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Modelling bird communities/landscape patterns relationships in a rural area of South-Western France

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Abstract

The new trends in agricultural policy in Western Europe conduct to new management problems in maintaining and utilizing biological resources. In the South-Western France, the evolution of agricultural practices occurs in two opposite ways. On one hand, the intensification of agriculture leads to simplify the landscape by hedgerows removal, grasslands ploughing and drainage for corn cultivation. On the other hand, the decreasing numbers of cattle and sheep conduct the less fertile parts of the territory to evolve into fallow. These two processes are closely linked on a same territory and important interactions exist between intensive agricultural areas and semi-natural communities. To understand the importance of these interactions and their role in ecological stability of landscapes, we use passerine bird communities as an ecological indicator.

We modelized the relationships between birds and landscape structure from 256 relevés. Each relevé includes **a** bird count point of 20 mn and a description of the landscape feature on the surrounding *6.25* ha. **An** ordination of the releves along the main ecological gradients was realized using Correspondence Analysis. Then, these ordinations where related to the landscape structure with Stepwise and Multiple Regression Analysis. The rate of woody area, the hedgerow network complexity and the rate of fallow land are the main ecological gradients. We have used this model to measure the importance of the changes induced on landscape by a range of management practices differing in intensity. To achieve this aim we compare the displacement of 116 relevés along the ecological gradients between **1983** and 1988. The changes occurring both in bird composition and landscape structure reveal the ecological impacts of the different management practices (hedgerow removal, drainage, ploughing, decreasing grazing pressure). We examine the behaviour of ecological diversity of landscape units differing in structure and use.

1. Introduction

The main goals of the current EEC agricultural policy are to reduce the production of agriculture by two complementary ways: the development of a low input agriculture with more ecological practices of production than in the past decades and the continuation of a high input agriculture on a reduced area (set-aside policy).

In South Western France, these two trends actually coexist within the same territory as a result of different individual past choices among the farmers. The resulting landscape is an unmanaged mosaic of interacting patches of low/high input agriculture. This situation constitutes a framework to answer the following general questions:

What are the consequences of these rapid changes in agriculture on the landscape patterns?

Is it possible to measure and predict the changes occurring in the ecological characteristics of these landscapes, and therefore provide a diagnosis tool to help decision making of land-planners in the spatial arrangement of the low/high input agriculture patches?

In order to study such questions one needs first an ecological indicator that reflects the ecological characteristics of a landscape, and secondly a strategy to diagnose the temporal and spatial changes occurring in both the ecological indicator and the landscape attributes.

Changes in composition and organization of communities generally reflect changes in the patterns of ecological systems. To measure these changes they provide a set of indices like species number or abundance, empirical indices like biotic index of the quality of fresh water (Verneaux and Tuffery 1967), information theory index like Shannon H′ diversity index (Tramer 1969; Whittaker 1972; ...) or like gradient indices based on multifactorial ordinations of a species x relevés matrix (Rotenberry and Wiens 1980; Prodon and Lebreton 1981; Balent 1986; Hacker 1986).

Blandin (1986) proposed a general framework to diagnose the effects of anthropogenic disturbances on the structure and functioning of complex ecological systems like landscapes. The method consists in two distinct steps. First it is necessary to know the patterns of evolution of the structure and the function of the system under a wide range of natural conditions including usual management practices by men; then it becomes possible to measure the deviation existing between the observed state of the system after a disturbance and the theoretical state without disturbance.

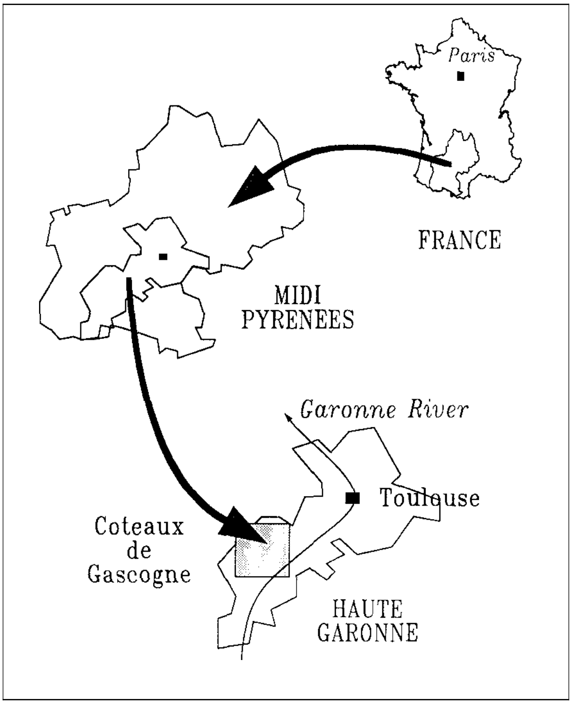
Baker (1989), in a recent review of models of landscape changes, distinguishes two main types of models: distributional and spatial models. Distributional models deal with the definition of landscape type based on the comparison of the importance of elements such as forest-types, land-use types or successional stages. The question is here to have an extend large enough to include the complete range of variation of the elements in order to correctly define the landscape units and describe the landscape patterns (Wiens 1989a). Ecologists need this kind of model to stress the mechanisms involved in temporal changes. Spatial models ‘use the location and configuration of landscape elements ..., and can thus explicitly output maps of these changing spatial configurations’ (Baker 1989). Here the problem is in the ecological consistence of the spatial changes observed on the map, their amplitude being strictly dependent of the extend of the map. This second kind of model constitutes useful tool for land-planners that rather dealt with spatial phenomena than with ecological processes.

In this paper, starting from the ideas and remarks of Blandin and Baker, we present a model based on an ordination of both landscape types and passerine bird communities along ecological gradients, transforming the geographical mosaic of heterogeneous landscape units into an ecological continuum (Balent 1989). The ordination of the landscape units along one or more ecological gradients from both passerine birds composition and landscape attributes characteristics provides powerful ecological indices to measure changes in landscape patterns. Such indices were successfully used by Prodon and Lebreton (1981) to study the bird species turn-over along a grassland-to-forest succession in the Mediterranean Basin. Our work is an extension of this method to heterogeneous landscapes. A detailed presentation of both theoretical and practical properties of this index is in preparation (Balent and Prodon in prep.). Breeding bird communities were chosen because they are sensitive to the changes in landscape structure and land use, and well suited to study territories of thousand hectares (Blonde1 1979; Opdam 1984).

2. The building of a regional model of landscape dynamics

2.1. *The studied area*

A multidisciplinary research work started in 1981 on the Coteaux de Gascogne area within the district of Aurignac (19000 ha; 70 km in the south-west of Toulouse; Map 1) to study the changes occurring in agricultural systems and their consequences on environment characteristics specially landscape patterns.



Map 1. Geographical location of the study area.

The district is a part of the region of the Pyrenean Foot-hills. The agriculture was there traditionally devoted to cattle farming and cropping but evolves now rapidly in two opposite ways. On one hand, the intensification of corn and sunflower cultivation leads to make the landscape uniform by hedgerow removal, grasslands ploughing and drainage. On the other hand, the decreasing number of cattle and sheep conduct to an extensive use of the less fertile parts of the territory evolving toward overgrown fallow land. The resulting landscape is a mosaic of patches of low or high input agriculture with no apparent spatial organization. The French Department of Environment asked for management tools for these spatial processes and this area was chosen for modelling purpose because of its diversity, as all the types of landscapes from forests to corn-fields can be found within the 19000 ha of the Aurignac district.

2.2. Sampling design

In spring 1981, we sampled the breeding avifauna of the whole district area with 780 point counts of unlimited distance located on a grid of 500 m in side. Counts were conducted between 5:00 and 11:00 in a morning during the month of May. All individuals heard or seen during 20-min period were recorded. Each plot was survey only once a year (Spitz 1974). From these data we mapped the different areas where the passerine bird communities where distinct (Balent unpublished data). Then, based on this map, a stratified sampling of 256 point counts was carried out in May 1982. The cell size was reduced to 6.25 ha (250 m in side) to better fit the home range extend of most of the species of passerine birds. The birds were recorded on a limited distance of 125 m around the point. **A** description of the main features of the landscape *i.e.*, land-cover and the vertical and horizontal structure of the remnant vegetation, within the cell surrounding each point count (Landscape Unit: LU) was realized both from field surveys and aerial photographs. Forty variables describing land use and hedgerows network were measured and/or calculated (Table 1).

These relevés were used to modelize the relationships between the structure of the landscape units and the passerine bird communities composition.

2.3. Data analysis

2.3.1. General principles

As pointed out by Opdam (1984), '... spatial changes in vegetation coincide with changes in animal communities, since most animal communities depend on the structure and species composition of the vegetation. However, the congruency between assemblages of plants and various animal groups is distorted by animal movements between vegetation patches, especially because the extent of these movements may vary widely between species'. For this reason, our main objective will be here to analyse ecological characteristics of landscape types defined *a posteriori* from bird communities patterns which is different from analyzing differences between bird communities characteristics of several *apriori* defined landscape types (Kalkhoven and Opdam 1984).

We firstly chose a working grain which is a com-

Table 1. List of the landscape attributes measured or calculated for the ***256*** landscape units.

Geographical attributes		
CRST		Landscape Unit located on a creast
VAL		LU in the bottom of a valley
SLOP		Slope: nil (0), light (1), medium (2), heavy (3)
EXPO		None
NOR		North
NE		North-East
EAST		East
SE		South-East
SOUTH		south
SW		South-West
WEST		West
NW		North-West
ROAD		Landscape Unit crossed by a road
LANE		" by a lane
RIVE		" by a river
BRKS		" by a brook
DITCH		Number of ditches
BANK		Number of banks
Area percentage of land-cover within the LU: (Brackets = Logarithm transformation)		
W	(LOGW)	% Wood
P	(LOGP)	% poplar tree
H	(LOGH)	% hedgerow
F	(LOGF)	% fallow land (canopy > 2m)
J	(LOGJ)	% juniper fallow land
G	(LOGG)	% grassland
M	(LOGM)	% meadow
I	(LOGI)	% improved grassland
C	(LOGC)	% crop
Landscape heterogeneity		
NLC	(LNLC)	Number of different land-cover within LU
CI		Horizontal Complexity Index from BAUDRY and BAUDRY-BUREL (1982)
Hedgerow attributes		
NLH		Number of linear pieces of hedgerows
L50; L100; L200; L300		Number of linear hedgerows >50m; >100m; >200m; >300m
H2; H4; H8; H16; H32		Hedgerow height >2m; >4m; >8m; > 16m; > 32m
W2; W4; W8; W18		Hedgerow width >2m; >4m; > 8m; > 16m
NH		Total number of hedgerows within a LU
TLH	(LTLH)	Total length of hedgerows within a LU
ARH	(LARH)	Total area of hedgerows within a LU
SCR	(LSCR)	Total vertical area of hedgerows within a LU (screen effect)
Connectivity (BAUDRY, 1984)		
CO		Number of hedgerows without connexion
CL		Number of hedgerows with a L connexion (angle of 90°)
CT		" a T connexion (perpendicular hedgerows)
CX		" a X connexion (crossing hedgerows)
CP		a P connexion (i.e. connexion with a woodlot)

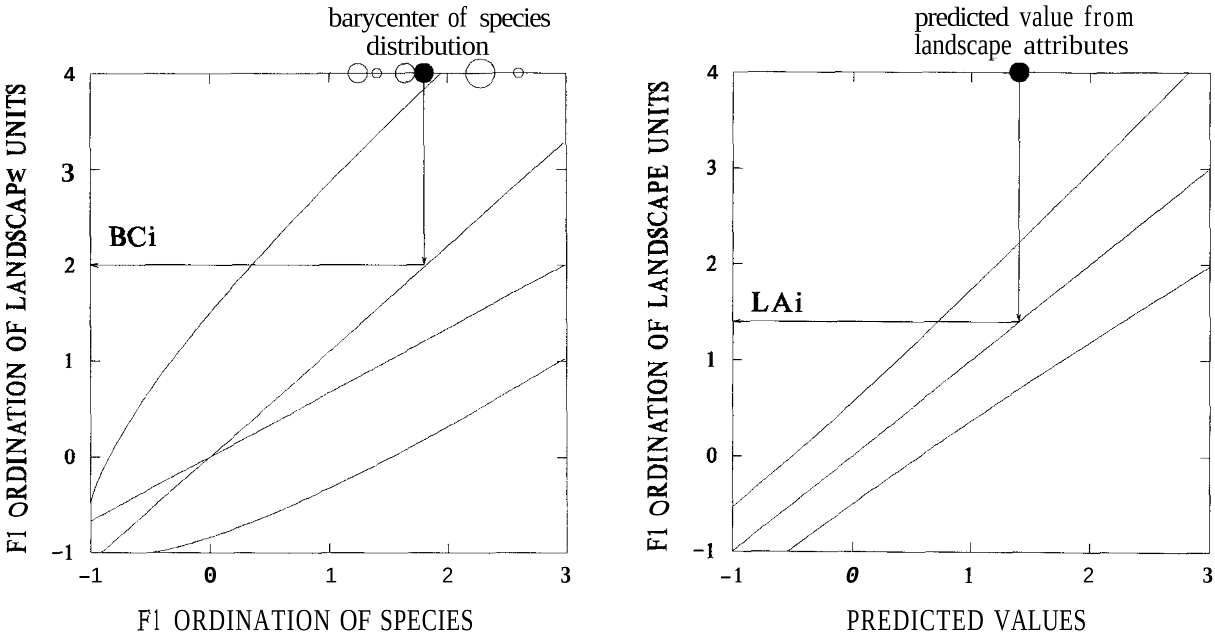


Fig. 1. Correspondence between Bird Composition index and Landscape Attribute index to calculate the score of a landscape unit along the first factorial axis (Adapted from Prodon and Lebreton 1981).

a. Canonical graph of the reciprocal ordination of species and relevés on the first axis. Exponential curves are the envelope of the data dispersion. Straight lines are the regression curves between releves X species (upper) and species X relevés (lower). First step is to calculate the barycenter of the distribution of the species occurring in a relevé; second step is to use the regression function to calculate BCi.

b. Multiple regression model between F1 ordination of relevés and some landscape attributes with confidence interval curves. LAi is calculated from the value of the different landscape attributes within the releve.

promise between the extend of the territory of the different bird species (A multi-scale approach is under study). The resulting studied territory is a sum of small patches (256 cells of **250** m in side) scattered in the Aurignac district territory.

To summarize the two step procedure: 1. A description of the relationships between bird communities and landscape attributes within a geographical extend large enough to include all the possible landscape types, the sample being *geographically discontinuous*. 2. The use of the model, as a diagnosis tool, on any given part of a *continuous territory* without care about its ecological representativeness.

2.3.2. Reciprocal ordination of the species and the relevés

Correspondence Analysis (CA: Benzécri *et al.* 1973b) was used to analyse the data matrix (45 species X 234 relevés), with different objectives:

– as a filter to eliminate outlier samples from the initial data set (22 landscape units were rejected);

– to establish the hierarchy of the main ecological gradient influencing bird community patterns;

– to calculate reciprocal ordination of bird species and landscape units along the main ecological axis; CA provides the best ordination of a species X relevés matrix (Benzecri *et al.* 1973a; Esteve 1978). We should notice after Chessel *et al.* (1982), Wartenberg *et al.* (1987) and others that this property is lost from manipulating the distances between species in Detrended Correspondence Analysis (Gauch 1982). The ordination of relevés based on bird data produces, on each axis, a single score for each relevé summarizing its composition relative to all other releves with respect to the various components of the bird composition variation. We will call these scores Bird Composition Index (BC_i: Prodon and Lebreton 1981).

– as a reference model to analyze the ecological

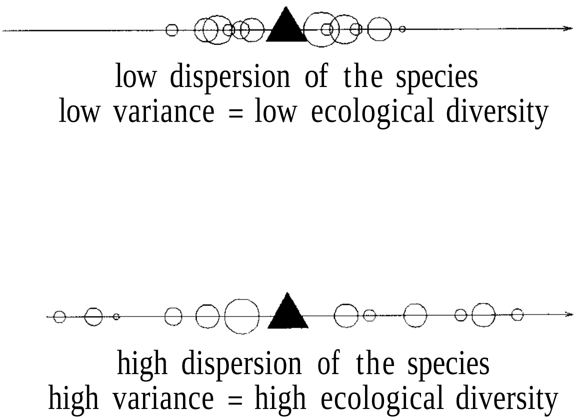


Fig. 2. Definition of the ecological diversity (from Prodon 1988).
Two theoretical releves differing in their bird composition are presented ordinated along the same ecological gradient. They have the same barycenter (dark triangle), the same number of species (empty circle) but these species differ in their ecological preferences. In the upper case the species occurring in the first relevé exhibit little differences in their ecological preferences (low dispersion along the gradient) while in the lower case the species occurring in the second relevé are very different (high dispersion along thegradient). The first relevé have a low ecological diversity. The second relevé have a high ecological diversity. Variance of the dispersion of species measures the ecological diversity.

characteristics of any given landscape unit of a rural territory. The procedure is to calculate the scores (BC_i) of an extra sample on the axes of the model from the score of its bird composition. This is done with the 'transition formula' described in Benzécri *et al.* (1973b) *i.e.*, the barycentre of the scores of its bird species, multiplied by a constant depending on the correlation between bird species and landscape units on the factorial axis (Fig. 1a). The quality of the result depends upon the way the species are ordinated in the CA model. Prodon and Lebreton (1981) have stressed the importance of an exhaustive sampling of all the possible landscape types where the species can be found to obtain a valuable species ordination.

2.3.3. Definition of landscape types

Hierarchical Ascending Clustering (HAC: Jambu 1977; Jambu and Lebeau 1978) was used to compute the landscape types from the scores of the landscape units on the first four axes of CA (Balent *et al.* 1988). The histogram of the inertias associated to the successive dichotomies of the dendrogram, helps us to decide on the number of cluster with a statistical meaning. A marked fall in the inertia after the 8th dichotomy indicates $8+1=9$ clusters to be conserved. The number of cluster is thus define on a statistical basis. This routine overcomes a difficulty mentioned by Baker (1989) to define an objective number of landscape types within a given set of data.

2.3.4. Ecological diversity

It has been clearly demonstrated by many authors that species richness and structural diversity index *e.g.*, information theory index like Shannon diversity H', are strongly correlated. The ecological diversity index (Chessel *et al.* 1982; Prodon 1988) is basically different from any diversity index because it depends mainly upon the ecological response of each species occurring in a relevé along an environmental gradient. The more landscape units are ecologically homogeneous *i.e.*, the more the species have a similar response to an ecological factor and by the way the more the ecological diversity indices are low (Fig. 2).

2.3.5. Modelling the relationships between the ordination of the landscape units from bird data and landscape attributes

To modelize the relationships between the ordination of the landscape units from bird data and landscape attributes we compute a multiple regression model between the scores of the landscape units along the F1 axis of CA (*i.e.*, the ordination from passerine bird composition) and a set of landscape attributes selected by a stepwise regression analysis. We call the score of landscape units along the F1 factor predicted from the multiple regression model, Landscape Attribute Index (**LA_i**; Fig. 1b).

Thus, we have two complementary ways to calculate the ecological value of any landscape unit on the F1 axis: from its BC_i or its LA_i. If BC_i and LA_i are similar a good correspondence exists between the landscape structure and the composition of the bird community. A difference between BC_i and LA_i means that the birds respond later than expected to a disturbance. This difference constitutes a

Table 2. List of the bird species used in the Correspondence Analysis.

Latin Names	English Names
Coturnix coturnix	Quail
Columba palumbus	Wood Pigeon
Streptopelia turtur	Turtle Dove
Cuculus canorus	Cuckoo
Picus viridis	Green Woodpecker
Picoides major	Great Spotted Woodpecker
Picoides minor	Lesser Spotted Woodpecker
Lullula arborea	Wood Lark
Alauda arvensis	Sky Lark
Hirundo rustica	Swallow
Anthus trivialis	Tree Pipit
Motacilla alba	White Wagtail
Troglodytes troglodytes	Wren
Erithacus rubecula	Robin
Luscinia megarhynchos	Nightingale
Saxicola torquata	Stonechat
Turdus merula	Blackbird
Turdus philomelos	Song Trush
Turdus viscivorus	Mistle Trush
Hypolais polyglotta	Melodious Warbler
Sylvia communis	Whitethroat
Sylvia borin	Garden Warbler
Sylvia atricapilla	Blackcap
Phylloscopus bonelli	Bonelli's Warbler
Phylloscopus collybita	chiffchaff
Regulus ignicapillus	Firecrest
Parus caeruleus	Blue Tit
Parus major	Great Tit
Sitta europaea	Nuthatch
Certhia brachydactyla	Short-toe tree Creeper
Oriolus oriolus	Golden Oriole
Lanius collurio	Red-backed Shrike
Garrulus glandarius	Jay
Pica pica	Magpie
Corvus corone	Carrion Crow
Passer domesticus	House Sparrow
Fringilla coelebs	Chaffinch
Serinus serinus	Serin
Carduelis chloris	Greenfinch
Carduelis carduelis	Goldfinch
Acanthis cannabina	Linnet
Pyrrhula pyrrhula	Bullfinch
Miliaria calandra	Corn Bunting
Emberiza citrinella	Yellowhammer
Emberiza cirlus	Cirl Bunting

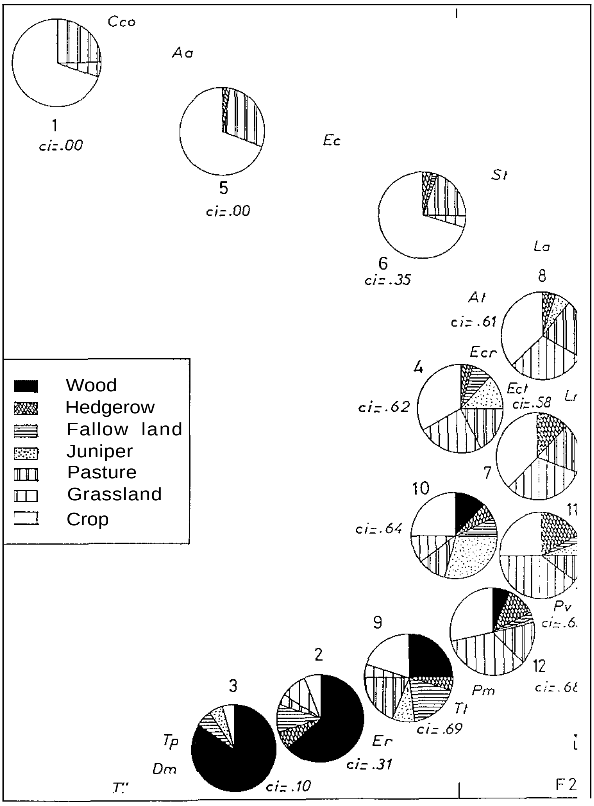


Fig. 3. Plan F1-F2 of the correspondence analysis. Only species most contributing to the axes are plotted. The pie diagrams are located at the barycenter of the distribution of the landscape units included in the twelve different landscape types resulting from HAC analysis. Land use values are the average by type.

Cco = Coturnix coturnix; Aa = Alauda arvensis; Ec = Miliaria calandra; St = Saxicola torquata; La = Lullula arborea; At = Anthus trivialis; Ecr = Emberiza cirlus; Ect = Emberiza citrinella; Lm = Luscinia megarhynchos; Pv = Phylloscopus collybita; Pm = Parus major; Tt = Troglodytes troglodytes; Er = Erithacus rubecula; Tp = Turdus philomelos; Tv = Turdus viscivorus; Dm = Picoides major; Ci = Complexity Index (see text).

measurement of the resilience of the ecological system to a disturbance (Prodon 1988).

BIOMECO Software (Lebreton *et* al. 1987) was used for CA and HAC analysis, SYSTAT Software (Wilkinson 1990) for the interpretation of the results and for Stepwise and Multiple Regression analysis.

2.4. *Results*

2.4.1. *The ecological factors affecting bird composition*

The *45* species of passerine birds involved in the analysis are listed in Table 2.

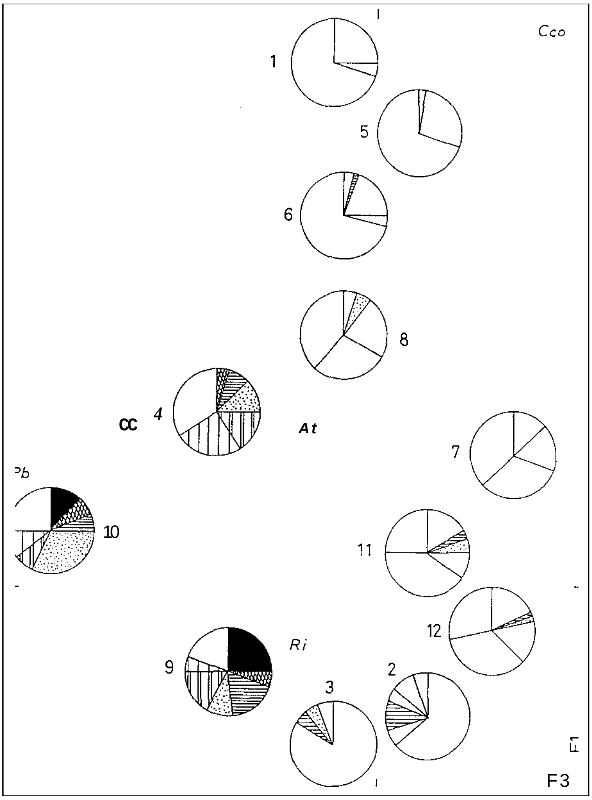


Fig. 4. Plan F1-F3 of the correspondence analysis.s The legend of the pie-charts **is** the same **as** Fig. 1.

Pb = Phylloscopus bonelli; Cc = Acanthis cannabina; At = Anthus trivialis; Ri = Regulus ignicapillus.

F1 axis (Fig. 3). Three typical species of very open landscapes, Alauda arvensis (Aa), Miliaria calandra (Ec), Saxicola torquata (St) and Coturnix coturnix (Cco) contribute to 53% of the inertia of axis F1 in the positive values of F1. On the other hand, woody species like Erithacus rubecula (Er), Turdus philomelos (Tp) and viscivorus (Tv) contribute to 14% of the inertia of the negative values of F1. Along this axis, landscape units vary progressively from very close forest types to open cultivated landscapes. This gradient of opening of landscape from the forest to the cropland (Forest-to-corn-field gradient) is consistent with the results of Karr & Roth (1971), Blondel *et al.* (1978), Stauffer and Best (1980), Prodon and Lebreton (1981), Arnold (1983) and many others.

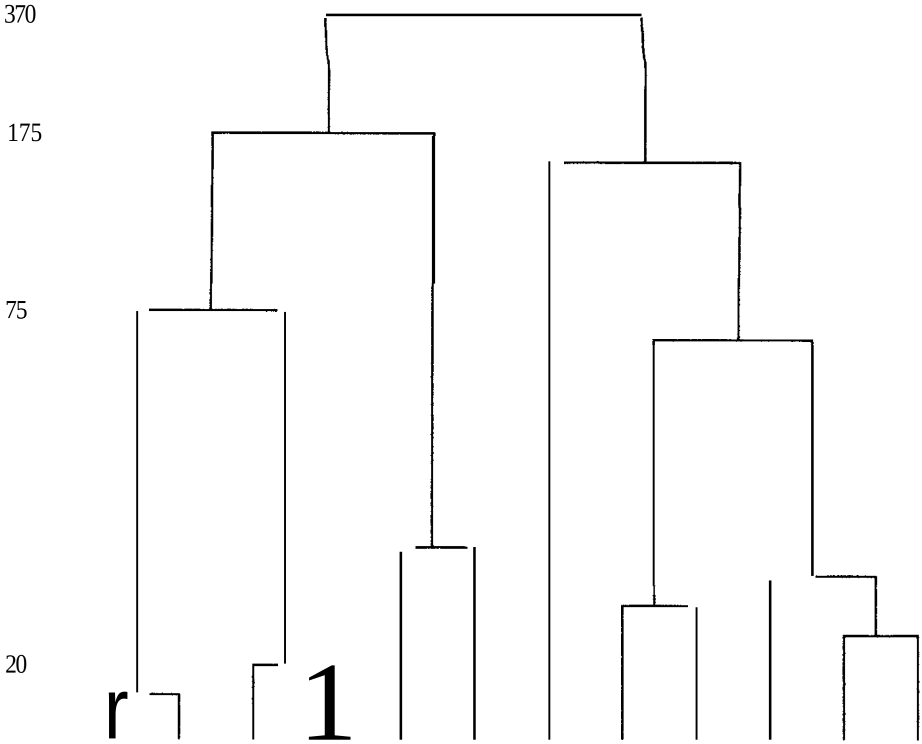
F2 axis (Fig. 3). Emberiza cirlus (Ecr), Emberiza citrinella (Ect), Sylvia communis (Sc), Picus viridis (Pv) and Luscinia megarhynchos (Lm) contribute to 17% of the inertia of F2 axis. The associated landscape units exhibit long hedges with a lot of Quercus pedonculata tall trees; the 'horizontal complexity' of these landscape units, measured with the complexity index (CI) of Baudry and Baudry-Burel (1982), is particularly high. On the opposite side of the axis, we find very simple landscape like forest or openfield. The score of the landscape units along the second axis are ranked according to the complexity of landscape.

F3 axis (Fig. 4)
Phylloscopus bonelli (Pb), Anthus trivialis (At), Acanthis canabina (Cc) and Regulus ignicapillus (Ri) contribute to 59% of the inertia of the third axis (F3). The first species is closely related to scrubs and shrubs located at the hedges of grazed woodlots of Quercus pubescens. Anthus needs some isolated trees with an understorey of short grass while, within the studied area, Acanthis cannabina is nesting in Juniperus communis. These three species are closely related to fallow land types of vegetation (*e.g.*, Juniperus and Rubus sp. on abandoned grasslands; woody species of the early stage of succession in clearcuts). The third axis **F3** ranks the landscape units and the bird species according to the increasing importance of fallow land area within landscape units.

2.4.2. The characteristics of landscape types

The cluster analysis distinguishes between two sets of open and close landscape types. The following steps of the clustering process define successively four, six and finally 12 types of landscape (Fig. 5).

Closed landscape types. Types 3 & 2 represent the woody habitats (forests and woodlots) and their outskirts. Types 11 & 12 are made of the typical undisturbed hedgerow networks with an average length of more than 250 m of hedges and an heavy percentage of grasslands within each landscape unit. The types 9 & 10, the vegetation is unmanaged. Re-growth of clearcuts are found in the type 9 and invasion of abandoned grasslands by Juniperus communis and Prunus sp. in the type 10.



CLASS	12	11	10	9	3	2	1	5	6	4	7	8
NBLU	44	16	9	12	27	46	9	6	14	17	19	10
WOOD	5	1 1	2 2	5 9	0 6	1	0	0	0	0	0	0
HEDGER	12	14	5	6	0	5	0	1	3	8	10	7
FALLOW	3	2	7 1	6	4 1	0	0	0	0	4	1	1
JUNIPER	1	6	28	12	0	1	0	0	1 1	3	0	2
GRAZLD	20	11	12	15	2	8	22	32	20	19	16	20
GRASSLD	29	41	10	7	1	9	6	0	6	22	33	33
ANGRAS	4	1	5	1	1	1	0	0 1	4	6 1	6	8
CROPS	25	24	20	17	1	3	73	67	56	27	22	30
HEDGL	254	270	94	113	4	97	0	0	54	164	141	62
CI	0.68	0.63	0.64	0.69	0.10	0.31	0.00	0.00	0.35	0.62	0.58	0.61

NBLU=**Number of landscape units;** WOOD=**woody area;** HEDGER=**hedgerow area;** FALLOW=**overgrown fallow land area;** JUNIPER=**juniper fallow land area;** GRAZLD=**grazing-land area;** GRASSLD=**permanent grassland area;** ANGRAS=**annual grassland area;** CROPS=**crop-fields area;** HEDGL=**hedgerow network length;** CI=**complexity index.**
(Areas are in % within LU; Lengths are in meters within LU).

Fig. **5.** Dendrogram of the Hierarchical Ascending Clustering and average value of landscape attributes within the 12 defined types. Only the most important landscape attributes are presented.

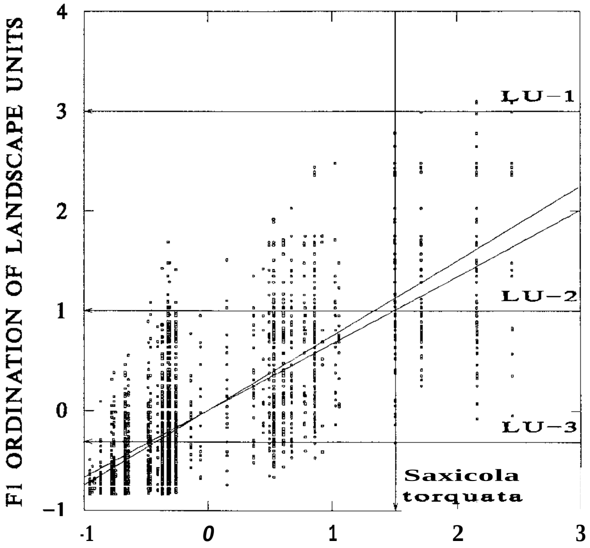


Fig. 6. Canonical graph of the reciprocal ordination of species and landscape units on the first axis.

Along a vertical line are the scores of the different landscape units where one species is found. Along an horizontal line are the score of all the species found in one landscape unit. This graph easily shows the dispersion of one species within the landscape units and the dispersion of all the species occurring within one landscape unit.

Open landscape types. Type 1 is the most simple type of landscape. Land use is exclusively devoted to cropping and grassland. The whole vegetation is shorter than 1 m. The lack of hedgerow and the presence of large ditches are the result of recent field reallotment. The landscape units of the classes 5 & *6* are located on the hill-sides overlooking the largest valleys. Remnants of low spiny hedgerows (1 to 3% of the landscape units area) are found between large fields of cereals and pastures.

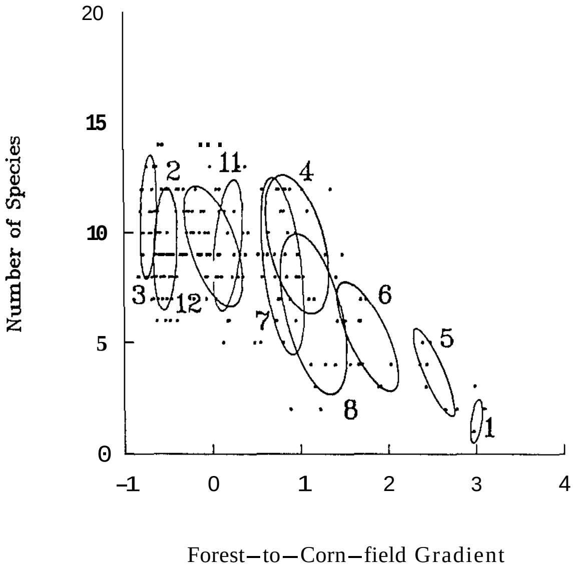
Types 4, 7 & **8** are intermediate between completely open and typical hedgerow network types. Types 4 & **8** are the most simple landscape resulting from the traditional agricultural systems of mixed crop-fields and animal husbandry while type 7 is the first stage towards an extreme simplification of landscape types by intensive agriculture.

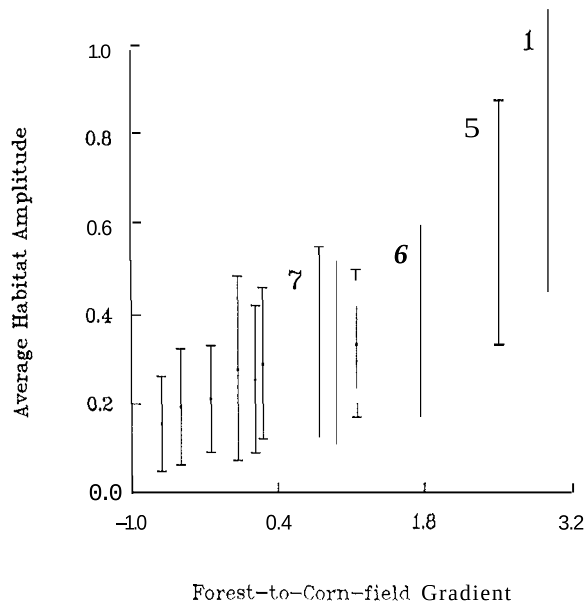
2.4.3. Characteristics of the landscape units along the first ecological gradient

One of the most interesting property of CA is the reciprocal ordination of species and relevés provided on the axes specially on the first one because of the high canonical correlation. On the Fig. *6* we plotted the scores of the 234 landscape units on the Fl axis against the scores of the **45** passerine bird species. The bird species exhibit differences in the niche breadth along the first axis. When the score of the species is lower than –0.5 we find strictly forest species with a narrow niche breadth (Sitta europaea, Erithacus rubecula, Turdus viscivorus ...); between –0.5 and 0, forest species that are also found in hedgerow habitats *i.e.*, with large niche breadth (Turdus merula, Sylvia atricapilla, Certhia brachydactyla ...); between 0 and 1, we find typical hedgerow habitat species like Emberiza cirlus and citrinella with large niche breadth; between 1.5 to 2.5, we find the open landscape species Saxicola torquata, Miliaria calandra, Alauda arvensis and Coturnix coturnix with very large niche breadth. The general pattern of niche breath is to increase from forest species to open landscape species.

The dispersion of the species within the landscape units *i.e.*, the ecological diversity exhibits a different pattern of evolution along the F1 axis. When the score of the landscape unit is lower than –0.25 we find forest landscape (LU-3) with a low ecological diversity; between –0.5 and 1.5, we find hedgerow network landscape (LU-2) where the ecological diversity is very high; for values greater than 1.5, we find open landscape units (LU-1) where the ecological diversity decreases strongly.

We plotted the number of species of the landscape units against the scores along F1 axis (Fig. 7a). On the first half of the gradient *i.e.*, from forest to the open hedgerow network, the number of species remains roughly constant around ten. That means that the important increase observed in the complexity of landscape has a little effect on the bird species richness of the landscape units. The number of species strongly decreases in the second half of the gradient specially for landscape types corresponding to intensive agricultural practices (Types *6*, 5 & 1) where nesting site are scarce. In respect of the species richness, a critical threshold seems to exist between the intensively managed types of landscape and the traditional ones. In the





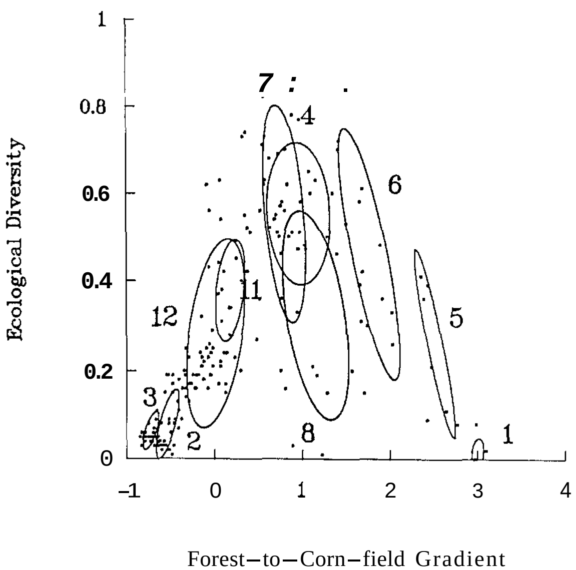


Fig. 7. Relationship between the ordination of the landscape units along the F1 axis and the number of species (a), the ecological diversity (b) and the mean and variance of the habitat amplitude within the different landscape types (c).

type 8, *i.e.*, the most open of the traditionally managed landscape types, the average number of species is around 6 vs 1.5 for the type 1.

The pattern of variation of the ecological diversity are completely different compared to the species richness (Fig. 7b). As pointed out before, forests and their immediate outskirts present a low ecological diversity *i.e.*, all the species present in forest landscape have their ecological optimum in forest habitats. The ecological diversity strongly increases with the complexity of landscape. The type 11 *i.e.*, remains of the old typical hedgerow network surrounding damp grasslands in the bottom of the valley, presents an intermediate diversity. The maximum of diversity is reached for fine grained landscape types located on the gentle slopes of the hill-sides (4) but also, for more degraded types of landscape (7 & *6*). At the end of the gradient, as prior indicated for species richness, the marked fall of the ecological diversity indicates an ecological threshold with the extreme simplification of the landscape. Baudry (1984) has found the same patterns of variation with a structural index called grain size diversity: 'Starting with a fine grain hedgerow network landscape, hedgerow removal increases grain size diversity as small grains remain in a more open landscape, diversity is constant for a while, then there is a sharp decrease when few hedgerows are left and an open field landscape emerges'. The community structure measured with ecological diversity, roughly follows the landscape structure measured with the grain size diversity.

However there are some differences in the within-type ecological diversity variations between the traditional landscape types and the modern types. As pointed out by the shape of the inertia ellipses, the within type variance of the ecological diversity is higher for the degraded types of landscape (7, 6, 5) than for traditional types. That probably means that the ecological structure of bird communities corresponding to the degraded forms of landscape is more unstable than for undisturbed ones. One reason is the poor number of species of the landscape units in the completely open landscape type. Another one in the ecological characteristics of the species within each landscape type (Fig. 7c). Along the Forest-to corn-field gradient the average habitat amplitude of species within the different landscape types regularly increases. The more the landscape is open the more the first dimension of the niche of the species is large. Species with narrow niche along the first axis are only found in forest types and hedgerow networks. The within-type variance of the habitat amplitude is maximum in the intensively managed landscape types (1, 5, 6, 7). This point reveals the great heterogeneity of the bird communities within the landscape types for our data set and our working scale.

Finally, it is important to notice that the three indices exhibit the same ecological threshold consecutive to the removal of hedgerows.

2.2.2. *Modelling the relationships between the F1 ordination of landscape units and landscape structure*

Table 3 gives the statistical characteristics of the multiple regression model fitting F1 ordination of landscape units to the six landscape attributes selected with a stepwise regression routine (alpha-to-remove value = .15). General fitting is fairly good as indicated by the high value of the multiple coefficient of correlation and F test on the results of the analysis of variance. However as our grain of study remains constant along the whole gradient, the grain of the landscape units changes along the same gradient. This is the reason why fitting is better for landscape units with an important percentage of woody area and hedgerow network than for widely open landscape (Fig. 8).

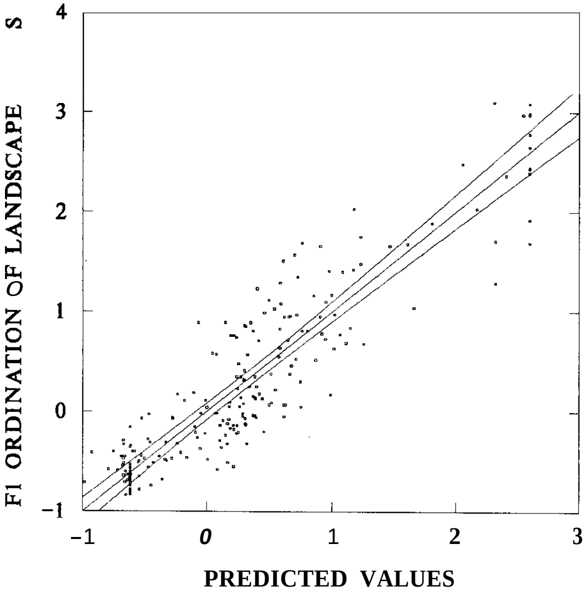


Fig. 8. Bird Composition Index plotted against Landscape Attribute Index.

The selected landscape attributes are of practical interest because they are very easy to calculate from field surveys and aerial photographs and even from aerial photographs alone. We should notice the particular importance of the percentage of woody area within the landscape unit, which contribution to the multiple coefficient of correlation (see Scherrer 1984) is about 0.85. Total length of hedgerows appears to be more efficient than structural characteristics such as connectedness. The reason is to be found in the low connectivity of landscape attributes, the number of hedges without connections (Baudry 1984) being largely dominant.

Table 3. Statistical parameters of the multiple regression model fitting the F1 ordination of the landscape units to the six selected landscape attributes.

Number of LU = 234 R = .927 R^2 = .860

VARIABLES	COEFFICIENTS
CONSTANT	+2.599
FALLOW LAND AREA	-0.010
JUNIPER FALLOW LAND	-0.005
HEDGEROW AREA*	+0.153
GRASSLAND AREA*	-0.167
WOODY AREA*	-1.607
HEDGEROW LENGTH*	-0.629

$F(6,227)=230.16$ $(P>0.0001)$

* Logarithm transformation.

3. The use of the model *to* evaluate changes in landscape

The use of the model as an evaluation tool for landscape changes has been conducted on a parish where we knew a field reallotment was planned.

3.1. The studied area

The parish of St.-Andre is located in the north of the Aurignac district where the model was elaborated. The studied area (725 ha) located in the southern part of the parish is divided into three distinct geographical units. In the middle, a flat valley of about 600 m wide with a river running from west to east is characterized by hedgerow fenced fields mainly devoted to haying and cropping. On its south, a steep slope hill side with residual woodlots and extensive pastures. On its north, a set of adjacent parallel talwegs with more gentle slopes occupied by pastures, hay-meadows and above all cereals. Human habitat is scattered on the territory but mainly located on the top line of the hills.

3.2. Sample design

The studied area has been covered with a grid of *250* m in side, *i.e.*, corresponding to the size of the landscape units entered in the model. Thus 116 contiguous cells were sampled twice with SCP and landscape attribute description: First in May 1983 and a second time in May 1988, after the field reallotment, carried out during winter 1987/1988. BC_i were calculated for the three main factors of CA model as abovementioned, and LA, for the first factor from the multiple regression model. The calculated indices were mapped after an exponential smoothing ($\mathbf{Y} = e^{-\alpha X}, \alpha = 1$) to take into account the spatial relationships of the different landscape units on the grid (Balent and Lauga, unpublished).

3.3. Intensification of agriculture

3.3.1. Changes in landscape

There is a strong effect of reallotment on LA, in the bottom of the valley and in one adjacent small valley (Figs. 9c and 9d). A detailed analysis of the variation of some landscape attributes between the two dates shows a decrease of 20% in hedgerow length, an increase of 40% of the cultivated area and an important increase of field size. There are now two large patches of open landscape with not any remnant hedgerow vegetation.

3.3.2. Changes in bird community

In 1983 the pattern of distribution on the territory of landscape units with an BC_i indicating an open landscape was a mosaic of isolated cells, mainly located in the valley (Fig. 9a). In 1988 they constitute two large patches. The boundaries of the patch upright on the Fig. 9b are roughly the same as those of the corresponding LA, patch (Fig. 9d). Actually, species of open landscape like Alauda arvensis, Saxicolatorquata or Miliaria calandra were already present in the previous coarse grain grassland-hedgerow network landscape.

On the other hand, the second patch (left of Fig. 9b) is far less extended than the corresponding patch on Fig. 9d. Here the patterns of transformation are quite different. The initial landscape was a

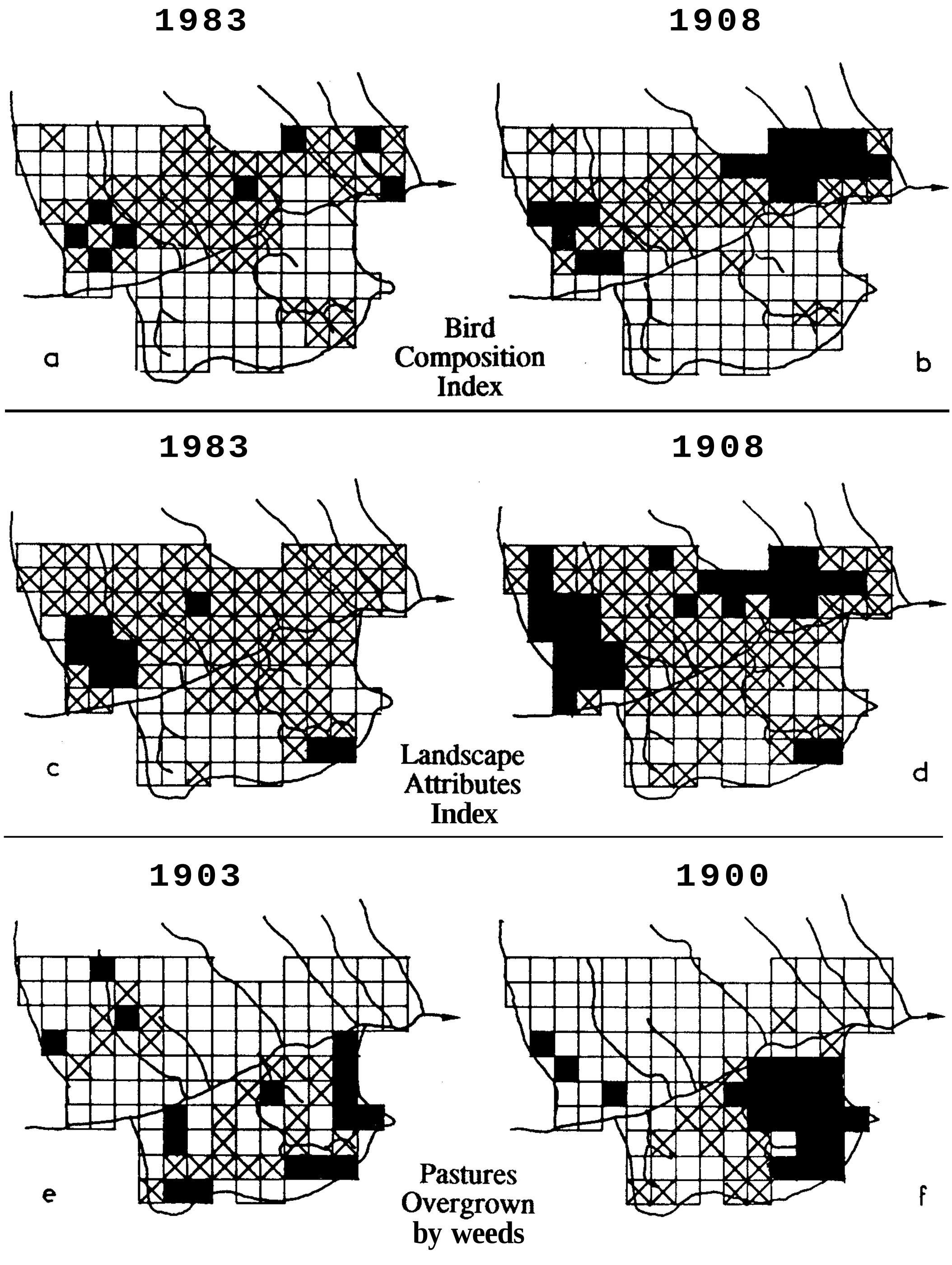
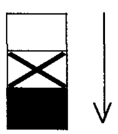


Fig. 9. Influence of the change in agriculture on the landscape of the parish of St.-André.

a & b: BC_i on F1 axis; c & d: LA, for the F1 axis; e & f: BC_i on the **F3** axis. The value of the indices have been clustered in three classes. Threshold values between classes are the same for the two years.

Increasing values of indices.



fine grain mosaic of small fields of wheat and barley, vineyards and pastures where the open landscape species above-mentioned were traditionally missing. The first spring after field reallotment, the species of the fine grain landscape are still present whereas those of open landscape are missing. This point illustrates the differences in the ecological response of fine and coarse grain landscapes to disturbance (Pickett *et al.* 1989) and the importance of the landscape history.

3.4. Abandonment of agriculture

On the southern part of the study area, the patterns of changes in landscape are different and appear mainly through changes in the BC_i on the third factorial axis (Fig. 9e and 9f). On the steep slope hill side the abandonment of intensive grazing on the pastures between the two dates has led to the appearance of a large patch of fallow land. The important changes in bird community composition are due to the invasion of pastures by weeds and woody species like Juniperus communis, Rubus fructicosus, Rosa canina ... this colonization providing a lot of nesting site to Acanthis cannabina, Serinus serinus, Carduelis carduelis, Carduelis chloris and Phylloscopus bonelli.

4. Conclusion

These first results confirm the interest of Correspondence Analysis to modelize community dynamics in heterogeneous environment. It allows a hierarchical ordination of the main factors structuring the data *e.g.*, Forest-to corn-field gradient, complexity of hedgerow network .... Moreover, the canonical correlation between species and relevés allows to calculate in an optimal way the functional distances between the different species and spatial units along ecological gradients. **As** a consequence, the habitat amplitude (niche breath) of species and the ecological diversity of landscape units as defined by Chessel *et al.* (1982) are also expressed in an optimal way. Despite their properties, these two indices have already been poorly used to study the functional response of communities to changes occurring in environmental factors excepted by Prodon and Lebreton (1981). Their accuracy to detect changes in the ecological structure and function of community near the threshold separating open landscapes and hedgerow networks answers the address by Turner *et al.* (1989a) to 'consider the importance of measuring and modeling variance, rather than means, particularly near critical thresholds'.

The method presented here allows us to establish the hierarchy of ecological factors structuring the landscape with a passerine bird point of view, to study the behaviour of bird communities both in the ecological space (CA factorial plans, ecological diversity) and in the geographical space (maps of smoothed BC_i). This point is of importance because, as above-mentioned, the accuracy of the landscape types depends strictly of the accuracy of the ecological extend of the initial sample. Now, from a practical point of view, we generally diagnose the ecological processes within a given part of the territory (commune, district) not necessarily involving all the landscape types existing in the region. The danger of such an analysis conducted on a small territory without referring to a general model is in resulting poor quality of the measurement and modelling of the habitat amplitudes of species and ecological diversity of landscape types.

We have built a model to diagnose the ecological changes occurring with the evolution of the management of landscape by agriculture. This tool can also be use for conservation purposes. Ecological diversity for instance is maximum for degraded types of hedgerow network landscape. In that case the aim of conservation of the highest level of ecological diversity is not necessarily a suitable objective. We have first to look carefully to the history of the landscape types that means to take a long time period in consideration. Secondly to compare the values of ecological diversity for a wide range of landscape types that means to study landscape patterns within a large geographical extend.

The further steps to be developed now deal with the significance of the distances between the different landscape units and types observed along

along the main ecological gradients after a disturbance. We specially aim to relate the measured ecological distances (*i.e.*, BC, and LA_j) to more concrete parameters like productivity of agro-ecosystems *i.e.*, management of energies by farmers (Sauget and Balent 1991); Our model works all over a wide range of landscape conditions in south-western France. We also need to establish relationships between the model results and remote sensing data to map the landscape changes at a broader scale and test the limits of its validity.

Finally, the model indicates an ecological breakdown when the opening of the agricultural landscape is extreme. But as pointed out by Allen (1987), Blondel (1986), Meentemeer (1989), Turner *et al.* (1989b) and others, changing spatial scale is of primary importance in the analysis of landscape patterns. Wiens (1989b) outlined the importance of both spatial and temporal scales in the predictability of ecological processes. The question is now to precise the ecological accuracy of this threshold by comparing several ecological points of view differing in spatial scale of study. Studying relationships between communities and landscape attributes has to be done at a proper spatio-temporal scale (Golley 1989). We are now starting multiscale researches including, on the same territory, ecological indicators operating at different spatio-temporal scales such as carabid beetles, passerine bird communities, wild ungulates and raptors populations.

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