

# Effect of landscape structure and dynamics on species diversity in hedgerow networks

Françoise Burel

*Centre National de la Recherche Scientifique, UA 696, Université de Rennes, Laboratoire d'Evolution des Systèmes Naturels et Modifiés du Muséum National d'Histoire Naturelle, Campus de Beaulieu, 35042 Rennes Cedex, France*

Keywords: landscape ecology, landscape structure, dynamics, hedgerow network, carabid beetles, spatial distribution

## Summary

Structure and dynamics of a hedgerow network landscape over the last thirty years are compared to the current spatial distribution of carabid beetles in hedgerows. Spatial and temporal scales are chosen according to the observed phenomena, and a multiscale approach used. None of the descriptors of landscape at any given period of time is related to carabid assemblages except heterogeneity in 1985. This measure of landscape structure in Brittany integrates part of the recent changes. Carabid assemblages are also related to overall landscape trajectories through time. Relationship between landscape and carabid spatial patterns may be modeled at the stand and landscape levels.

## Introduction

Spatial and temporal distribution pattern of species are related to various ecological factors and processes. Many authors insisted on this, major papers are on disturbance (Pickett and White 1985), succession (Watt 1947) or physical conditions, altitude and climate (MacArthur 1972). The earliest attempt to use spatial structure as an ecological factor were in bird studies (MacArthur 1972). Island biogeography (MacArthur and Wilson 1967), in its explanation of ocean islands species richness, was a major breakthrough in ecological thinking. The partially spatially explicit model that was proposed could yield testable hypotheses. It constituted one of the reasons for the emergence of landscape ecology in North America (Risser *et al.* 1983; Burgess and Sharpe 1981). The development of landscape ecology (Schreiber 1988; Turner 1987; Zonneveld and Forman 1989) stresses the importance of structural pattern on species distribu-

tion and behaviour. Nevertheless field studies still mainly focus on either habitat fragmentation (Opdam *et al.* 1985) or effects of network connectedness (Baudry 1984; Merriam 1984; Burel 1989). Milne *et al.* (1989) propose a model predicting presence of one species, the white tailed deer, based upon site characteristics and proximity at different scales. Parameters describing overall landscape structure were used by O'Neill *et al.* (1988) and Burel and Baudry (1990a). In fact, few studies give an integrated view of landscape (Phipps *et al.* 1986; Van Dorp and Opdam 1987); time is rarely taken into account.

The aim of this research is to isolate, among several interacting organisation levels, the relationship between the landscape structure and the species diversity. Landscapes vary through time (Baudry and Burel 1985; Romme and Knight 1982; Odum and Turner 1990). Intensity of changes, as for example removal of hedgerows and ploughing of meadows (Rackham 1986) increased in western

European rural areas since the fifties (Leonard and Cobham 1977; Agger and Brandt 1988). Landscape structure is dynamic so the dominant paradigm of landscape ecology on the synchronic relationship between species distribution and landscape pattern is questionable. Changes in spatial structure and changes in species assemblages are not synchronous. Current species distribution depends on past as well as present landscape states, for example bird species assemblages in mediterranean areas are directly related to the vegetation history (Blondel 1986). Landscape is a changing system, its dynamics may be a driving factor for species space occupancy, species or species assemblages being influenced by a previous state of the environment can be a memory of the past.

In this paper I analyse how landscape structure and dynamics over the last thirty years have affected carabid beetles in hedgerows.

The relevant spatial scale at which to study those interactions depend on the scale at which specific phenomena occur. This scale is explicitly defined according to Morris (1987). On the contrary Allen and Starr (1982) and Urban *et al.* (1987) argue that sampling scale is an artefact of the scientist and insist on the necessity to study different scales in order to reveal the correct scale of each ecological phenomenon. One way to study multiscale phenomena is to analyse the landscape in terms of its fractal geometry, which integrates complexity at a variety of scales (Mandelbrot 1982; Milne in press; Voss 1988) and defines self similarity over a range of scales.

Landscape structure parameters are chosen according to their known relationships with ecological processes. Ecology of hedgerow networks has been widely studied (Pollard *et al.* 1974; INRA *et al.* 1976; Burel and Baudry 1989, 1990b) and allows us to link spatial structure and some ecological processes.

Previous studies carried out on the distribution of carabid beetles pointed out their sensitivity to landscape structure (Thiele 1977; Ranta and As 1982; Clavreul 1984). There is little overlap between species assemblages in hedgerows and in fields, except for a few ubiquitous species (Lyngby and Nielsen 1980; Bonkowska 1970). The richness and

abundance of forest species in hedgerows has been shown to be related to distance from woods, network connectivity, presence of lanes bordered by two parallel hedgerows and hedgerow vegetation structure (Burel 1988, 1989). Constraints determining the spatial distribution of these species change with the size of the universe studied and the level of spatial organisation, from the hedgerow level to the landscape level. Removal of hedgerows often leads to isolation of some populations finding refuge in remnant landscape elements, these populations are subject to extinction (Blondel 1986). Den Boer (1985) showed that isolated populations of carabid species appear to survive for only restricted periods. Species of stable habitats (with low powers of dispersal) will survive around 40 years, and species mainly occupying unstable habitats (with high powers of dispersal), around 10 years. This allows us to hypothesize that carabid species assemblages reflect past landscape structure and dynamics. Isolated populations can survive for a while in a landscape where they were previously connected to other populations. This is the reason why this material has been chosen.

While some insights may be gained on the spatial distribution of carabids within hedgerows, the emphasis of this contribution is upon methods of landscape ecology analysis with particular focus upon changes through time.

## Methods

### *Study area*

The research was carried out in Lalleu, a 1500 ha municipality, 50 km South of Rennes, France.

The Lalleu landscape is farmland (grassland, cereals, maize) with most of the fields surrounded by hedgerows. Hedgerows are mainly composed of pruned oak, pollarded every nine years according to local rules. There is no woodlot larger than 0.5 ha. Roads between small villages are an important landscape structure. Formerly, they were bordered by hedgerows that were removed for road enlargement. It happens that some hedgerows regrew since then. The bedrock is an alternation of shale sup-

porting gently rolling landscapes and sandstone, which forms steep slopes. Two plateaus on these slopes have shallow soil. The geological constraints on cultivation kept these areas as common pastured moorland until the end of the last century. The moorland was eventually divided among farmers, into rectangular fields. Spontaneous heathland-type vegetation developed on boundaries, to form hedgerows. Farming is mostly mixed dairy cattle husbandry associated with cereal cultivation.

Carabids were sampled in 352 ha area, subdivided into 22 contiguous 16 ha square quadrats (Burel and Baudry 1990a). Many changes occurred here as shown by records from 1952, 1961, 1972 and 1985: total hedgerow length decreased by one third, connectedness by more than a half, connections between hedgerows and lanes by 40%, and the average quadrat heterogeneity increased. At each period there is a large diversity of situations in quadrat landscape structure. Though the general trend is progressive enlargement of a dense hedgerow network, some quadrats had few hedgerows in 1952 while in others, network remains dense in 1985. Trajectories of change were calculated by computing overall landscape characteristics at the different dates. Types of change were determined and they differ not only by their initial and final stages but also by their rates of change. Intensity of changes was not homogeneous; it was maximum between 1961 and 1972, due to subsidies from the French government to farmers in the sixties to remove hedgerows. The rate of change varies also between quadrats.

#### *Carabid sampling*

Carabids were collected, in 1986 and 1988, in circular pitfall traps 13 cm diameter by 25 cm deep. Sets of 3 traps, 1 m apart were located on top of earthen banks in hedgerows, where, in Brittany landscapes, 'forest' species are found preferentially beyond a few 100 meters out of a forest edge (Burel 1988). Two or three nearby hedgerows were sampled this way in each 16 ha quadrat (Fig. 1). In 1986, 29 hedgerows were sampled, and 44 in 1988. Traps were open for three consecutive days every week

from mid-April to mid-July thereby providing estimates of spring assemblages and catches of 95% of the species present all year (Burel 1987). Names are according to Bonadonna (1971).

#### *Data analysis*

Data were analysed with ordination methods. Correspondence analysis and classification are from Addad software (Jambu and Lebeaux 1978). In correspondence analysis, a point in the multi-factorial space is represented by the line profile, here species frequencies, and the weight of this line within the whole data set. Thus, there is no standardization over habitats and each sample site is characterized by its own richness. This is important because differences between habitats are essential.

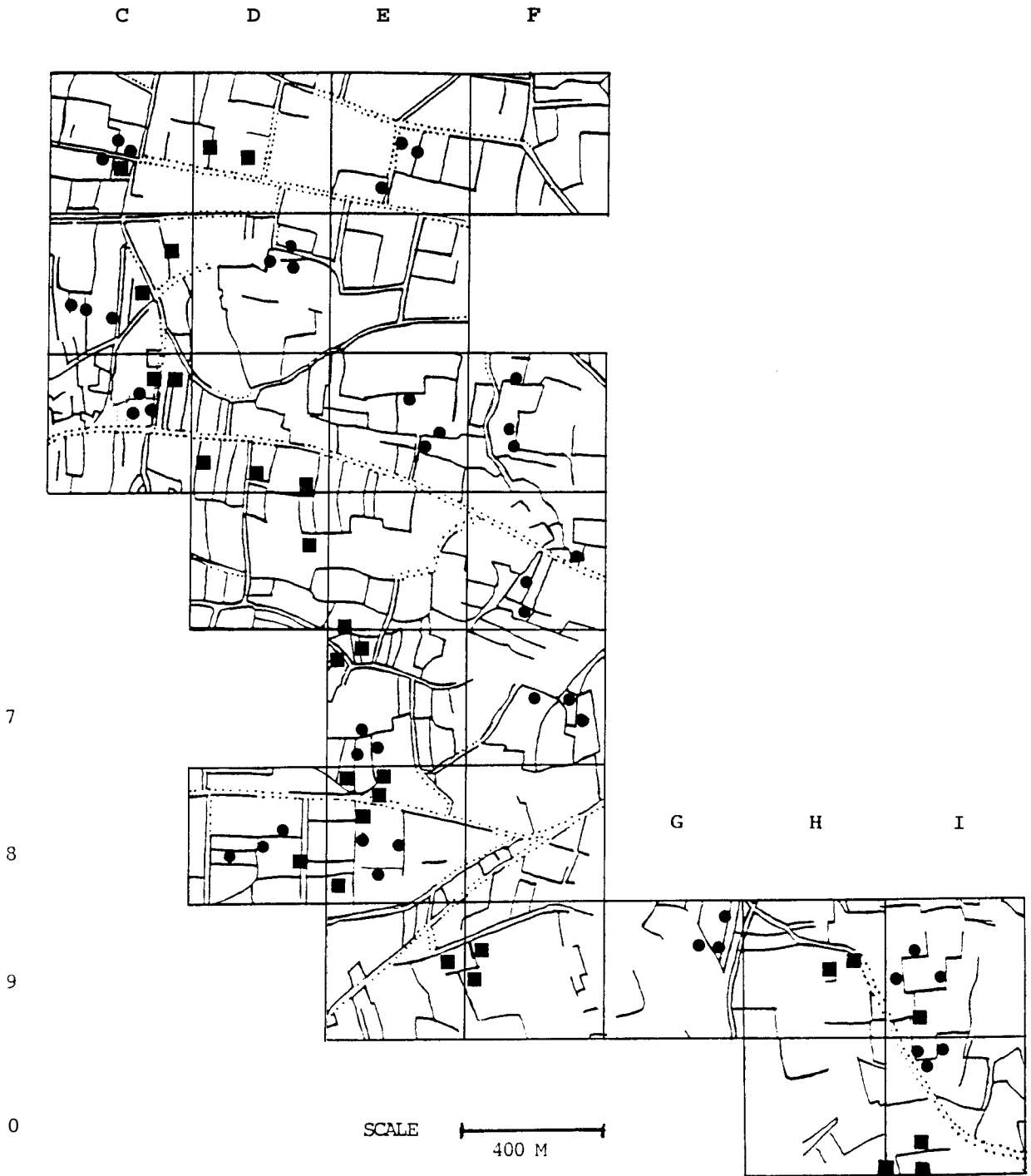
Results of Burel and Baudry (1990a) on landscape structure and dynamics are used here to evaluate relationships between landscape structure and carabid assemblages. All these data were measured in 16 ha quadrats.

They are:

- \* hedgerow length
- \* connectedness (number of connections among hedgerows) (Baudry and Merriam 1988).
- \* number of no-connections (hedgerow not connected to any other at one end)
- \* grain size heterogeneity (Baudry and Burel 1985)
- \* type of trajectory of change: for each quadrat, the scores on the axes of a correspondence analysis (CA1) using the four parameters listed above, measure the landscape structure at the four periods of time (Burel and Baudry 1990a). Trajectories of changes are the results of a correspondence analysis (CA2) where each quadrat is characterized by its factorial scores at the four sampled years on the two first axes of (CA1).

The first four parameters were measured at four periods: 1952, 1961, 1972, 1985.

The grid fractal dimension (Voss 1988; Milne 1991) of hedgerow network was measured on 16 ha quadrats which were subdivided into 50 m x 50 m cells, for the quadrats individually and for the whole landscape. Cells were aggregated in groups



**Fig. 1.** Study area and sampling sites. — hedgerow; ..... lane without hedgerow; ■ samples in 1986  $n=29$ ; ● samples in 1988  $n=44$ .

of four at each of four levels. Each grid cell at each scale was characterized by the presence or absence of hedgerows. The log of the number of cells where

hedgerows were present at each scale of measurement was regressed against the log of resolution (*i.e.*, the number of cells along one side of the 16 ha

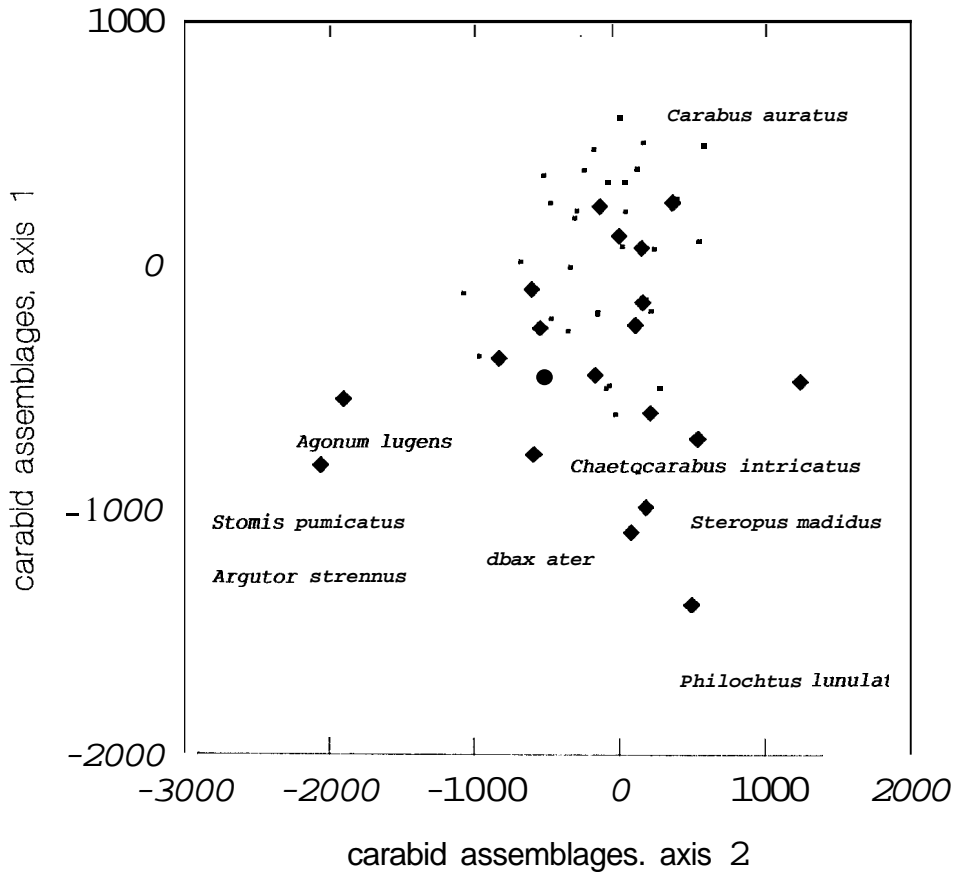


Fig. 2. First plane of the correspondence analysis. ■ single hedgerow; ◆ one of the two parallel hedgerows bordering a lane.

quadrats at a given measurement scale). For the whole landscape, counts are the sums of the counts obtained for the 16 ha quadrats. The slope of the regression is the fractal dimension (Voss 1988), and provides a measure of the tendency for hedgerows to fill the plane at a variety of scales. The linearity of the relationship between measures and scales is a characteristic of fractals due to their invariance under changes of magnification.

### Results: Carabids and landscape

#### \* hedgerow species assemblages

During the two studies years 59 taxa were captured. Among those with a frequency higher than 2% only 2 are 'forest' species: *Abax ater* and *Chaetocarabus intricatus*. All the sample periods were lumped together in order to focus on spatial interactions (Doledec and Chessel 1987).

The data matrix contains 73 hedgerows  $\times$  59 carabid taxa recorded as numbers of individuals per species. Species assemblages may be expressed by sample scores on the first axis of a correspondence analysis performed on this matrix. Axes 1 and 2 explain 18% of the total inertia, which is significant at  $p < 0.05$  (Lebart *et al.* 1977).

Axis 1 contrasts on the positive end *Carabus auratus* and quadrats e8, d8, i10, which are either located on ancient moorland or on quadrats of very low hedgerow density, and, on the negative end *Steropus madidus*, *Abax ater*, *Chaetocarabus intricatus* (Fig. 2). The latter three species are more frequent and abundant on the negative part of the axis, as shown for *Abax ater* on Fig. 3. Quadrats which contribute the most to this negative end of the first axis have a high hedgerow density. Nevertheless the spatial distribution of the 3 species is not significantly related to any of the landscape para-

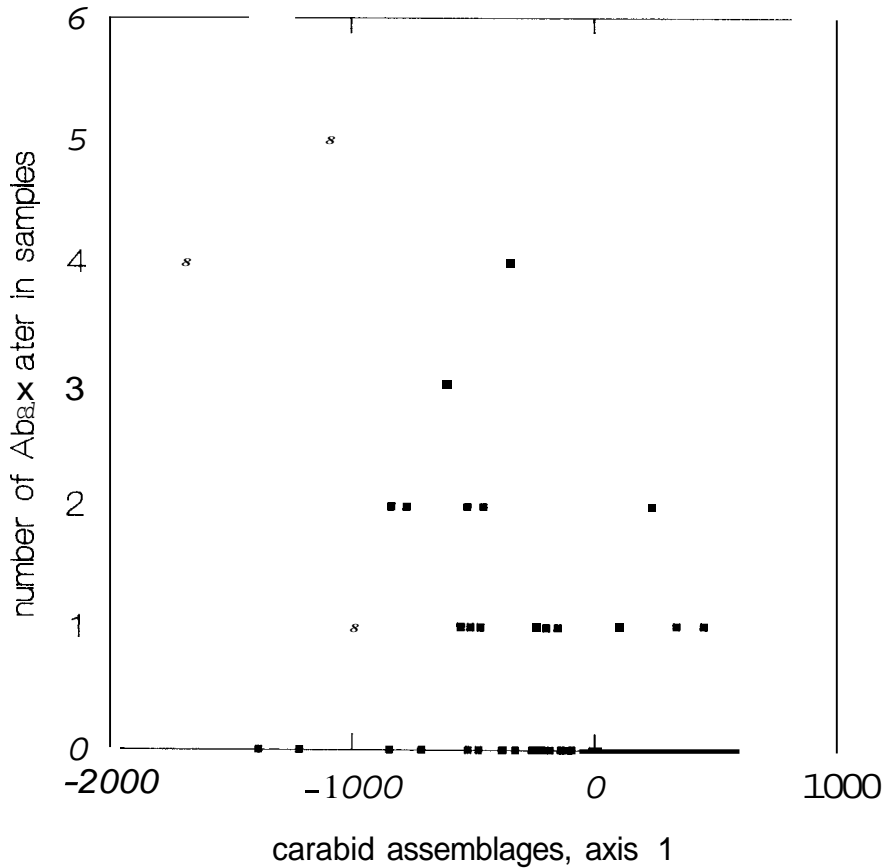


Fig. 3. Abundance of *Abax ater* along axis 1 of the correspondence analysis.

meters as they have been computed for the four periods (Spearman test,  $p > 0.05$ ). The second axis opposes *Philochtus lunulata* on one end to *Argutor strennus*, *Stomis pumicatus*, *Agonum lugens* on the other one (Fig. 2).

#### \* Meaning of the 16 ha scale for carabids

The effect of spatial proximity on species composition is a basic assumption of landscape ecology theory. For example plant species composition in ungrazed patches in Normandy depends on the presence of adjacent hedgerows which are sources (Burel and Baudry 1990b). Proximity effects depend on dispersal behavior and capabilities for each species. Baudry and Merriam (1988) pointed out the differences between connectedness which is a quantitative measure of links between mappable elements, and connectivity which is a measure of the processes of animals moving among landscape

elements. Burel (1989) showed that carabid assemblages in hedgerows differ according to landscape structure. Connectedness, distance from forest sources and presence of lanes bordered by two hedgerows determine presence and abundance of the forest species which are able to use hedgerows as corridors for their dispersal. If the resolution scale of 16 ha is relevant to express these relations between carabids and landscape structure, the aggregation of the carabid assemblages of the different sample sites within a 16 ha quadrat must be more similar than a random association of sample sites. To test this hypothesis the following null hypothesis has to be rejected:

$H_0$  = the average similarity of groups of samples is the same whether the samples are assigned randomly to a quadrat or are considered at their actual place in the landscape within a given quadrat.

\* Similarity computation: the distance, in the

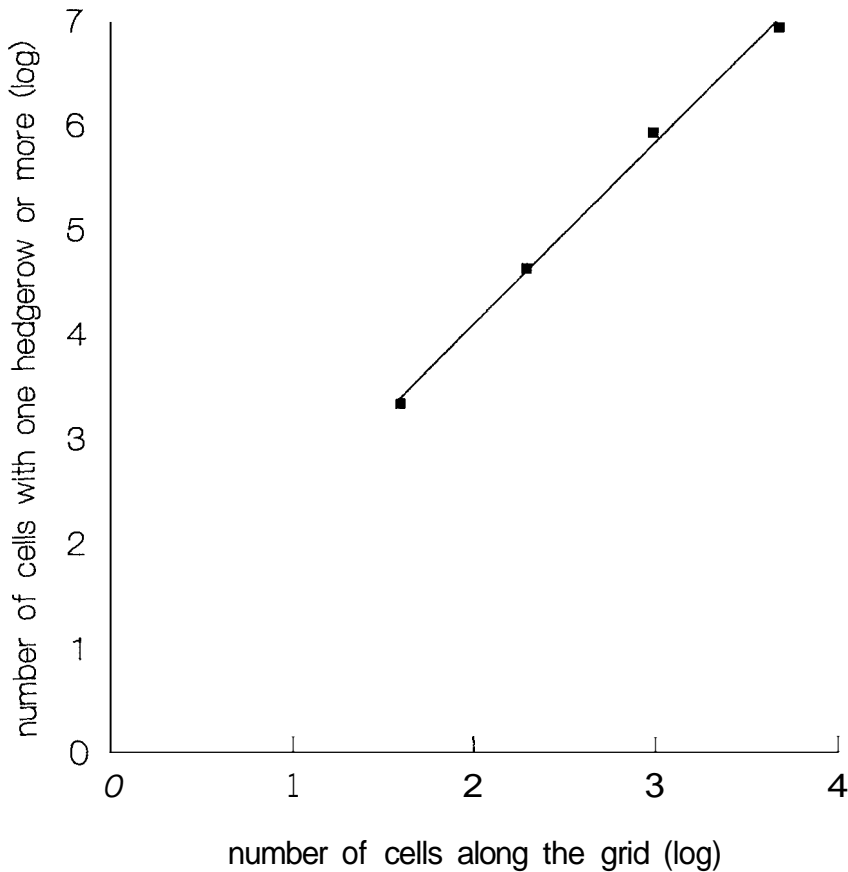


Fig. 4. Fractal dimension of hedgerow network in the whole landscape.

factorial space, between each sample and the center of mass of all the samples of the 16ha quadrat it belongs to is calculated in the two first dimensions of the factorial space of the correspondence analysis presented above. The average distance of all the samples was computed. Small value of this average distance indicates that samples within a quadrat have similar species composition, a high value a dissimilar one.

\* Test: two average distances were calculated: one for actual position within a 16ha quadrat (da), one for random position of samples within 16 ha quadrats (dr). We found  $(da) = 392 \pm 65.7$ ,  $(dr) = 624.14 \pm 90.7$ . The mean intervals are calculated with a confidence level of 5%. The two mean intervals do not overlap, the two average distances are different, the actual one (da) being lower than the randomly generated one (dr). Distances obtained for two random assignments are similar.

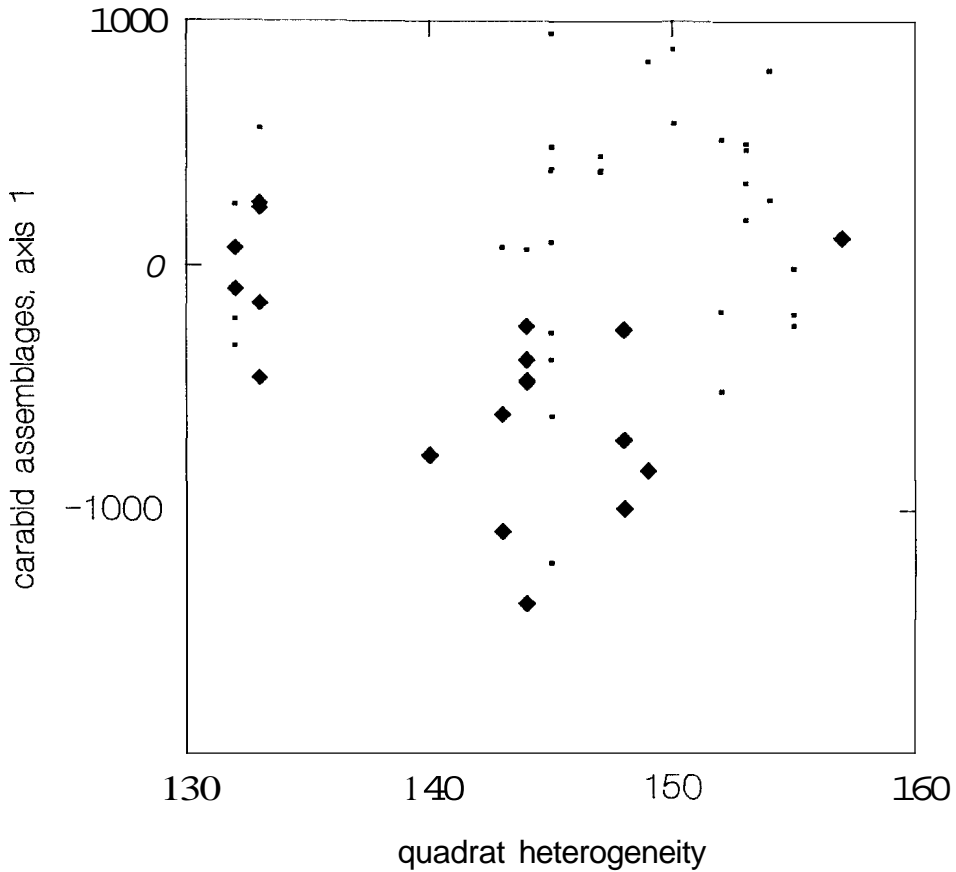
$H_0$  is rejected, nevertheless the value of (da) shows that important differences between samples within a quadrat exist.

#### \* *Fractal dimension of the landscape*

The graph (Fig. 4) plotting cells against resolution scale in the case of our Lalleu landscape shows that points are in a row. This means that the hedgerow network is a fractal within this species range of scale. The fractal dimension, here 1.75,  $p = 0.002$ , measures network complexity all over this range. The fact that a landscape exhibits a fractal dimension over only a certain range of scale is expected (Milne 1991). Individual quadrats fractal dimension varies from 1.24 to 1.92.

#### \* *Carabid assemblages and landscape features*

A Pearson correlation matrix was computed between carabid species assemblages and landscape



**Fig. 5.** Relationship between carabid assemblages and heterogeneity of landscape structure in 1985.  $\blacklozenge$  lanes bordered by two hedgerows;  $\blacksquare$  single hedgerow.

descriptors of the quadrats at the four periods of time. Carabid assemblages are represented by their scores on the first axis of the correspondence analysis which is used as indicator of environmental conditions, assuming that species are distributed along some environmental gradient (Whittaker 1967) in an abstract ecological space (Jongman *et al.* 1987). Among the descriptors of the current landscape within quadrats, including the fractal dimension, only heterogeneity in 1985 is significantly correlated to the scores ( $n = 73$ ,  $p = 0.05$ ,  $r^2 = 0.233$ ) (Fig. 5). Correlation is stronger without taking into account quadrats of low heterogeneity, C4 and E7 ( $n = 60$ ,  $r^2 = 0.355$ ,  $p = 0.01$ ). None of the descriptors of previous states is correlated to carabid assemblages.

At the local spatial scale, lanes bordered by two parallel hedgerows have carabid species assem-

blages that strongly contrast with that of single hedgerows (Fig. 2). The correlation matrix between overall landscape (measured by ordination score) at the four periods and the carabid assemblages shows no correlation at any time. There is nevertheless a strong trend with quadrat trajectories of change as determined by CA2 (see methods) (Fig. 6). On the first 'CA2' axis, the quadrats which determine the positive end had a low hedgerow length (3155 m in 1952, mean = 3693 m, and 1778 m 1985, mean = 2325 m) and their rate of changes is slower than for the average. The negative end corresponds to quadrats which had high density of hedgerows in 1952 and went through the highest intensity of changes during the following thirty years (group 2 of Burel and Baudry 1990a). Quadrats of the positive end have carabid assemblages of ancient moorland or open areas. At the other end quadrats are charac-

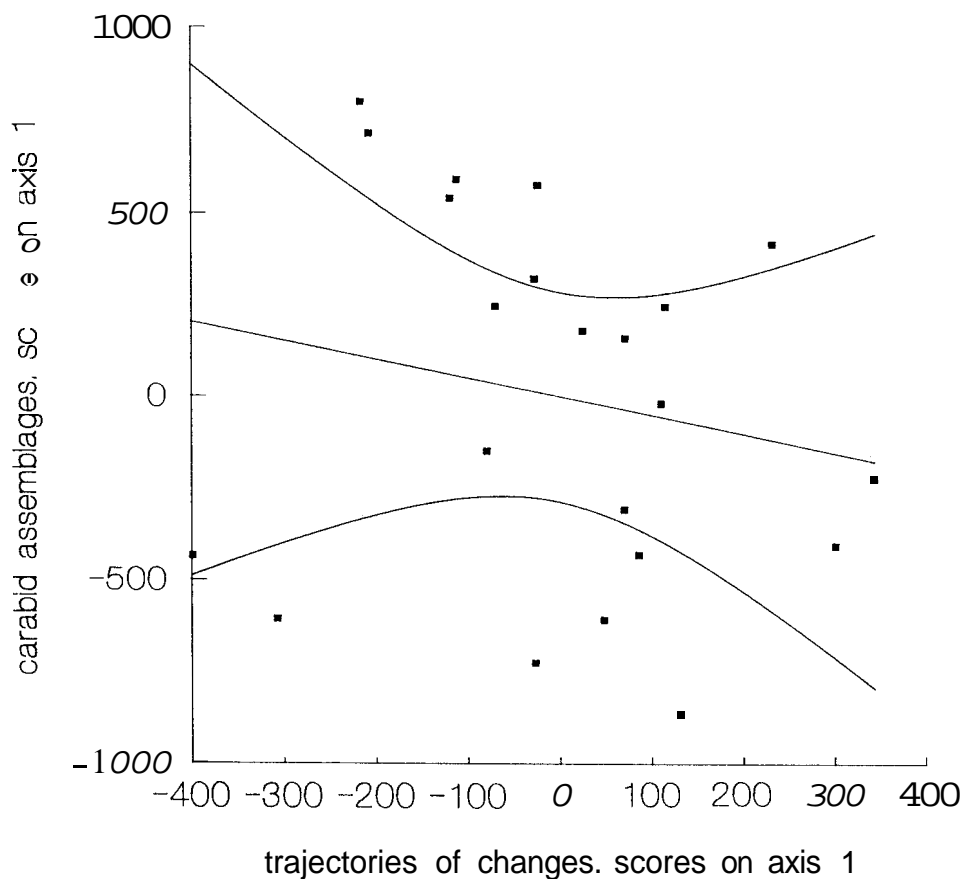


Fig. 6. Relationship between carabid assemblages and the quadrats trajectories of change. The figure shows the regression line between the 2 variables. The envelop is the confidence interval for  $p = .95$ .

terized by the presence of forest species. This relationship with recent history is confirmed when looking individually at species determining axis 1 of carabid assemblages. *Abax ater*, for example is present in any kind of landscape structure in 1985, as represented by scores on axis 1 of the correspondence analysis performed on landscape attributes of quadrats (CA1), but is mainly restricted to a certain type of quadrats in 1952 (Fig. 7). Those quadrats were characterized by a high density of hedgerows, a large number of connections with lanes bordered by two hedgerows, and a large number of connections between hedgerows.

## Discussion

### *Fractal approach*

Traps belonging to the same 16 ha quadrat have similar carabid species composition, which differs from other quadrats. Carabid beetles perceive this partition of space as some entity in spatial continuity. We selected 16 ha quadrats (Burel and Baudry 1990a) both because they represented an economical unit and for convenience for map aggregation. This scale also proved to be relevant for beetles. Relationships between the territory in one quadrat and species composition may be of different kinds. Explanatory factors may be physical ones such as geology, topography, or agronomy *e.g.*, type of crop, farmer practices, or topology *e.g.*, landscape structure. The fractal dimension expresses the way

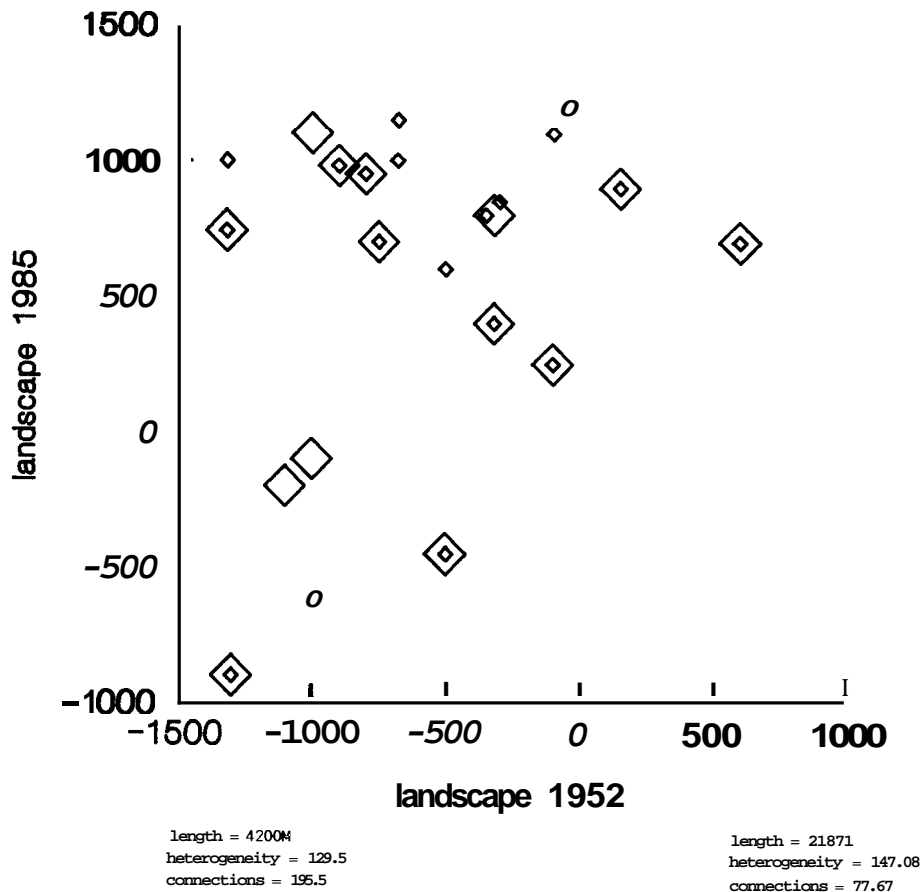


Fig. 7. Distribution of *Abux ater* according to overall landscape structure in 1952 and 1985. Landscape structures are represented by their scores on the first axis of CA1.  $\diamond$  presence of *Abux ater*;  $\circ$  absence of *Abux ater*.

hedgerow density changes over the range of scales. The hedgerow network landscape is fractal. Based on this, I consider shape to be invariant when scaling up through the studied range of scales.

Within the range of scales of self-similarity, the same process may be responsible for all the observed patterns. Landscape changes within the 16 ha quadrats over time is due to socio-economic factors (Burel and Baudry 1990a). Farming activity also generate network pattern at that scale, which seems an appropriate scale for processes affecting carabid populations (Baars and Van Dijk 1984). Thus fractal geometry is a relevant way to link socio-economic activity and ecological processes which operate at different scale. This study also shows that 16ha is a relevant scale to study carabid assemblages. This is important in terms of sampling within a landscape to address questions pertaining

to landscape dynamics. I suggest that in fractal landscape, sampling design at a coarse scale (16 ha) is sufficient to characterize patterns occurring at a finer scale (1 ha).

#### *Landscape structure and species diversity dynamics*

Except for heterogeneity there is no relation between carabid species composition and any descriptor of 1985 landscape structure. Heterogeneity is, here, measured with information theory, and takes into account mesh size delimited by hedgerows (Baudry and Burel 1985). Using this measure of heterogeneity, we have shown that in a hedgerow network hedgerow removal progressively leads to an increase of heterogeneity, and after some threshold there is inversion and heterogeneity decreases.

When the network is dense there are only small fields. In Brittany after some removals, small and large fields coexist. Further removal of hedgerows creates only large fields (Baudry and Burel 1985). In Lalleu from 1952 to 1985 we observed only the first phase of network dismembering. Quadrats of high heterogeneity are those where hedgerow removal has been most frequent. As heterogeneity increases scores of carabid assemblages increase on axis 1 of the correspondence analysis (Fig. 5) which corresponds to a decrease in abundance of the 'forest' species present in the hedgerows of the study area.

Neither length of hedgerows nor landscape structure are related to carabid assemblages. This may be explained by two different causes. First, the landscape may have been studied at the wrong scale. Second, rates of change are different for landscape and for beetles. The first hypothesis must be rejected because the calculated fractal dimension, which describe landscape structure within a range of scales, is not related to carabids distribution, while 16 ha resolution is a relevant scale to study assemblages. In the light of the second hypothesis one may hypothesize that after removal of hedgerows in an area, 'forest' species find refuge in the few remaining woody habitats. There probably is a period of supersaturation followed by an increasing rarity. If hedgerows are no longer connected to the network, isolation may lead to extinction of some species. Delay until extinction depends on biological characteristics of each species and they will not all be in phase. Quadrats C4 and E7 which stayed dense all over the last 30 years have a peculiar status on the plot of heterogeneity against carabid species composition (Fig. 5). This may be explained by the fact that forest corridor species find suitable habitats in many contiguous farm lanes where the supersaturation phenomenon does not occur.

Lag in reaction of beetles to landscape changes leads to a temporary independence of the two spatial patterns of landscape elements and species assemblages.

The relationship between quadrats trajectories through time and carabid assemblages (Fig. 6) confirms the possibility of the second hypothesis: rates of change are different for landscape and for bee-

gles, C4 and E7 have a peculiar status here too. Carabid assemblages in 1985 do not reflect landscape structure at that time. They reflect a combination of past and present structure. Hedgerow network landscape in Brittany, built by the rural society according to farming techniques and social values, changed through time since the prehistorical period (Meyer 1972). Intensity of changes increased during recent decades. The trajectory variable includes indications about landscape dynamics in each quadrat since 1952. The relationship between trajectories of change and carabid assemblages is as if there were some memory of 1952 landscape structure reflected in the spatial pattern of the species assemblages. In those quadrats which had a highly dense and connected network in 1952 carabid assemblages remain characteristic of the 1952 type of landscape even though landscape structure has changed drastically since then. Species which determine the structure of assemblages on axis 1 of the correspondence analysis are *Abax ater*, *Chaetocarabus intricatus* and *Steropus madidus*. The first two are forest species, which have been shown to be able to use certain type of hedgerows as dispersal corridors to move from forest sources across the rural landscape (Burel 1989). *Steropus madidus* is restricted to shady places (Deveaux 1978). In farmland areas of Normandy and southern France, it has been found preferentially in recent woodlots and hedgerows (Burel *in press*). Distribution of these 3 species is not related to any of the landscape structure parameters. Nevertheless it is dependent on landscape history. They are restricted to quadrats where, in 1952, they could find suitable habitats to live in and to disperse through. It could be either lanes bordered by two hedgerows or very small enclosed fields where shade and humidity are more similar to forests than in large fields. Hedgerows destruction leads to field enlargement, reduced connectivity and increased heterogeneity. These species are still found in some sites, which now are mainly lanes.

It is of interest to build hypotheses on the future of those populations which become more and more isolated as discontinuities in the lane network increase. Either enlargement of lanes which often leads to the removal of one of the bordering hedge-

rows, or cutting of old trees are stochastic environmental events which will lead to extinction of those fragmented populations. Gradually these species will disappear at the landscape level.

As quadrat heterogeneity decreases through time, the relationship between quadrat heterogeneity and carabid assemblages (Fig. 5) may help to understand how carabid assemblages react to changes at both local (stand) and landscape levels. In dense hedgerow networks (low heterogeneity), some forest species may find good habitats and disperse through the landscape. They are present in many elements and their mean abundance is low. When some hedgerow removal occurs, network heterogeneity gradually increases. Carabid assemblages are highly diversified, and depend more on local effects. Forest species find refuge in the remaining lanes or very dense wooded hedgerows, their abundance being higher. This high density of individuals per species may be explained by a super-saturation phenomenon, found when availability of potential habitats in a given landscape suddenly decreases (Clavreul 1984; Blondel 1986). As network dismembering increases or time since removal is long, forest species diminish or become extinct, this may be due more to environmental stochastic events than to stochastic population hazards.

The knowledge of landscape structure at one period of time is not sufficient to predict carabid assemblages in changing landscapes. Their species composition and abundance are linked also to previous states of the landscape. Influence of recent history is more important for high levels of the spatial hierarchy, where rates of change are slow. Dwyer and Merriam (1985) found similar results when looking at the ground fauna of two different forest stands. Small soil samples kept their own composition and dynamics when moved to a different environment. For the lower levels, fast moving, local influence is predominant and history may be considered as a background noise.

For management purposes two main principles are derived from these results. First, forest species present in hedgerows remain, for a while, in the landscape even when landscape structure slows down their dispersal. This retains colonization potential and may allow future species diversity at

the landscape level, if recolonizations occur before regional extinction. Second, lanes bordered by two hedgerows are fundamental landscape features in a conservation perspectives for these beetles in Brittany. The common practice of removing one hedgerow to allow their enlargement will lead to a reduced species richness at the landscape level.

## Conclusion

This research was performed in a man-dominated landscape where changes in structure are rapid in recent decades. It emphasizes the necessity to look not only at landscape structure but also at its dynamics. All the processes occurring in a landscape are not synchronous and predominance of time as an explanatory factor of spatial distribution depends on the time scale resolution of the study.

## Acknowledgements

I thank J. Baudry, J.C. Lefeuvre, H.G. Merriam and B.T. Milne for their constructive review of early drafts of the manuscript, P. Fouillet for technical help. This work was partly funded by grant number 87230 from the Ministry of Environment, France.

## References

- Agger, P. and Brandt, J. 1988. Dynamics of small biotopes in Danish agricultural landscapes. *Landscape Ecology* 1: 227–240.
- Allen, T.F.H. and Starr, T.B. 1982. *Hierarchy: perspectives for ecological complexity*. The University of Chicago Press, Chicago and London.
- Baars, M.A. and Van Dikk, Th. S. 1984. Population dynamics of two carabid beetles in a Dutch heathland. I. Subpopulation fluctuations in relation to weather and dispersal. *J. Anim. Ecol.* 28: 211–230.
- Baudry, J. 1984. Effects of landscape structure on biological communities: the case of hedgerow network landscapes. *In* *Methodology in landscape ecological research and planning*. Vol. 1: 55–65. Edited by J. Brandt and P. Agger. Roskilde University Centre Denmark.
- Baudry, J. and Burel, F. 1985. Systeme écologique, espace et théorie de l'information. *In* *Paysage et Système*. pp. 87–102. Edited by V. Berdoulay and M. Phipps. Presses de l'Université d'Ottawa.

- Baudry, J. and Merriam, H.G. **1988**. Connectivity and connectedness: functional versus structural patterns in landscapes. *In* Connectivity in Landscape Ecology. Proceedings of the 2nd International Seminar of the International Association for Landscape Ecology. pp. **23–28**. Edited by K.F. Schreiber. *Münstersche Geographische Arbeiten* **29**.
- Blondel, J. **1986**. *Biogéographie évolutive*. Masson.
- Boer, P.J. den **1985**. Fluctuations of density and survival of carabid populations. *Oecologia* **67**: **322–330**.
- Bonadonna, P. **1971**. Catalogue des coléoptères carabiques de France. Publication de la nouvelle revue d'entomologie.
- Bonkowska, T. **1970**. The effect of shelterbelts on the distribution of Carabidae. *Ekologia polska* **28**: **559–569**.
- Burel, F. **1987**. Effets de la structure spatiale des paysages ruraux sur les populations animales et végétales. Rapport Ministère de l'Environnement, SRETIE, **97** p.
- Burel, F. **1988**. Biological patterns and structural patterns in agricultural landscapes. *In* Connectivity in Landscape Ecology, 2nd IALE seminar. Edited by K.F. Schreiber. *Münstersche Geographische Arbeiten* **29**: **107–110**.
- Burel, F. **1989**. Landscape structure effects on carabid beetles spatial patterns in Western France. *Landscape Ecology* **2**: **215–226**.
- Burel, F. (in press). Ecological consequences of land abandonment on carabid beetles distribution in two contrasted grassland areas. *Options méditerranéennes*.
- Burel, F. and Baudry, J. **1989**. Hedgerow network patterns and process in France. *In* Changing Landscapes: an ecological Perspective. pp. **99–120**. Edited by I.S. Zonneveld and R.T.T. Forman. Springer Verlag, New York.
- Burel, F. and Baudry, J. **1990a**. Structural dynamic of a hedgerow network landscape in Brittany France. *Landscape Ecology* **4**: **197–210**.
- Burel, F. and Baudry, J. **1990b**. Hedgerow networks as habitats for colonization of abandoned agricultural land. *In* Species dispersal in agricultural environments. pp. **238–255**. Edited by R.H.G. Bunce and D.C. Howards. Belhaven Press, Lympington.
- Burgess, R.L. and Sharpe, D.M. **1981**. Forest island dynamics in man dominated landscapes. *Ecological studies* **41**, Springer Verlag, New York, Heidelberg, Berlin.
- Clavreul, D. **1984**. Contribution à l'étude des interrelations paysage/peuplements faunistiques en région de grande culture. Thèse de doctorat de 3<sup>ème</sup> cycle. Université de Rennes 1, **317** p.
- Deveaux, D. **1978**. Recherches sur la répartition spatio-temporelle des peuplements en carabiques (Col. Carabidae) en zones bocagères, Thèse de doctorat de 3<sup>ème</sup> cycle Université de Rennes. **264** p.
- Doledec, S. and Chessel, D. **1987**. Rythmes saisonniers et composantes stationnelles en milieu aquatique. *Acta Oecologica Oecol. Gener.* **3**: **403–426**.
- Dorp van, D. and Opdam, P.F.M. **1987**. Effects of patch size, isolation and regional abundance on forest bird communities. *Landscape Ecology* **1**: **59–73**.
- Dwyer, L.M. and Merriam, H.G. **1985**. Decomposition of natural litter mixture in a deciduous forest. *Can. J. Bot.* **62**: **2340–2344**.
- I.N.R.A., C.N.R.S., E.N.S.A. and Université de Rennes, **1976**. Les bocages: Histoire, Ecologie, Economie. **586** p.
- Jambu, M. and Lebeaux, M.O. **1978**. Classification automatique pour l'analyse des données. Dunod.
- Jongman, R.H.G., ter Braak, C.J.F. and van Tongeren, O.F.R. **1987**. Data analysis in community and landscape ecology. Center for Agricultural Publishing and Documentation (Pudoc) Wageningen, The Netherlands.
- Lebart, L., Morineau, A. and Tabard, N. **1977**. Techniques de la description statistique. Dunod.
- Leonard, P.L. and Cobham, R.O. **1977**. The farming landscape of England and Wales: a changing scene. *Landscape plan.* **4**: **205–236**.
- Lynby, J.E. and Nielsen, H.B. **1980**. The spatial distribution of carabids (Coleoptera, Carabidae) in relation to a shelterbelt. *Ent. Meddr.* **48**: **133–140**.
- MacArthur R. **1972**. Coexistence of species. *In* Challenging Biological Problems. pp. **251–259**. Edited by J.A. Behnke. Oxford University Press.
- MacArthur, R.H. and Wilson, E.O. **1967**. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.
- Mandelbrot, B.B. **1982**. The fractal geometry of nature. WH Freeman and Co, New York.
- Merriam, H.G. **1984**. Connectivity: a fundamental characteristic of landscape pattern. *In* Methodology in Landscape Ecological Research and Planning. vol. 1. pp. **5–15**. Edited by J. Brandt and P. Agger. Roskilde University Centre, Denmark.
- Meyer, J. **1972**. L'évolution des idées sur le bocage en Bretagne. *In* La pensée géographique française contemporaine. Presses universitaires de Bretagne, **453–467**.
- Milne, B.T. **1991**. Lessons from applying fractal models to landscape patterns. *In* Quantitative Methods in Landscape Ecology. Edited by M.G. Turner and R.H. Gardner. Springer Verlag.
- Milne, B.T. *in press*. Spatial aggregation and neutral models in fractal landscapes. *American naturalist*.
- Milne, B.T., Johnston, K.M. and Forman, R.T.T. **1989**. Scale dependent proximity of wildlife habitats in a spatially-neutral Bayesian model. *Landscape Ecology* **2**: **101–110**.
- Morris, D.W. **1987**. Ecological scale and habitat use. *Ecology* **68**: **362–369**.
- Odum, E.P. and Turner, M.G. **1990**. The Georgia landscape: a changing resource. *In* Changing Landscapes an Ecological Perspective. pp. **137–164**. Edited by I.S. Zonneveld and R.T.T. Forman. Springer Verlag, New York.
- O'Neill, R.V., DeAngelis, D.L., Waide, J.B. and Allen, T.F.H. **1986**. A hierarchical concept of ecosystems. Princeton University Press.
- O'Neill, R.V., Krummel, J.R., Gardner, R.H., Sugihara, G., Jackson, B., DeAngelis, D.L., Milne, B.T. and Turner, M.G. **1988**. Indices of landscape pattern. *Landscape Ecology* **1**: **153–162**.

- Opdam, P., Rijdsdijk, G. and Hustings, F. **1985.** Birds communities in small woods in an agricultural landscape: effects of area and isolation. *Biol. Conserv.* **34:** 333–352.
- Phipps, M., Baudry, J. and Burel, F. **1986.** Ordre topoécologique dans un espace rural, les niches paysagiques. *CR Acad Sc Paris, T 302, Série 3,* **20:** 691–696.
- Pickett, S.T.A. and White, P.S. **1985.** The ecology of natural disturbance and patch dynamics. Academic Press, New York.
- Pollard, E., Hooper, M.D. and Moore, N.W. **1974.** Hedges. Collins and Sons, London.
- Rackham, O. **1986.** The history of the countryside J.M. Dent & Sons Ltd, London, Melbourne.
- Ranta, E. and As, S. **1982.** Non-random colonization of habitats islands by carabid beetles. *Ann Zool Fennici* **19:** 175–181.
- Risser, P.G., Karr, J.R. and Forman, R.T.T. **1983.** Landscape ecology directions and approaches, The Illinois Natural History Survey, Natural resources Building 607 East Peabody Drive, Champaign, Illinois **61820,** 16 p.
- Romme, W.T. and Knight, D.H. **1982.** Landscape diversity: the concept applied to Yellowstone Park. *BioScience* **32:** 664–670.
- Schreiber, K.F. **1988.** Connectivity in landscape ecology, Proc. 2nd int. seminar of the international association for landscape ecology. *Münstersche geographische Arbeiten,* **29,** 255 p.
- Thiele, H.U. **1977.** Carabid beetles in their environments. Springer-Verlag, Berlin, Heidelberg, New York.
- Turner, M.G. **1987.** Landscape heterogeneity and disturbance. *Ecological studies* **64.**
- Urban, D.L., O'Neill, R.V. and Shugart, H.H. Jr. **1987.** Landscape ecology. *BioScience* **37:** 119–127.
- Voss, R.F. **1988.** Fractals in nature: from characterization to simulation. *In* The science of fractal images. pp. 21–70. Edited by H.O. Peitgen and D. Saupe. Springer Verlag New York.
- Watt, A.S. **1947.** Pattern and process in the plant community. *J. Ecol.* **35:** 1–22.
- Whittaker, R.H. **1967.** Gradient analysis of vegetation. *Biol. Rev.* **42:** 207–264.
- Zonneveld, I.S. and Forman, R.T.T. **1989.** Changing Landscapes: an ecological perspective. Springer-Verlag, New York.