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Research article

Patterns of organisation in changing landscapes: implications for the management of biodiversity

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Abstract

Despite the widespread need to predict and assess the effects of landscape change on biodiversity, the array of tools available for this purpose is still limited. Species' patterns and human activities such as land use respond to the environment on their own suite of scales in space and time so that their interactions are overlapping but complex. It is difficult, therefore, to relate biodiversity to patterns described solely by metric assessments of spatial heterogeneity. In this methodological paper, we therefore propose consideration of two measures of landscape organisation which focus on the relationships between different properties of the landscape system (e.g., soil type distribution, land use distribution), rather than on their description alone. Alpha organisation measures the degree to which the distribution of features such as land use deviate from a random distribution, measured here as fractal dimension from the semivariogram of a variable describing agricultural intensity. Beta organisation measures the degree of deviation by which the spatial distribution of one property (e.g., human land use) is independent of the distribution of another (e.g., soil type) and was derived from relative mutual information (= redundancy) between the 'agricultural land use' and 'soil types'. These measures are illustrated in a rural landscape of the lower Seine valley, at two scales of observation, and at two dates (1963 and 1999) separated by substantial agricultural change due the European Common Agricultural Policy (= CAP). The results show that analysis of patterns of agricultural activity across a range of spatial scales (α organisation), or across the pattern of spatial variation in soil types (β organisation) reveal how the agricultural actors respond to environmental constraints at different scales. This organisation concept relates to the metastability of landscape systems, and suggest possible correlation between high values of landscape organisation and high levels in biodiversity.

Introduction

Disturbances due to human land uses have a role at least as great as that of natural disturbances in shaping many landscapes (Baker 1995). There are clear consequences for ecological processes (Godron and Forman 1983; Turner et al. 1991; Wiens et al. 1993b), as changing landscape patterns influence fluxes of matter, energy and species at the landscape scale (Pickett and Cadenasso 1995; Vitousek et al. 1997). Nutrient cycling (Dale 1997), hydrology (Girel 1994), energy partitioning (Wylie and Currie 1993), and the availability of habitat for species (Law and Dickman 1998; Morris 1992; White et al. 1997) are all affected.

Despite potential adverse effects, some long-term human disturbance regimes have promoted biodiversity. In western Europe, traditional low intensity agriculture often promotes high levels of diversity, or favours site specific rare taxa (Robinson and Sutherland 2002). Hot spots of biodiversity occur, for example, in grazed chalk grasslands throughout northern Europe (Dutoit and Alard 1996; Gigon and Leutert 1996), and in many wetlands (Bornette et al. 1998; Hughes 1995). Recently, however, changes in agricultural policies (CAP of 1962), and intensification have altered subtle equilibria between biota and patterns of use in farmed landscapes even on areas with strong constraints to development (dry or water logged soils, strong slopes, infertile soils).

Faced with the task of managing landscapes for biodiversity, there is increasing interest in understanding the potential impacts of such agricultural changes through their influence on landscape pattern (White et al. 1997; Noss 2000; Levin 1992; Baudry et al., this issue). Landscape patterns are the superimposition of spatial heterogeneity caused by both natural and anthropogenic agents (e.g., human land use). Spatial heterogeneity is considered here as the variability of system properties in space (Kolasa and Rollo 1991; Li and Reynolds 1995). This heterogeneity is deemed to be an essential element of the environmental filters which explain the occurrence and distribution of species from local to global scales (Eriksson 1993). Landscape patterns are thus a key element in understanding biodiversity.

Many tools have been proposed to characterise spatial heterogeneity (Gustafson 1998; Cullinan and Thomas 1992; McGarigal and Marks 1995). But, as each species, including humans, respond to the environment on its own suite of scales in space and time (Kolasa and Rollo 1991; Wiens et al. 1993a), the spatial pattern of their activities (e.g., species movement, human land use, . . .) is very complex and interwoven. It is thus a difficult task to relate patterns described by such metrics to biodiversity as a whole (O'Neill et al. 1996; McGarigal and Marks 1995). In an attempt to simplify this issue, classical metrics measure human activity patterns on the one hand (e.g., index of land use diversity, index of connectivity, . . .) and patterns of biodiversity and species activities in the landscape on the other (e.g., index of species diversity, dispersal rate).

The systems approach offers opportunities to address these issues (Figure 1). The activities of species and people are considered as properties of the ecosystem. The variability of these system properties in space (whether continuous or discontinuous) account for the spatial patterns observed in landscapes. Comparison within and between the layers of spatially explicit information on the variability of these properties (e.g., human land use, soil types, . . .), describe the organisation of the landscape system (Figure 1). Organisation measures, unlike classical indices, do not aim at providing a synthetic value of the properties of the system (e.g., indices of land use diversity, land use richness), but aim instead at providing a measure of the relationships between them (Levin 1999).

Quantifying the amount of information that one propriety of a system, provides on another element, is one of the most obvious ways that system organisation can be assessed (Kolasa and Pickett 1989). In this context, an agricultural landscape system can be described through different properties, for example agricultural intensity, agricultural land use, vegetation distribution and soil types. Each property, in turn, may have different expressions and different spatial distributions. Assessing the organisation of such a system can be achieved by quantifying the information derived either by a particular expression of a given property on a subsequent expression (in time or space) of the same property (hereafter named α organisation), or by one property on another property (hereafter named β organisation). These parameters are conceptually equivalent to measures of alpha (richness) and beta (turnover) components of species diversity. Alpha organisation provides information on the scales of organisation of the studied property in time (as a series of expressions in time) or space (series of expressions with distance).

This methodological paper aims at assessing the value of organisation measures for understanding the impact of human activities on landscape patterns. We propose the use of two measures of landscape organisation that result in the spatial distribution of agricultural activities are organised. We determined (1) how these agricultural activities are organised spatially in the landscape, (2) the scales at which agricultural activities are organised in the landscape. The measures are tested at two different scales of observation and their potential uses discussed. In particular, we formulate a hypothesis about the potential impact of changes in the scale and organisation of agricultural activities on biodiversity. Overall, this paper aims at contributing a generic method that allows the parametrisation of the potential effects of agricultural change on landscape patterns.

Study Site

The study area is a meander of the Seine river 20 km west of Rouen, France. The Seine valley illustrates most of the changes in rural areas in western Europe.

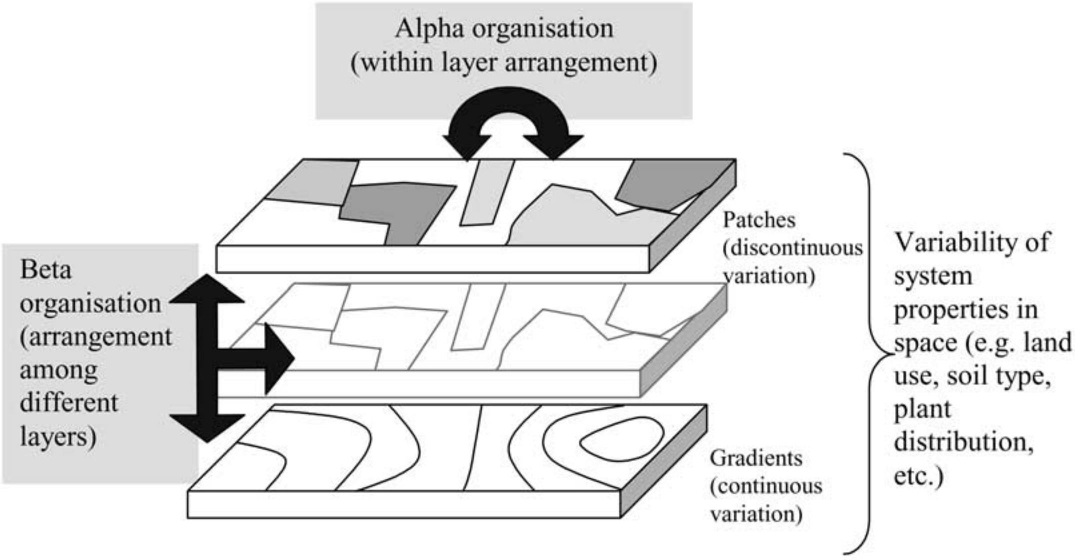

Figure 1. A systemic approach to spatial patterns in landscapes. Comparison between the spatially explicit layers of information can inform on relationships within one layer (e.g., spatial arrangement of land use patches) also called alpha organisation, or on relationships between different layers (e.g., relation between soil type distribution and land use distribution) also called beta organisation.

The strong environmental constraints of these lands on agricultural land use have increasingly been overcome. These lands, essentially disturbed by river flooding until the middle of the 19th century, have been drained to secure navigation and provide agricultural land. The pattern imposed by traditional agriculture is now shifting again with the recent Commons Agricultural Policies (CAP) and technical changes that led to intensification. This site is representative of local rural areas in its diversity, its changes and its peri-urban constraints (Alard and Poudevigne 1999; Poudevigne et al. 1997). The whole area presents as a landscape mosaic dominated by a wide range of grassland habitats from wetlands to dry chalk grasslands. Two nested scales of observation were investigated (Figure 2). The global scale includes what we refer to as the valley system and comprises the river valley in its broad sense from the plateau to the river. The local scale includes what we refer to as the wetland system comprising the former alluvial floodplain of the Seine river.

Methods

Among the many possibilities (Antrop and Van Eetvelde 2000; De Pablo et al. 1988; Johnson et al. 2001; Phipps 1981; Ricotta 2000), we chose semivariance with distance and fractal dimension to measure α organisation, and relative mutual information to measure β organisation. Considering the focus of this paper, we chose the diversity of states of the variable 'agricultural intensity' to measure the α organisation, and the relationships between the variables 'agricultural land use' and 'soil types' to measure β organisation. Data on each of these variables were collected at different dates to assess potential impacts of agricultural policies between 1963 and 1999, dates that incorporate very marked change and dynamism due to the CAP in Europe generally. Alpha and β organisation were assessed at the two nested scales of observation: valley and wetland scales (Figure 2).

Data collection

Land use data were obtained from aerial photographs at two selected dates of 1963 and 1999. The photographs were scanned and fed into a Geographical Information System (Arc View 3.2; ESRI). Photographs were georeferenced and rectified with the Image Analysis module of Arc View, then analysed and classified into 8 classes (crops, chalk grassland, orchards, buildings and orchards, alluvial forest, poplar plantations, plateau forest, wet grasslands). Validation was performed on a 1 km^2 of the 1999 image by ground truthing through field identification which provided a 87% accuracy (Burrough and McDonnell 1998). This analysis provided us with a numerical map on a 1/25 000 scale of the land uses at the two dates.

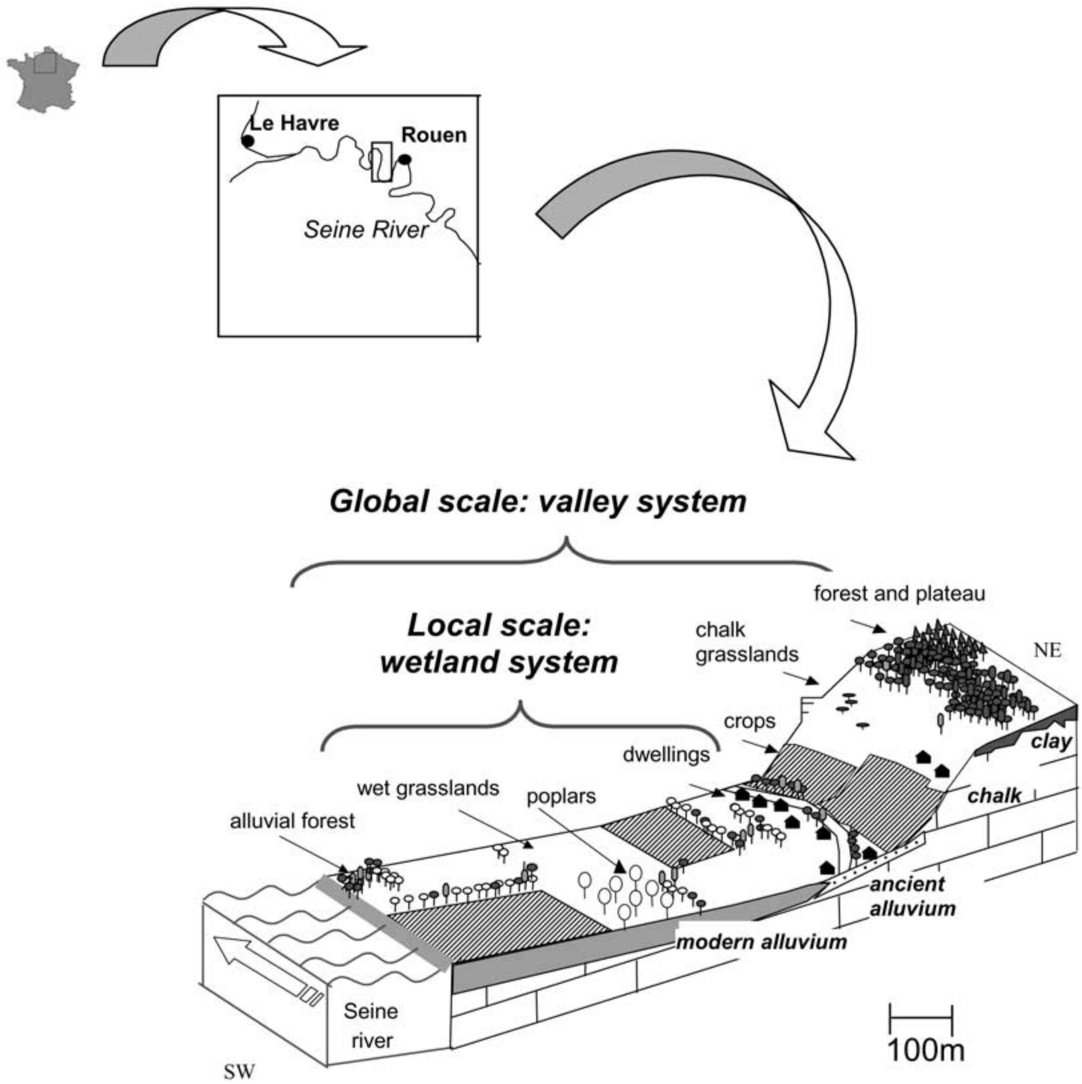

Figure 2. The study area: a meander of the Seine river some 20 km west of Rouen. The transect band represents the main environmental patterns and land uses of the valley. Two levels of observation are described : the local wetland scale and the global valley scale.

The whole map covered an area of 1480 ha incorporating 570 managed land plots, while the wetland area covered 1140 ha and counted 430 managed land plots. Simple cartographic analysis was done (mean land covers, mean land cover changes) within the GIS and historical data were collected (see Poudevigne et al. 1997) to provide insight on the global landscape dynamic trends.

At the coarse resolution of the valley scale, four main soil series were described and defined as soils developed from the same parent material (USDA, 1996). These were soils developed on the clay plateau, soils on the chalk slopes, soils on the ancient alluvial floodplain and soils on the modern wet alluvium. These series were obtained from a local geological map at a 1:50,000 scale (BRGM 1980), a topographic map and a coarse-scale field survey. At the finer scale of the wetland system, a more precise map was produced. Auger holes in the surface soil horizon were described on 35 random sampling points in the wetland area. The map provided through interpolation distinguished soil phases on the modern alluvium series on the basis of 4 measured variables: texture (from sand to clay), hydromorphy (measured through the appearance of Go horizon), depth of organo-mineral horizon, depth of the peat layer if present). Soil phases are superficial horizons of a soil series modified by natural or anthropic processes (USDA, 1996). Both maps were processed within the GIS (Arc View 3.2; ESRI).

The 'agricultural intensity' variable was computed so that its value increased with the level of intensification. Agroecosystems can be arranged according to their degree of intensification, i.e., the temporal intensity of land use and the range of practices applied (Swift et al. 1996). This can be done empirically by classifying land use practices subjectively from 'less' (e.g., extensive grazing by sheep) to the 'more' intensive ones (e.g., tilling of the soil, use of chemicals). Alternatively, intensification may be assessed by calculating an index that takes into account the frequency and intensity of human interventions. We used for this purpose an index modified from Giller et al. (1997) and Decaens and Jiménez (in press; Table 1). The index values were adapted for this case study.

Measuring α organisation in agricultural intensity

Semivariance is a measure of the degree of spatial dependence between samples, and summarises the variance of a variable as a continuous function of scale (Palmer 1988). The semivariance is calculated as the sum of squared differences between all possible pairs of points separated by a chosen distance. The semi-variogram or variogram is a plot of the semivariances at different distances. Analysis of this semi-variogram consists of trying to fit a mathematical function to the semi-variogram values. Among the most common models (Figure 3) are two classes: firstly, bounded models which rise to a more or less constant value called the sill (C + Co) at a given separation distance called the range of spatial dependence (A); secondly, unbounded models where variance appears to increase without limit (Rossi et al. 1992). Bounded models such as the spherical and exponential models (the first being a strictly bounded model while the second can be described as an asymptotically bounded model) generally reveal aggregated spatial structures, while unbounded such as linear models show gradient structure. In bounded models, the range distance is important in distinguishing correlated samples (samples separated by distances closer than the range) from uncorrelated samples (samples separated by distances greater than A). The range thus gives a clue as to the size of the aggregated structures within the landscape. Model curves often intersect the y-axis at a point called the nugget variance (C0). This point represents unexplained variance which can arise from measurement error or microvariability undetected at the sampling scale used. The relative structural variance (C/C+Co) represents the part of the variance that can be attributed to spatial autocorrelation.

A first set of variograms were computed from series of 160 points sampled for agricultural intensity along four transects along an environmental gradient from the forest to the river (Figure 2). The number of samples was chosen to achieve a stable variogram (Burrough and McDonnell 1998). The transects were 300 meters apart, and the points were sampled every 50 m along the transects. This distance of 50 m was chosen in consideration of the mean plot size in this area (an average of 4 ha). The choice and fitting of the theoretical models to the sample variogram was done by the least squares method included in the interactive routine of the Variowin software (Pannatier 1996). The range values were derived from the theoretical model equation. On the variogram, only distances less than two thirds of the mean total transect length (1500 m) are shown, because greater distances are more affected by low sample sizes and spurious properties of the data (Journel and Huijbregts 1978). A second set of variograms were computed from a selection of 90 sampled points located only on the wetlands. Again, only distances less than two thirds of the mean total transect length (900 m) are shown.

We estimated the fractal dimension in agricultural intensity distribution using the relationship between the fractal dimension of a series and the slope of the corresponding log-log semivariogram (Burrough 1981; Palmer 1988). On a double logarithmic scale the slope (m) of a semivariogram is related to the fractal dimension (FD) as FD=(4-m)/2 (Burrough 1981). Fractals have the ability to summarise the heterogeneity of a spatial property of a system in a single value, the fractal dimension, independent of scale (Leduc et al. 1994). In homogeneous systems, the degree of spatial dependence between sampling points is low and the fractal dimension close to 2. In heterogeneous systems, this value is close to 1, since the degree of spatial dependence is strong. Most environmental variables display variability clustered at particular scales (Palmer 1988). Burrough (1981) suggests that the examination of D values might be useful in separating scales of variation that might be result of particular processes. We therefore estimated the fractal dimension of agricultural variability in our landscape at both local and global scales, in order to separate scales of variation in the land use, i.e. distinguish the scales at which agricultural activities are organised. Ob-

Table 1. Calculation of the Index of Agricultural Intensity. This index, modified from Giller et al. (1997) is given by the equation: AI = (MTF+MMP+MPCF+MASR+PBE+MFR+D)/N, where AI is the agricultural intensity index, MTF the mean tillage frequency (per year), MMP the mean motorised practise (per year), MPCF the mean pest control frequency (per year), MASR the mean animal stocking rate (per year), PBE the plant biomass exportation (t/ha/y), D the presence or absence of drainage and N is the total number of variables. Values for each variable were extracted from data of an agricultural field survey performed in 2000 on 38 farms on the meander.

Systems	MTF		MMP		MPCF		MASR		PBE		MFR		D		**AI**
	y^{-1}	MTF	y^{-1}	MMP	y^{-1}	$MPCF$	y^{-1}	$MASR$	$T.ha^{-1}$ y^{-1}	PBE	y^{-1}	MFR	%	D	
Alluvial forest	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00	0	0.00	0	0	**0.00**
Plateau forest	0.00	0.00	0.10	0.02	0.00	0.00	0.00	0.00	7	0.12	0	0.00	0	0	**0.02**
Chalk grassland	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.60	0	0.00	0	0.00	0	0	**0.09**
Poplars	0.05	0.03	2.00	0.33	1.00	0.66	0.00	0.00	0	0.00	15	0.10	1	1	**0.30**
Grassland in orchards in grazing	0.00	0.00	0.00	0.00	1.00	0.66	0.20	0.60	0	0.00	0	0.00	1	1	**0.31**
Grassland in orchard & dwellings	0.00	0.00	0.00	0.00	1.00	0.66	0.33	1.00	0	0.00	50	0.34	1	1	**0.42**
Wet grassland (cut+grazed)	0.20	0.10	6.00	1.00	1.00	0.66	0.33	1.00	20	0.33	100	0.67	1	1	**0.68**
Crops	2.00	1.00	5.00	0.84	1.50	1.00	0.00	0.00	60	1.00	150	1.00	1	1	**0.83**

jects with different fractal dimensions are said to be modelled by different sets of processes (Mandelbroot 1977). We derived these measures in both 1963 and 1999 to see whether we could detect a change in the nature or the scales in the organisation of agricultural activities during this period.

Measuring β organisation in agricultural land use and soil type

As with many old European rural areas, the Seine valley landscape is the result of strong interaction between environmental pattern (variability in space of local natural conditions such as soil types) and agricultural pattern (variability in space of agricultural use of the land) (Poudevigne et al. 1997). The correlation (β organisation) between these two depends on the farming systems, in other words the extent to which agricultural practices have shaped the environment, and the extent to which the natural conditions have constrained agricultural practices. We measured the latter by calculating the conditional mutual information (also called redundancy), (R) between the two variables 'land use' and 'soil types' conditional to knowing 'soil types':

$$R_S(L) = \frac{H(L) + H(S) - H(L.S)}{H(L)} \tag{1}$$

where H(L) is the marginal entropy of land use distribution calculated with the Shannon equation as

$$H(L) = -\Sigma_{(i \text{ land use})} \text{pi. log pi.} \tag{2}$$

with (pi.) the probability of finding land use (i) in the study area, and where H(S) is the marginal entropy of soil types distribution calculated as

$$H(S) = -\Sigma_{(j \text{ soil types})} \text{p.j log p.j} \tag{3}$$

with (p.j) the probability of finding soil type (j) in the study area, and where H(L.S) is the total entropy of the 'landuse' by 'soil types' matrix

$$H(L.S) = -\Sigma_{(i \text{ land use})} [\Sigma_{(j \text{ soil types})} p_{ij} \log p_{ij}] \tag{4}$$

with (p_{ij}) the probability of finding land use (i) on soil type (j) in the study area, At the scale of the valley system, we used the soil series to express the 'soil type' variable, and at the local observation level of the wetland system we used the soil phases. Thus, for a smaller extent of the study area, we employed a finer resolution of soil typology. Redundancy reaches its upper limit value of 1, when all land uses are located according to specific environmental niches, thus achieving the largest co-occurrence between land use and soil type. Redundancy tends to reach zero when land uses are located anywhere.

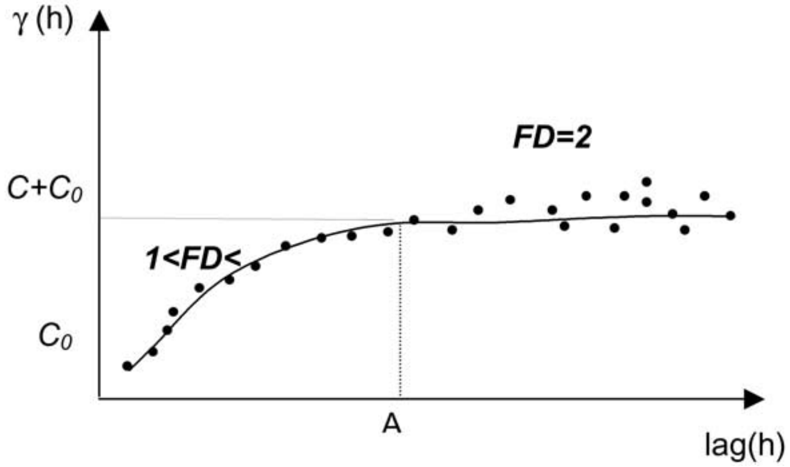

Figure 3. Components of a theoretical semivariogram. (C_0) the nugget variance, (A) the range, the sill ($C + C_0$) and fractal dimension (FD) associated with different phases in the increase of the semi-variance. The lag (h) refers to the various inter-point distances at which we calculated the semi-variance γ(h).

Redundancy measures were calculated using software provided by Phipps (1994), which also provides explicative side calculations such as the contribution of each soil type to total entropy, and niche specificity of each land use. Niche specificity of land uses is a similar concept to niche breath for an organism (Phipps et al. 1986). This value is highest when one land use is only found on a few components of soil types, and lowest when that land use can be found on any component.

Results

Scales in the organisation of agricultural intensity

The variogram on the whole data set of land use in 1963 (160 samples) showed a nested structure accounting for two patterns with distinct ranges (Figure 4a). A spherical model was fitted to the proximal section of the variogram (Co = 0, C = 615, A = 376 m). The distal section of the variogram showed a relatively linear trend in the data. A similar nested structure could be observed for the 1999 data (Figure 4b) so that a spherical model could be fitted to the first part of the variogram (Co = 0, C = 620, A = 275 m, structural variance 100%). The distal section of the 1999 variogram was more difficult to model showing an exponential trend with a range around 900 meters. Both the 1963 and the 1999 semivariograms showed strong spatial structure in the pattern of agricultural intensity. These results show that in 1963 the whole valley could be considered, at a resolution under 900 m, as a globally heterogeneous landscape with aggregate patches of ca. 376 m. By contrast, at the same resolution in 1999, the valley could be considered as a globally homogeneous landscape with aggregated patches of ca. 275 m. These results show that during the 1963–1999 period, increased spatial fragmentation of agricultural activities into smaller and less connected aggregates has led to a homogenisation of the landscape at a global scale. The increase in fractal dimension (higher α organisation) over the same period (from 1.60 to 1.75) confirms the same trend towards global-scale homogenisation. The shift in fractal dimension between those two periods also suggests a change in the scale, or in the nature of the factors which determine agricultural activities in the valley.

The semivariogram from data comprising only the wetland scale (90 points) also showed very distinct spatial structure (Figures 4c and 4d). The semivariograms for both 1963 (Co = 0.03, C = 0.64, A = 397 m, variance of 95.5%) and 1999 (Co = 0.17, C = 1.65, A = 285 m, variance of 90.6%) were described by exponential models although their key parameters differed. In particular, the two wetland semivariograms showed very different range sizes. This indicates that the size of the aggregates within the wetlands have decreased by 28%. Furthermore, the decrease in fractal dimension (lower α organisation) between 1963 and 1999 (from 1.73 to 1.23) also indicated decreasing homogeneity in the wetland system. The data also suggest that the scales of the factors which determine agricultural activities in the wetlands

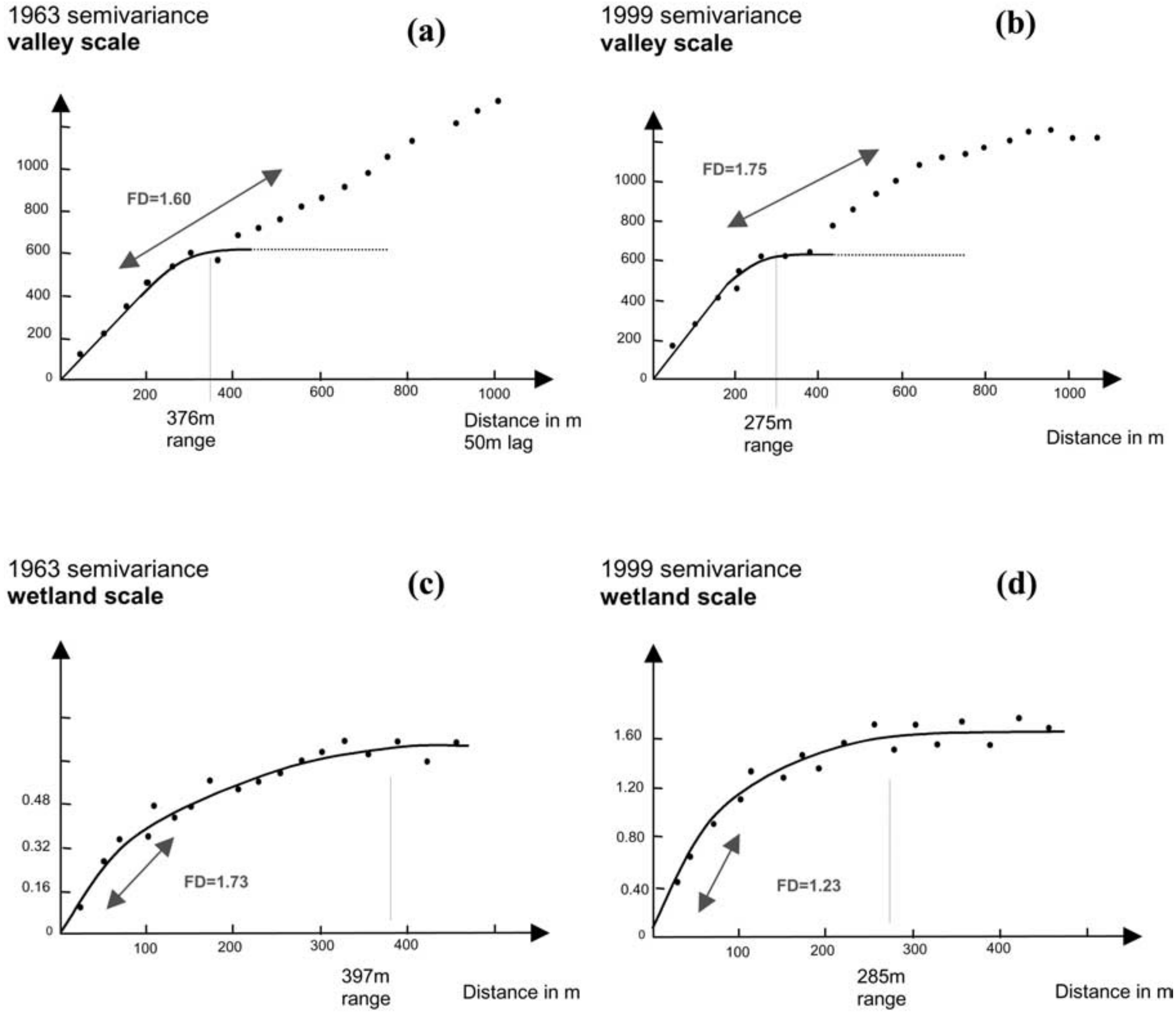

Figure 4. Semi-variograms of agricultural intensity AI (see Table 1 for calculations) at two scales of observation : global valley scale (160 sampling points) and local wetland scale (90 sampling points). The curves represent the fitted theoretical models. Range values are derived from these models.

have changed, with the factors of organisation for agricultural activities larger in 1963 than in1999.

Landscape pattern and the dynamics of the valley at different resolutions

At the valley scale, the superposition by GIS of the data layers accounting for the soil series and the land use pattern revealed a strong spatial redundancy, or in other words a strong organisational relationship between the two. From the plateau to the Seine banks, the landscape was characterised by a sequence of land uses (forest/dry grasslands/crops and habitations/bocage wet grasslands) which closely followed the topography and geology (clay plateau/chalk slopes/ancient alluvium/modern alluvium) (Figure 2). The redundancy was stronger for 1963 (0.51) than for 1999 (0.36), values declining by over 29% between these dates.

The redundancy between 1963 and 1999 reflects quantitative and qualitative changes in the land use mosaic of which some are known to have occurred over this period (Figure 5). Although the wet grasslands on alluvial soils may seem homogeneous at a coarse level of observation, this landscape unit has the particularity of having undergone both intensification and extensification trajectories between 1963 and 1999. A total of 12.5% of these wet grasslands

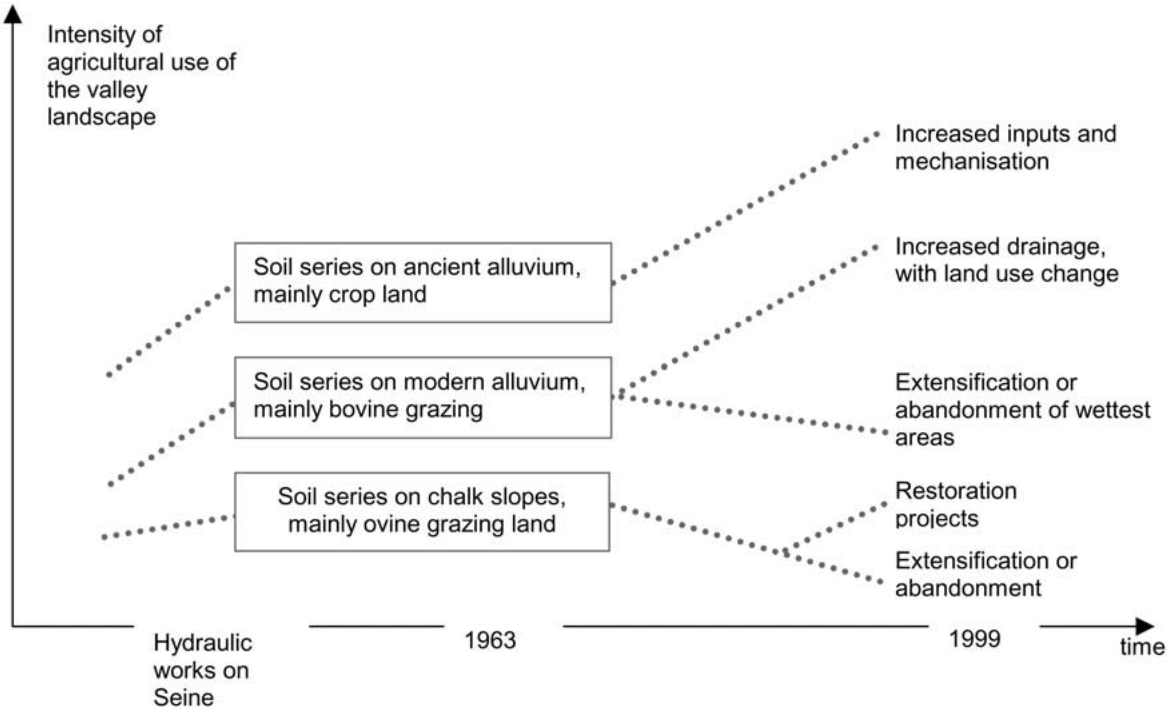

Figure 5. Main composition changes in land use at the valley scale. The grey lines represent trends in the intensity of agricultural use of the main soil series of the valley, since the first hydraulic works on the Seine (see Poudevigne et al. 2002, for details).

were transformed from pastures to crops. At a finer resolution, however, heterogeneity can be detected in the physico-chemical attributes of the wetland soils (texture, hydromorphy, organic content, depth of the organic horizon) thus characterising the soil phases. Measures of redundancy at the wetland scale between the environmental pattern (i.e., the soils phases) and the land uses pattern reveal a slight rise in $R_S(L)$ between 1963 and 1999 (from 0.40 to 0.43), in turn indicating slightly more diversified use of the soil phases. It is to be noted also that redundancy measures do not vary in consistent ways between the two observation levels (valley system and wetland system).

Table 2 provides insight as to the relative contribution of the soil phases to the land use pattern. Hydromorphy and peat appearance are factors that explain most of the patterns in land use in 1999 while thickness of the organic horizon were more important in 1963. The results concerning the niche specificity of land use with respect to soil type also reveals trends through time, showing for example that crops were cultivated on a broader range of soil phases in 1999 than in 1963.

Discussion

Although some methodological aspects need improvement, our example illustrates how measures of organisation relevant to agricultural land use, agricultural intensity and natural soil structure can be parameterised in ways that meaningfully describe patterns of human activities in landscapes. Not only do the data and their treatment reveal spatial aspects of landscape organisation, they illustrated marked changes through time that have tracked agricultural intensification and development over a 36 year period of pronounced agricultural dynamism.

Although this methodology requires substantial data collection and treatment, some steps can be simplified. Indices of 'land use intensity' can be obtained through local expert judgement. The relationships between indices that measure human activity and those which measure disturbances liable to affect species need further development. Another debatable point concerning data collection is the assumption that the soils have not changed over the studied period. Hydromorphy is a questionable variable since regulation works on the Seine river and intensification of the drainage system in 1970–1972 have seriously changed

Table 2. Values for 1963 and 1999 of the main environmental variables explaining land use and specificity of the 5 land use niches. These calculations were performed though statistics derived from the information theory and calculated with a procedure described by Phipps (1981).

	1963	1999
Main environmental variables explaining land use (contribution to total entropy)	texture: 73.8% hydromorphy: 6.4% thickness of A: 19.8% peat appearance: 0.0%	texture: 73.4% hydromorphy: 15.7% thickness of A: 6.7% peat appearance: 4.2%
Specifity of land use niche	dwellings/orchards: 0.54 grasslands: 0.36 crops: 0.32 orchards: 0.21 wood: 0.08	dwellings/orchards: 0.60 grasslands: 0.43 crops: 0.14 orchards: 0.14 wood: 0.20

the extent to which the floodplain was waterlogged. The depth at which the Go horizon appears (defining the hydromorphy characteristic) is nevertheless liable to remain rather constant as such alluvial soils integrate such variations only slowly. Therefore, in 1999, even with water tables lower than in 1963, this variable would still capture most of the heterogeneity of hydromorphy in the soils at the scale of the wetland.

The 1963 landscape of the lower Seine valley site illustrates a situation common to many rural landscapes inherited from the 19th century, where landscape mosaics were originally composed of elements in large patches with a strong spatial organisation (Burel and Baudry 1999). In the lower Seine valley, some 1500 m wide, our results have shown that at a coarse resolution, the landscape could be described in 1963 as a heterogeneous mosaic of large patches some 400 m in size. Though at a coarse resolution, spatial organisation appears relatively low (α organisation relative to 1999), the organisation within these patches appears strong (strong α organisation). The strong spatial correlation (β organisation) between the environmental pattern defining the constraints and the agricultural pattern also shows a strong agro-ecological organisation (Balent et al. 1998). As a result, the Seine valley was composed of large units of homogeneous land use (agro-ecological units): bovine breeding in the alluvial valley, crops on the driest alluvial soils and sheep grazing on the slopes. During the 1963–1999 period, the global increase of α organisation (increased homogeneity) and the global decrease in β organisation (lower redundancy between habitat and land use patterns) mark the transformations of the Seine valley landscape. The landscape changed from a coarse grained structure (with a high inter unit diversity) to a finer grain structure (with a high intra-unit diversity). This pattern is common to many rural areas of Europe (Balent et al. 1998) and can be attributed to technical advances in agriculture that is now less constrained by environmental patterns (Robinson and Sutherland 2002). At the valley scale, these changes led in 1999 to a homogenised landscape, where the weight of the physical environment in land use organisation decreases, probably replaced by within farm constraints, such as field size or choice of production system. It could be suggested from results of the correlation between land use and soil type patterns (β organisation), that the observed shift in fractal dimension marks the transition between an agricultural use of the land linked to the environmental pattern which exhibit large scale variability, to an agricultural use of the land linked to more anthropogenic patterns (e.g., farming system) showing finer scale variability.

Some of these results can partly be explained by changes in technical capability in agriculture through time. In 1963, pastures were the dominant use of most of the alluvial lands regardless of variations in the finer characteristics of these soils (texture, hydromorphy, organic content and depth). These fine differences were not at that time an important factor in explaining land use, only the general quality of these alluvial and rich but waterlogged soils that seemed to have determined agricultural purposes. By 1999, with enhanced technical capacities, farmers could seek to use these different characteristics to their advantage. Results show that in 1999, hydromorphy and peat appearance became stronger factors of land use decisions while thickness of the organic layer become less important. For the farmer, lower hydromorphy could be a criterion to choose plots for new land uses, leaving the pastures on the wetter lands. Peat appearance probably excludes other land uses than pastures. Thickness of the organic layer appears a less important factor, as technically this constraint can be avoided by increasing nutrient input. These results exemplify how human perception of environment affect its use. In 1963, technical agronomy forwarded a perception of these lands as nutrient rich but waterlogged soils improper for tillage. In 1999, technical advances, drainage of the floodplain and economic drivers have changed this perception to a finer level, thus enhancing heterogeneity in land use.

Conclusion: measuring spatial organisation for the management of biodiversity

Relating human activities such as agricultural land use to species activities pattern and activity is one of the key issues for managing biodiversity at landscape scales. Trends in landscape ecology propose, as a possible answer, to assess relationships and overlap between the spatial pattern of these activities. Among the possible research paths, the organisation measures described in this paper have several advantages.

Alpha organisation refers to the spatial distribution of a system property (e.g., human land use). As defined in this paper, it measures the degree to which the distribution of features such as land use deviate from random distribution. A major asset of this metric is that it describes the variability of spatial distribution as a function of scale. Scale dependency is a major impediment for most classical metrics (Palmer and White 1994) and probably explains some of the difficulties in relating these indices to diversity in species assemblages.

Beta organisation refers to the spatial distribution of one property of the system (e.g., human land use) as compared with the spatial distribution of another property of the system (e.g., soil type). As defined in this paper, it measures the degree of deviation by which the spatial distribution of one property is independent of the distribution of another. In our example, beta organisation is directly linked to land use decisions, and drives the changes in alpha organisation. A decrease in beta organisation means that the degrees of freedom for land use decision, regarding physical constraints, is higher therefore planning could be easier. A model of the relationships between the two types of organisation could provide a relevant tool for planning. This measure could also be used to investigate relationships between with different properties (e.g., land use distribution and species distribution), in order to understand or even predict the impact of land use changes on biodiversity at a given scale.

Testing these two measures of organisation in our case study, has prompted some hypothesis. We showed that lower alpha organisation, and hence more random distribution, in human land use led to more heterogeneous (non random) distribution patterns at two scales of observation. It could hypothesised that decrease in the organisation of human land use at a given scale has negative effects on species whose activities concern those scales. We also showed that lower beta organisation, in which there was a more random distribution of human land use on soil types, increased the total heterogeneity of environmental pattern. The resolution of a species is the scale (grain and extent) at which they are able to perceive and respond to spatial heterogeneity in their environment (With 1994). It could be hypothesised that lower beta organisation has negative effects on species deemed to perceive heterogeneity at his scale.

In systems theory, the concept of organisation relates to metastability (Levin 1999). A landscape system in a metastable state is described as being in a state of relative ‘equilibrium’ with external constraints. Metastability depends on the nature and intensity of the interactions among the systems properties, as well as on the nature of the disturbance. When the disturbance crosses a vital threshold value, the landscape system is pushed out of its previous metastable state, and may take much time before reaching a new metastable state (Baker 1995). If landscape metastability is related to increased probability of niche partitioning among species (Huston 1994), then one could hypothesise that high values of alpha and beta organisation could then suggest stable and diverse species assemblages.

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