper.

Collection of litter layer and analysis of decomposition stage

Collection of litter layer occurred in June 1993 at the 26 points. Two layers were distinguished: the first with intact leaves, corresponding to the first centimeter (surface layer); the second with fragmented leaves and fine organic matter was about 2 cm thick (subsurface layer). All samples were dried in a ventilated oven at 60 °C until constant weight, ground in a cyclone mill through 1-mm mesh, and scanned with a near-infrared reflectance spectrophotometer (NIRSystems 6500). The stage of decomposition of leaf litter expressed as the percentage of ash-free litter mass remaining (LMR) was predicted following a procedure described by Joffre et al (1992) and Gillon et al (1993).

LAI measurements

Leaf area index (LAI) was estimated with the LI-COR LAI-2000 plant canopy analyser (LI-COR Inc, Lincoln, NE, USA). This instrument measures the gap fraction of the canopy based on diffuse blue light attenuation at five zenith angles simultaneously. Detailed description of theory and inversion method for LAI-2000 sensor can be found in Welles and Norman (1991). Measurements were made at each of the 26 litter collector locations. In this coppice, reference readings of sky brightness could be obtained quickly in sufficient large clearings nearby. Because direct sunlight on the canopy causes errors exceding 30% in the LAI-2000 measurements, we collected data on cloudy days during July 1993.

Statistical analysis

The spatial distribution of leaf litter, LAI and decomposition stage of forest floor was investigated using a geostatistical analysis. In its simplest form, this procedure involved a two-step process: i) defining the semivariogram, that is, the degree of autocorrelation among the data, and ii) interpolating values between measured points based on the degree of autocorrelation encountered (see Webster and Oliver 1990 for a comprehensive account). The basic assumption of geostatistical analysis of spatial dependence is that the difference in value of a regionalized variable observed at two positions depends only on the distance between sample points and their orientation. Semivariance γ (h) is defined as half the expected squared difference between sample values z separated by a given distance h:

$$2\gamma(h) = E[z(x_i) - z(x_i + h)]^2$$

The semivariance at a given lag h is estimated as the average of the squared differences between all observations separated by the lag:

$$\hat{\gamma}(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} E[z(x_i) - z(x_i + h)]^2$$

where N(h) is the number of pairs of observations at lag h.

The semivariogram is usually displayed as a plot of semivariance against distance. The shape of a semivariogram may take many forms, which

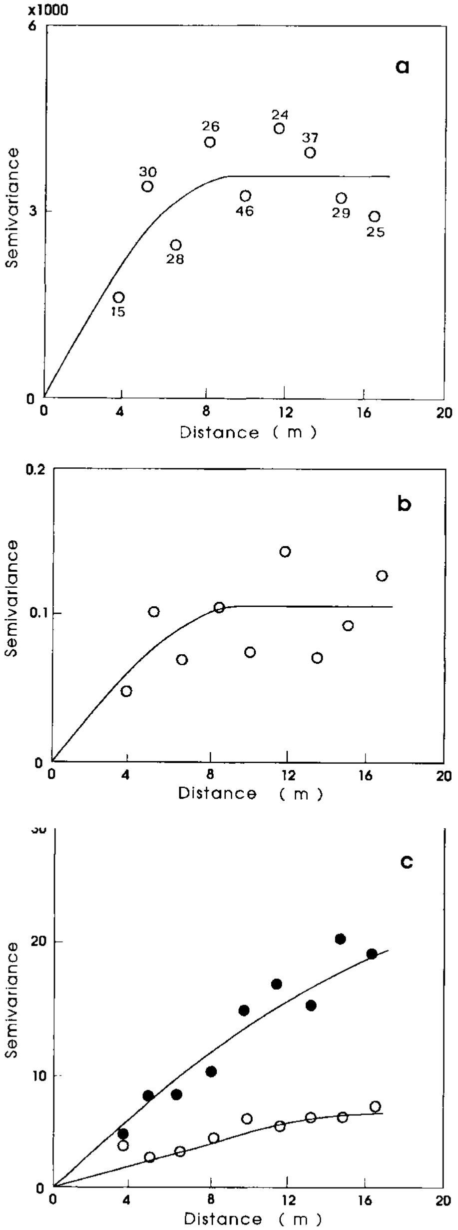


Fig 1. Semivariograms of mean annual leaf litterfall (**a**), leaf area index (LAI) (**b**) and LMR (ash-free litter mass remaining expressed in % of original organic matter) of surface (O) and subsurface (●) layers (**c**). The number of pairs of points considered in each variogram lag class is indicated in **a**.

can be related to several models. The experimental semivariograms obtained for our set of data have been fitted to bounded spherical models:

$$\gamma(h) = c\left(\frac{3h}{2a} - \frac{1h^3}{2a^3}\right) \text{ when } h \le a$$

$\gamma(h) = c$ when $h \ge a$

the semivariance rise to a more or less constant value (the sill c) after a given range a. The value of $\gamma(h)$ for $h = 0$ is not always the origin: in some cases a spatially independent variance may exist (nugget variance). For the decomposition stage, our data were also fitted to a bounded linear model:

$$\gamma(h) = c\left(\frac{h}{a}\right) \text{ for } h \le a$$

$\gamma(h) = c$ for $h \ge a$

Estimation of these parameters were obtained using the GEOPACK software (Yates and Yates, 1989). Calculations were made considering 10 lag classes using a lag spacing of 1.8 m. Using these parameters, the number of pairs of points considered in each variogram lag class is indicated in figure 1. The second step uses semivariogram parameters to interpolate values for points not measured using kriging algorithms (Trangmar et al, 1985). For all variables under study, values for exact points on a grid within the sampling unit are estimated using punctual kriging. Maps were based on these kriged data provided by GEOPACK and obtained using the SURFER package (Keckler, 1994).

RESULTS

Within the site, spatial variations of the four sampled variables (LAI, annual leaf litterfall, LMR of surface and subsurface layers) differed greatly (table I). Coefficients of variation (calculated as standard deviation/mean) ranged from 10% for LAI and 19% for leaf litterfall to about 4% for the LMR of the two considered layers.

Mean average leaf litterfall over 10 years (1984–1993) was 254 g.m^{-2} with a standard deviation of 48 g.m^{-2}. Interannual vari-

Table I. Mean values and standard deviations (SD) of leaf area index (LAI), mean annual leaf litterfall (g.m^{-2}) and litter mass remaining (LMR expressed in %) of surface and subsurface layers obtained at the Puéchabon site ($n = 26$).

	LAI	*Annual leaf litterfall*[a]	*LMR*	
			Surface layer	*Subsurface layer*
Mean	2.96	254	85.6	63.4
SD	0.30	48	3.7	2.4
Minimum	2.33	114	79.4	59.3
Maximum	3.61	324	93.6	69.2

[a] Mean annual litterfall was calculated over the period 1984–1993.

ability was very high, with annual values ranging between 104 g.m^{-2} in 1988 to 497 g.m^{-2} in 1987 (table II). Spatial variations within the plot led to high standard deviations. The coefficient of variation calculated for each year ranged from a minimum of 21 in 1992 to a maximum of 33 in 88 with a mean of 26.5. For each year, the semivariogram of leaf litterfall have been fitted using the spherical model. Table III shows that the values of the range parameter (indicating the limit of the spatial dependence) of fitted semivariograms did not display large variations among years. The slope of the linear regression between annual leaf litterfall and range parameter was not significantly different from zero, and the intercept value was 9.4 m (95% confidence interval 7.2 to 11.6), very close to the value (9.2) of the range parameter obtained when fitting the semivariogram of mean leaf litterfall over 10 years (fig 1). Such an absence of significant relationships between litter production and spatial distribution indicates that the spatial pattern of leaf litterfall was time-persistent. Using the spherical variogram of mean annual leaf litterfall, a contour map of kriged estimates of annual leaf litterfall in the studied plot was obtained (fig 2).

Within the plot, LAI ranged between 2.3 to 3.6 with a mean value of 2.96 (SD = 0.30). The experimental semivariogram of LAI increases until it reaches the sill variance at about 8.5 m (fig 1). This range is similar to that obtained with mean annual leaf litterfall. A kriged map of LAI is also shown (fig 3).

Table II. Annual values of leaf litterfall (g.m^{-2}) from 1984 to 1993 at the Puéchabon site ($n = 26$).

Leaf litterfall	*1984*	*1985*	*1986*	*1987*	*1988*	*1989*	*1990*	*1991*	*1992*	*1993*
Mean	228	423	179	497	104	203	282	216	220	186
SD	62	105	41	127	34	60	90	49	46	50
Minimum	68	146	68	229	51	82	100	111	90	89
Maximum	325	619	266	722	286	348	521	320	351	268

Table III. Values of the range parameter (expressed in m) of the spherical models fitted to the variograms of annual leaf litterfall at Puéchabon from 1984 to 1993.

1984	*1985*	*1986*	*1987*	*1988*	*1989*	*1990*	*1991*	*1992*	*1993*	*Average*
10.2	8.8	8.2	6.4	7.9	7.7	9.9	8.9	10.3	8.4	9.2

The stage of decomposition defined as the percent of LMR decreased strongly between the surface and the subsurface layers (table I). Experimental semivariograms for LMR of these two layers are given in figure 1. Semivariances were considerably higher for the surface layer. The two semivariograms could be fitted to spherical models, the sill being reached at a range of 21.4 and 18.7 m for the surface and subsurface layers, respectively. In this case, however, the fitted values of ranges showed large confidence intervals and were not significantly different. These semivariograms could also be related to bounded linear models obtaining ranges of 15.8 and 16.8 m for the two layers, but fitting to spherical models led to a better reduced sum of squares. Figures 4 and 5 show kriged maps of LMR for the two sampled layers.

DISCUSSION

The mean value of LAI on the studied site was in agreement with the range of values obtained in oak coppices of southern France (Debussche et al, 1987; Pinault, 1992). It corresponded to levels reached in stands growing with a very low soil water avaibility. In more mesic stands, LAI of mature

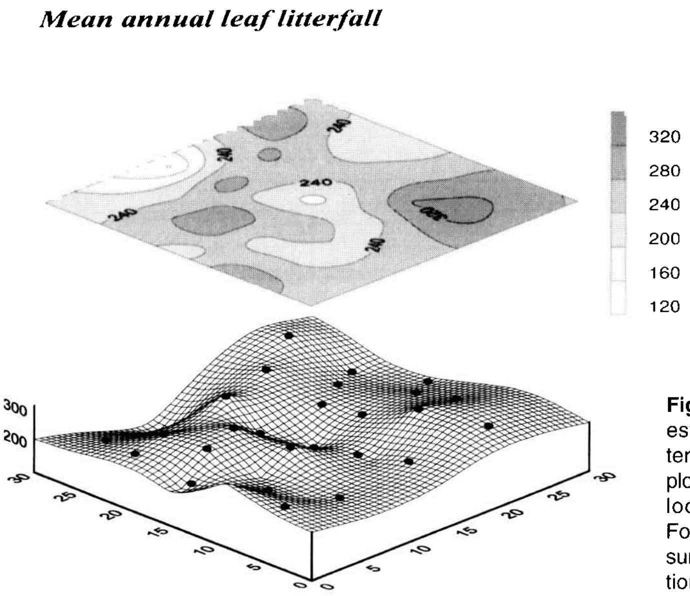
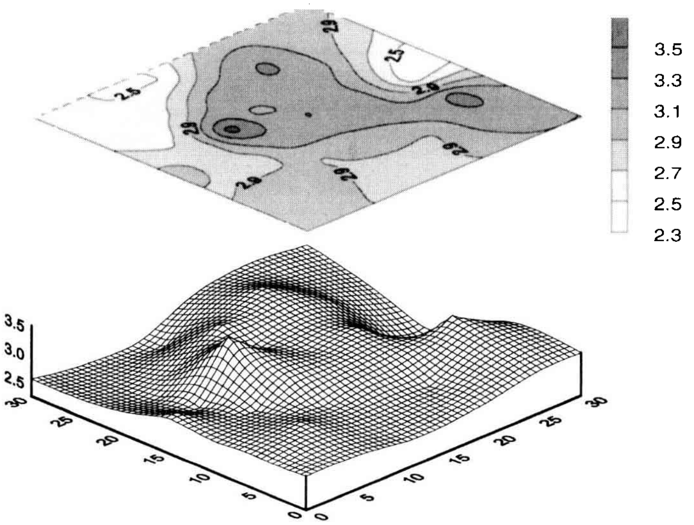

Mean annual leaf litterfall

Fig 2. Contour map of kriged estimates of annual leaf litterfall (g.m^{-2}) in a 30 x 30 m plot of a *Quercus ilex* coppice located in the Puéchabon Forest. Dotted points on the surface plot indicate the locations of the litter collectors.



Leaf area index

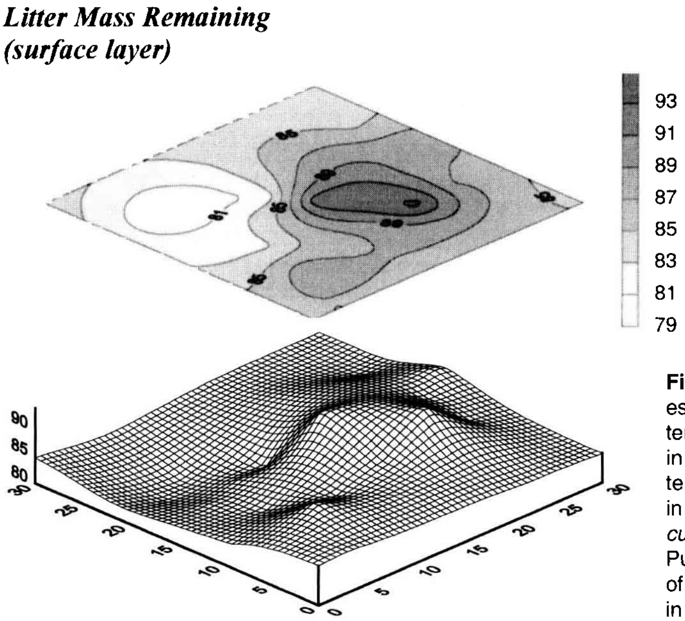
Fig 3. Contour map of kriged estimates of leaf area index (LAI) in a 30 x 30 m plot of a *Quercus ilex* coppice located in the Puéchabon Forest. Locations of measurements were the same as in figure 2.

coppices of *Q ilex* could reach values above 4 (Eckart et al, 1977). The mean annual leaf litterfall (254 g.m^{-2}) at the Puechabon site fill in the range of the Mediterranean *Q ilex* coppices (244 g.m^{-2} at Le Rouquet and 273 g.m^{-2} at La Madeleine; Lossaint and Rapp, 1971; 250 g.m^{-2} and 290 g.m^{-2} in southern Tuscany; van Wesemael and Veer, 1992).

All variogram models present no nugget variance. Only for leaf litterfall, a very low nugget variance (230 compared to the sill variance of 3 600) could be included in the model without changing the effectiveness of the fitting. The four studied variables should be regarded as continuous variables and as emphasized by Webster and Oliver (1990), in this case, "the nugget variance may arise partly from measurement error, though this is usually small in relation to the spatial variation."

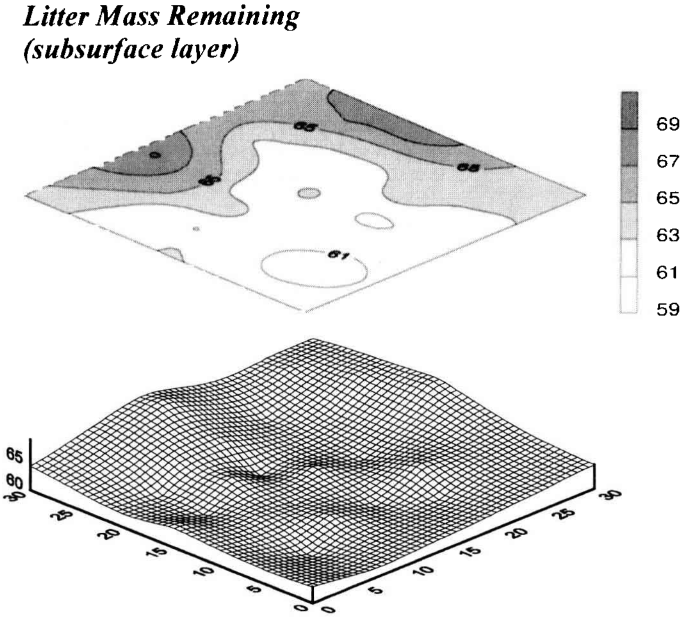
The two variables closely related to the structure of the canopy (LAI and leaf litterfall) exhibited close spatial dependence and differed from the two soil process-related variables (stage of decomposition) whose ranges were approximately double. LAI and mean annual leaf litterfall exhibited close spatial patterns with a range parameter of about 8 m. Lacaze et al (1984) measured radiation interception and structure of foliage every 1.25 m along two 80 m transects in a very similar holm oak coppice near Montpellier. They observed a range of about 4 m for radiation measurements and foliage thickness under the canopy. This corresponds to the mean diameters of the stools. The differences in ranges between the two studies may be partly attributed to differences in the sampling procedures. Indeed, in our study, the number of sampled points separated by less than 4 m was too small (8) to be considered in the variogram modelization, and spatially dependent variation that occurs over distances much smaller than the shortest sampling interval could not be identified.

The spatial patterns of decomposition stage (LMR) are totally different, with a distance of spatial dependence greater than



Litter Mass Remaining (surface layer)

Fig 4. Contour map of kriged estimates of LMR (ash-free litter mass remaining expressed in % of original organic matter) of the surface litter layer in a 30 x 30 m plot of a *Quercus ilex* coppice located in the Puéchabon Forest. Locations of sampling were the same as in figure 2.



Litter Mass Remaining (subsurface layer)

Fig 5. Contour map of kriged estimates of LMR (ash-free litter mass remaining expressed in % of original organic matter) of the litter subsurface layer in a 30 x 30 m plot of a *Quercus ilex* coppice located in the Puéchabon Forest. Locations of sampling were the same as in figure 2.

15 m, that is, approximately twice the values obtained with LAI and leaf litterfall. This could be due to the buffering effect of canopies and soils on the functional process of decomposition. In oak forests of southern Tuscany, van Waesemel and Veer (1992) showed that the spatial variations of organic matter accumulation in organic horizons are smaller at sites with a closed tree layer than at sites with a relatively open tree layer and concluded that "this could be attributed to a better protection of the organic-rich layer against local disturbance under a closed canopy." Nevertheless, as they used a quantitative criteria (amount of organic matter) rather than a qualitative one (LMR), they did not observe a clear trend in spatial patterns when comparing ectorganic and endorganic horizons.

The concept of environmental patterning as defined by Addicott et al (1987), that is, the nonuniform spatial and temporal distribution of resources and abiotic conditions that influence species interactions, makes it possible to express determined spatial variation of ecological processes at different scales. However, there are no general methods to determine such patterns. The use of geostatistical procedures in ecological studies brings novel tools to the interpretation of joint spatial dependence between organisms, functional processes and environment (Rossi et al, 1992). The semivariograms reveal the level of variation of an independent variable as a function of scale and shows the spatial scales at which vegetation and soil can be considered homogeneous. This has important implications for ecological theories and sampling procedures. By examining the semivariogram, we have shown that this technique can help formulate hypotheses concerning the spatial scale of process–pattern interactions. This should prove extremely useful for developing scaled studies to correlate processes operating at different spatial hierarchies.

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