

Bird assemblages in mosaic forests: the relative importance of vegetation structure and floristic composition along the successional gradient

Louis-Félix Bersier ⁽¹⁾ and Dietrich R. Meyer

Institute of Zoology, University, Bd. Pérolles, CH-1700 Fribourg, Switzerland.

Abstract

We examined the hypothesis that birds choose their habitat on a large scale according to structural features of the vegetation, but that, within homogeneous habitat types, bird assemblages are more structured by the taxonomic composition of the plants. We studied bird assemblages in riparian forests near lake Grand Lieu, Brittany, France. These forests are mosaics composed of patches of different vegetation types, which cover the entire range of the forest succession. We used partial canonical correspondence analysis to investigate the contributions of the floristic and structural components of vegetation along the successional gradient, restricting the scale of investigation from the entire range of the succession toward mature forest. Vegetation structure accounted for the highest individual fraction of variation at the large scale, but the importance of floristics increased at smaller scales. These differences in contribution of sources of variation are statistically significant. We analysed the individual contribution of each variable, and it became apparent that this pattern was due to a strong increase of the importance of the richness of tree species, in contrast to the decrease of the importance of variables describing the structure of trees. These results are consistent with the hypothesis.

Keywords: Bird assemblages, riparian forests, community structure, spatial scale, forest succession, partial canonical correspondence analysis.

Résumé

Nous avons testé l'hypothèse que les oiseaux choisissent leur habitat sur une grande échelle d'après la structure de la végétation et que, dans des habitats homogènes, la composition en espèces végétales devient prédominante dans ce choix. Nous avons étudié les assemblages d'oiseaux dans les forêts riveraines du lac de Grand Lieu, en Bretagne. Ces forêts sont composées d'une mosaïque de différents types de végétation. Ces types de végétation couvrent toute la succession forestière. Des analyses canoniques des correspondances, contraintes par les variables de la structure de la végétation et de la composition floristique, montrent que les variables expliquant le plus de variation dans la distribution des oiseaux sont celles liées à la succession forestière. Nous avons utilisé des ordinations partielles pour calculer les contributions dues exclusivement à la structure, exclusivement

⁽¹⁾ Present address: Scripps Institution of Oceanography, UCSD, San Diego CA 92093-0202, USA.

à la floristique, et conjointement à ces deux éléments. La structure de la végétation explique la plus grande fraction de variation à grande échelle, lorsque toute la succession est prise en compte. La contribution de la composition floristique devient plus importante à petite échelle, lorsque seul le dernier stade de la succession est pris en compte. Ces différences sont statistiquement significatives. L'analyse individuelle des variables montre que cette évolution est due à une forte augmentation de l'importance de la richesse en espèces d'arbres et à une diminution de l'importance des variables décrivant la structure des arbres. Ces résultats sont en accord avec l'hypothèse.

INTRODUCTION

The study of relationships between the bird assemblages and the environment provides information on how birds occupy their habitat. Traditionally, studies of avian habitat selection have concentrated on the structure of the habitat (e.g. HILDÉN, 1965; WIENS, 1969; WILLSON, 1974; JAMES & WAMER, 1982; CODY, 1985*b*, 1985*c*). The plant taxonomic composition was disregarded, although some plant-bird associations were documented (e.g. ROTHSTEIN, 1971; SNOW & SNOW, 1971, 1980; SMITH, 1977; HOLMES *et al.*, 1979). WIENS and ROTENBERRY (1981) found strong relationships between the composition of bird assemblages and the floristics in steppe habitat on a regional scale, whereas these same bird assemblages, on the continental scale of North America, were correlated with the vegetation structure (ROTENBERRY & WIENS, 1980). Other studies found that floristics and bird assemblages were correlated (e.g. LOVEJOY, 1974; TOMOFF, 1974; POWER, 1975; HINO, 1985). This led ROTENBERRY (1985) to propose that birds distinguish between broad habitat types according to the vegetation structure, and that, at a smaller scale, they use floristic features to identify an appropriate habitat. He proposed that the underlying mechanism responsible for the association between birds and plants is related to food and foraging behaviour. If this association is evident for frugivores (see KARR, 1971), it is less obvious for insectivores (most of the species in our study are insectivores during the breeding season). ROTENBERRY (1985) proposed that such species respond to a group of particular plant species.

The present study of bird assemblages was carried out in the riparian forests of lake Grand Lieu (Brittany, France). These forests are not homogeneous, but are composed of a mosaic of different vegetation patches. Vegetation structure as well as plant taxonomic composition vary among vegetation patches and with them vary the habitats for birds. In forests, these mosaic structures are natural as well as man-made (BLONDEL, 1986; REMMERT, 1991; HANSSON, 1992; MEYER, 1993). The present study takes into account the structural and floristic components of vegetation separately. First, we investigate the relationships between bird assemblages and the structural and floristic components of the vegetation in all vegetation patches using canonical correspondence analyses. Second, we analyse the evolution along the successional gradient of the relative importance of the vegetation structure and of the plant taxonomic composition in explaining the variation in the bird data matrix. We use partial ordination for that purpose. Third, we test the hypothesis of ROTENBERRY (1985) in riparian forests: we compare the relative importance of vegetation structure and of floristics between small-scale homogeneous habitats and large-scale heterogeneous habitats.

The influence of the mosaic structure of forests on the bird assemblage, and particularly the importance of neighbourhood effects, will be treated elsewhere (BERSIER *et al.*, in prep).

METHODS

Study area, vegetation

The riparian forests at the site of lake Grand Lieu were chosen because they are particularly species-rich and are thus presumed to yield general relationships between habitat and community structure more easily (see MAGURRAN, 1988). Their histories of origin and succession have been described (MARION & MARION, 1975).

The four study plots are 100 m wide transects, ranging from 1 600 to 2 000 m in length (fig. 1). The vegetation in the plots is not homogeneous, but composed of mosaics of different vegetation types. We distinguished 31 vegetation types according to their structure and their floristic composition. The mosaic patches of each vegetation type were then mapped using aerial photography. The maps are presented in Appendix 1. They are shown in a linear way for ease of presentation. The sizes of the vegetation patches ($n=276$) are distributed log-normally, and varied between 54 and 20 080 m², with a median of 1 290 m². Every vegetation type was described by two complementary methods, the method using a "stratiscopes" (BLONDEL & CUVILLIER, 1977) and the "point centered quarter" method of COTTAM and CURTIS (1956). At least 50 measurements with the stratiscopes and 25 with the point centered quarter method were made for each vegetation type following a transect, with measurements separated by 4 and 8 m respectively. The measurements using a stratiscopes gave the percentage cover in each horizontal stratum. The limits of these strata were fixed at 0.25, 0.50, 1, 2, 4, 8, 16 and 32 m. The measurements using the point centered quarter method gave the average and standard deviation of the distances between trees and between shrubs (less than 5 m high), of the heights of trees and of shrubs, and of the diameter (dbh) of trees. Together with this method, we noted the species of each recorded tree and shrub (at least 100 records per vegetation type). This gave us the taxonomic composition of the vegetation type. Each vegetation type was assigned an age class (0-6, 7-15, 16-30, 31-60 years, more than 60 years old), based on the growth form of the vegetation and maximum tree age. We assigned to each vegetation type a nominal variable describing perturbations by forestry that were performed recently: "no" for no perturbation, "plantation" for young plantation, "clearing" for undergrowth clearing in the last few years.

The 31 vegetation types were analysed using the coefficient of Gower and intermediate linkage clustering (see LEGENDRE & LEGENDRE, 1983). The most similar types were combined into one. This led to the establishment of 21 different types. From the raw vegetation data we calculated several indices, thereby condensing the information into a small set of variables: the foliage height diversity (MACARTHUR & MACARTHUR, 1961); the herb layer per cent coverage, the shrub coverage, the tree coverage, the coefficient of variation (CV) for the distances between trees and between shrubs (ROTH, 1976); the CV for the heights of trees and of shrubs; the CV for the diameters of trees. From the taxonomic composition, we calculated the proportion of each tree and shrub species, the species diversity (Shannon index, MAGURRAN, 1988) for trees, for shrubs, and for both combined. The processing and mathematical treatment of surface areas and coordinates were performed with the geographical information system software GEOBASE (BLAISE & GESSLER, 1992) and IDRISI (EASTMAN, 1992) on a personal computer.

Bird census

Bird counting was based on the spot mapping method (BLONDEL, 1969; VERNER, 1985). We mapped all registered pigeons, woodpeckers and passerines on the maps shown in Appendix 1, but on a scale of about 1 : 700. We noted the birds even in they were outside the limits of the plots. The maps are 25 m broader on each side for that purpose (see Appendix 1). This was done to correctly assess the

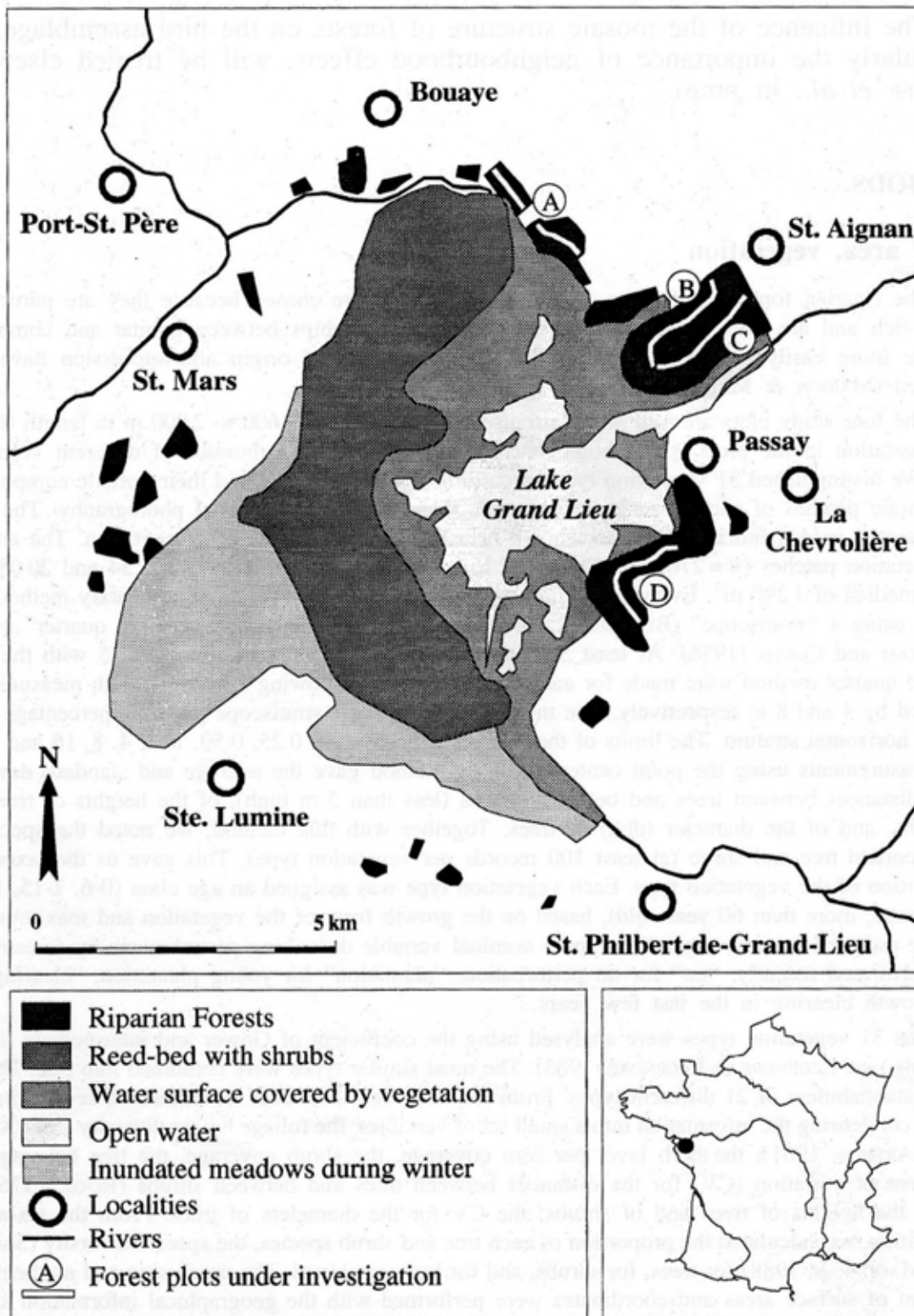


FIG. 1. – Location of the study area and of the survey plots.

territories that overlap the borders of the plots. We made ten censuses in each plot during the breeding season, 7 of them early in the morning and 3 in the evening, between the end of March and the end of June 1989. We estimated a "paper territory" as a cluster of at least three contacts, indicating the presence of a territory holder, at different days (BERTHOLD, 1976). We computed the densities of paper

territories in each vegetation patch. Territories that overlapped two or more vegetation patches were divided between the patches according to their proportion of bird contacts in each patch. The efficiency of finding paper pairs was tested by comparing the results of the described method with an intensive search in the same forest (the grid census method of BLONDEL, 1969). Tests were done in a riparian forest at Lake Neuchâtel, Switzerland, in 1987. Seven censuses were performed on a surface of 8 ha. Ninety per cent of all pairs present at the site were recorded as paper pairs, essentially the difficult and rare species were overlooked.

Data analyses

We studied the effects of the floristic and structural components of vegetation on the whole bird data matrix using canonical correspondence analysis (CCA) (TER BRAAK, 1986, 1988a; JONGMAN *et al.*, 1987). We used the CANOCO software (TER BRAAK, 1988b). We retained vegetation patches with surface areas more than 500 m² and less than 10000 m² ($n = 210$). We eliminated small patches to reduce errors due to stochastic variation. We eliminated one large patch, which was an outlier in the size distribution of patches. We used the logarithms of the bird species densities for the construction of the bird data matrix. The densities were downweighted in proportion to their frequency according to an algorithm available in CANOCO. The environmental variables were normalized. We have retained the variables of vegetation that explained most of the variance in a step-by-step procedure of selection. The significance of the axes of the ordinations was tested using a permutation procedure available with CANOCO.

Partial correspondence analysis was used to distinguish between the effects of vegetation structure and of the plant taxonomic composition. To do this, we used the variation partitioning method described by BORCARD *et al.* (1992). In this method, we alternatively removed the effect of each set of variables (floristic and structure), and performed the ordination with the other set of variables as explanatory variables. The variables whose effects are removed are called covariables. This allowed us to calculate the percentage of variation due exclusively and in common to the two groups of vegetation variables. In both sets of variables, we chose the six variables that were best correlated with the bird data matrix. It is important that the number of variables be equal in each set, since set with more variables will be comparatively overvalued in partial analyses.

To evaluate the contribution of a single variable to the total fraction of variation due exclusively to a set of variables, we performed a partial ordination, retaining as explanatory variable only the variable of interest. Repeating this procedure for each variable allowed us to calculate their relative contribution (in per cent).

To study the evolution of the different fractions of variation along the successional gradient, we performed the above analyses for all the vegetation patches (age classes 1 to 5), except those influenced by forestry; then, we computed the partial ordinations for vegetation patches of age classes 2 to 5, and so on until the last stage of the succession (fig. 2). The result of these analyses gives us the pattern of the evolution of the relative importance of vegetation structure and of floristics along the successional gradient.

To statistically test the hypothesis of ROTENBERRY (1985), that is, that structure is more important at large scale and floristics at small scale, we used the following procedure. We created 1 sample composed of 5 replicates containing vegetation patches covering the whole succession, and 1 sample composed of 5 replicates containing vegetation patches of one or of two successive age classes. The former 5 replicates are heterogeneous and represent large-scale habitats; the latter 5 are homogeneous and represent small-scale habitats. Each replicate consists of 15 randomly chosen vegetation patches. We randomly extracted 3 patches from each age class for the heterogeneous replicates. One chosen patch could not be picked up again in another replicate of the same sample. We performed partial CCA for each replicate. We compared the percentage contribution of vegetation structure with that of floristics for the homogeneous small-scale sample and for the heterogeneous large-scale sample using a *t*-test for paired comparisons.

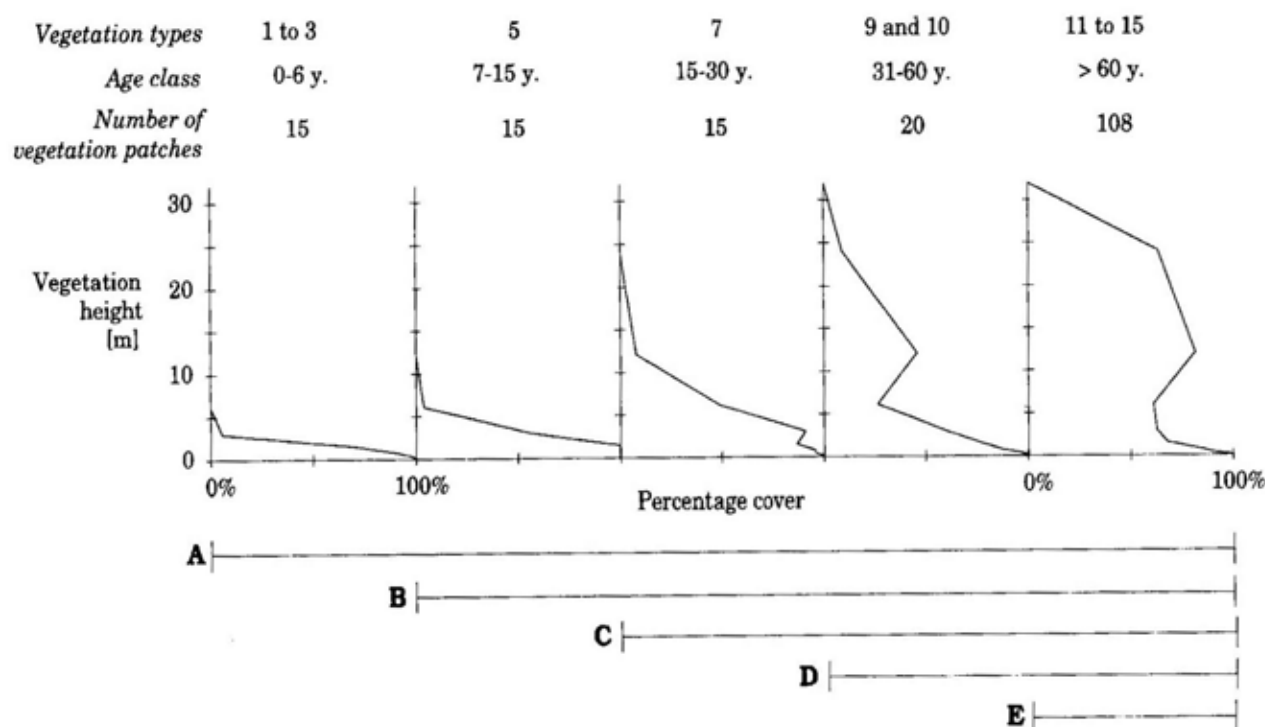


FIG. 2. – Vegetation types, together with their vegetation profile, involved in the analysis of partial canonical correspondence analyses. The five samples of the analysis are indicated as A to E.

RESULTS

The description of the vegetation types is presented in Appendix 2. The basic result of the bird mapping for the 4 forest plots and for 16 most widespread vegetation types is given in Appendix 3. It reveals a high number of nesting bird species (37), compared to the total number of forest species in Brittany (~43 species, GUERMEUR & MONNAT, 1980).

The bird data matrix was subjected to canonical correspondence analysis, first with the variables of plant taxonomic composition, then with the variables of plant structure (fig. 3). In both cases four variables significantly explain the variation of the bird data. For plant taxonomic composition they were: proportion of furze *Ulex europaeus* ($p \leq 0.001$, 999 permutations), proportions of oaks *Quercus pedunculata* ($p = 0.002$), proportion of brambles *Rubus fruticosus* ($p = 0.038$) and number of shrub species ($p = 0.034$), for plant structures they were: percentage cover of trees ($p \leq 0.001$), percentage cover of shrubs ($p \leq 0.001$), foliage height diversity ($p = 0.024$) and coefficient of variation (CV) of distances between shrubs ($p = 0.047$). In both ordinations, the relationships between the bird assemblages and the environmental variables are significant only for the first axes ($p \leq 0.001$ in both cases). The p-values for the second axes are 0.109 for the ordination with plant taxonomic composition, and 0.098 for the ordination with the vegetation structure. The first ordination axis for the taxonomic composition as explanatory variables shows a gradient reflecting the succession by contrasting the influences of the proportions of furze and of oak trees (fig. 3a). The first ordination axis with plant structure separates early-successional stages with high percentage cover of shrubs and high horizontal heterogeneity for shrubs from other vegetation patches that

show a high vertical diversity and a high percentage of tree coverage (fig. 3b). Both analyses with the floristic and the structural components of vegetation demonstrate the relationships between bird assemblages and forest succession.

To gain insight into the relationships between plant structure variables and plant taxonomic composition variables, we subjected the data to partial canonical correspondence analyses. We analysed the evolution of the relative importance of both components of the vegetation along the successional gradient, according to figure 2. The results of the partial ordinations are presented in figure 4. The total variation of the bird data matrix is composed of four fractions: (a) the fraction of variation explained exclusively by the plant taxonomic composition, (b) the fraction due in common to plant taxonomic composition and vegetation structure, (c) the fraction explained exclusively by the structure of the vegetation, and (d) the unexplained variation. Figure 4a shows the total amount of variation explained by the environmental variables (fractions a, b, and c). The relative contributions of each explained fraction are shown in figure 4b. Both sets of variables have their highest individual contribution at the sample C. For the entire succession (sample A), the fraction of variation due to vegetation structure is greater than that due to floristics. Floristics becomes more important than structure as the

a)

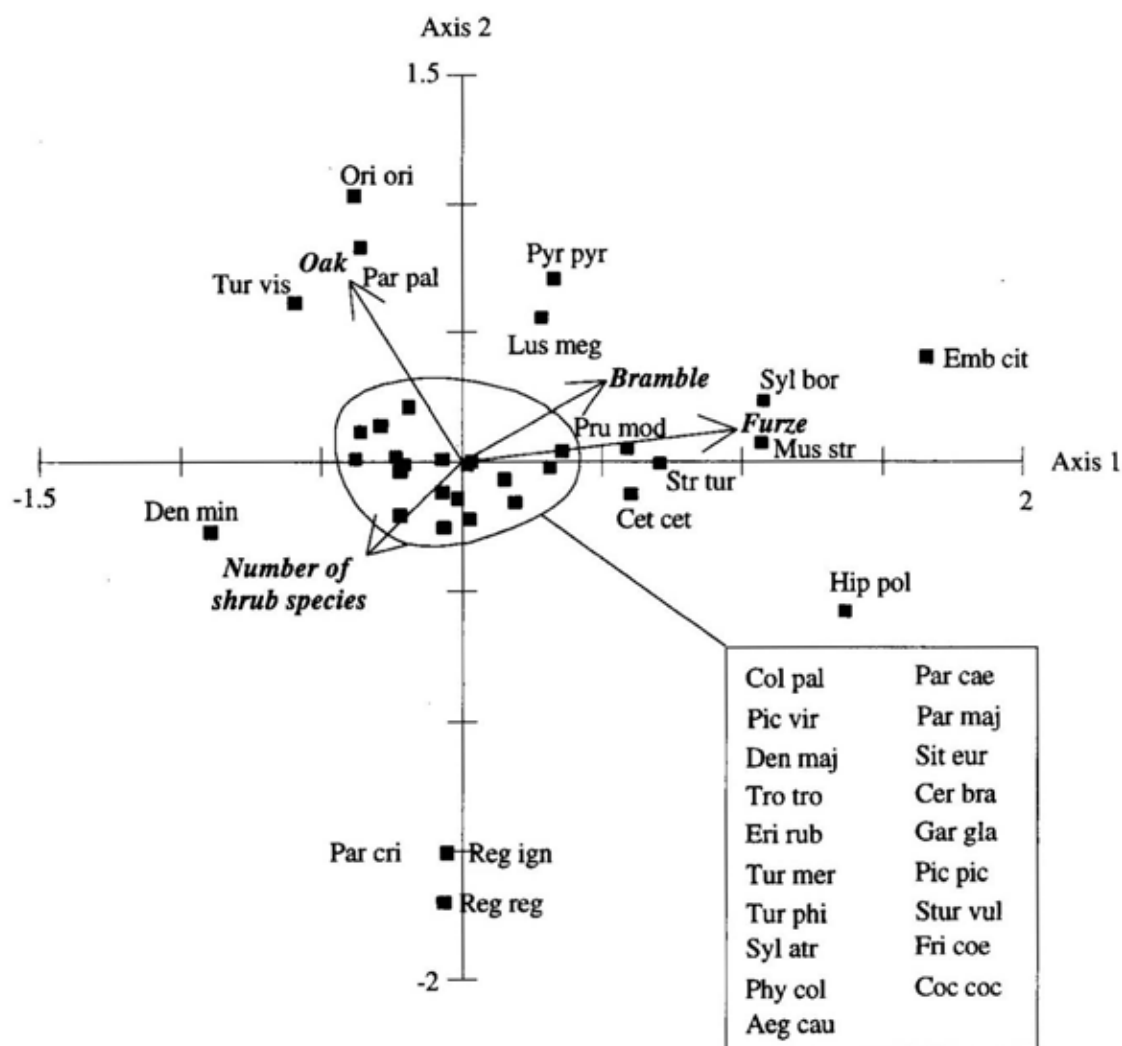


FIG. 3 a.

b)

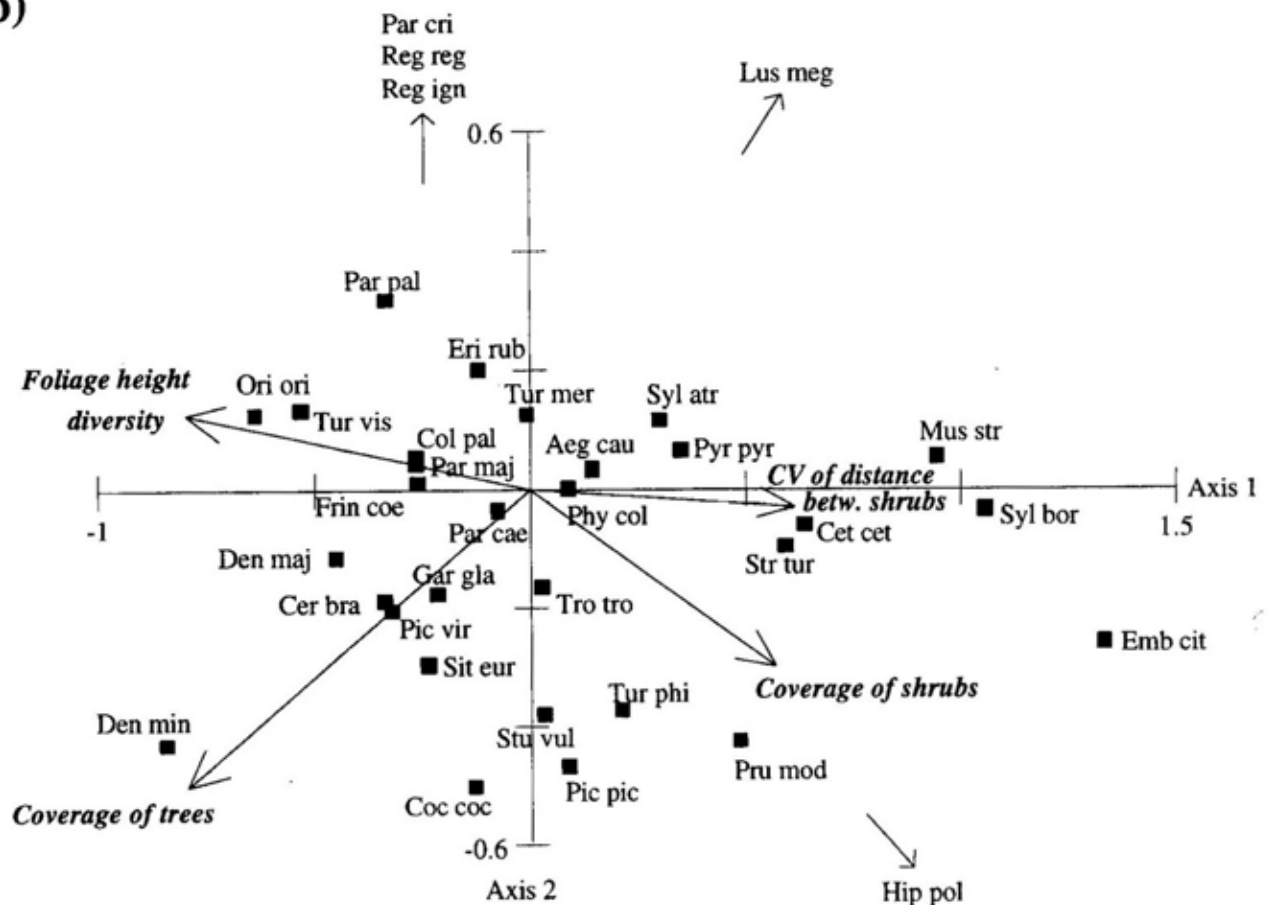


FIG. 3. – Canonical correspondence analyses diagrams of the distribution of the bird species (■) in the studied mosaic forests according to **a**) the plant taxonomic composition (floristics), and **b**) the structure of the vegetation. Arrows represent the environmental variables that significantly explain the variation of the bird data matrix. The scientific species names are abbreviated as in Appendix 3. Small arrows indicate that the corresponding species lie outside the diagram.

analyses are restricted to mature forest (sample E). However, these differences are quite small. To see if these differences are significant, we performed partial CCA with a heterogeneous (large-scale) and a homogeneous (small-scale) sample, each composed of 5 replicates. The results are shown in table I. The percentage variation due to structure is significantly larger than that due to floristics at large-scale, and significantly smaller at small-scale.

What is the contribution made by each individual variable along the successional gradient? To answer this question, we performed partial ordinations in retaining only one environmental variable, and repeated the procedure for all variables. We obtained the relative individual contributions of each variable in the total amount of variation explained exclusively by the vegetation structure or by the floristics (fig. 5). From this, it is apparent that the increase in importance of the floristics in comparison to the vegetation structure in the last successional sample E is due to a strong increase of the contribution of the richness of tree species, in contrast to the decrease of the contribution of the CV of distances between trees.

TABLE I. – Percentage of explained variation due exclusively to the floristics and exclusively to the vegetation structure for a homogeneous small-scale sample and for a heterogeneous large-scale sample.

Homogeneous small-scale sample			Heterogeneous large-scale sample		
replicate	Fraction of variation due to		replicate	Fraction of variation due to	
	floristics	vegetation structure		floristics	vegetation structure
1	13.36 %	7.02 %	1	18.06 %	19.72 %
2	11.77 %	7.38 %	2	22.45 %	25.05 %
3	13.20 %	7.45 %	3	22.26 %	23.28 %
4	21.44 %	17.40 %	4	17.77 %	18.08 %
5	17.61 %	15.83 %	5	20.49 %	21.96 %
<i>t</i> -test for paired comparisons: <i>t</i> = -5.63, <i>p</i> (two-tail) = 0.005			<i>t</i> -test for paired comparisons: <i>t</i> = -3.75, <i>p</i> (two-tail) = 0.02		

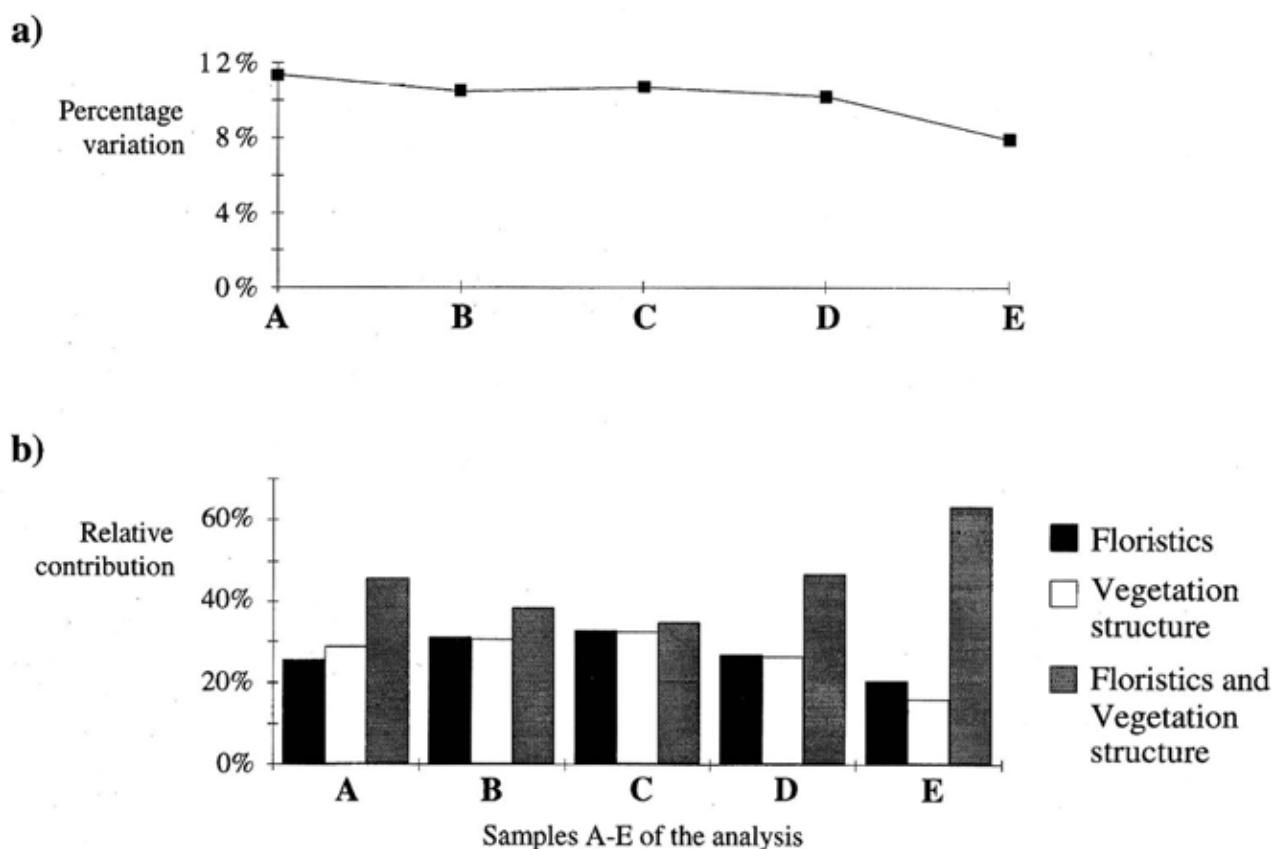
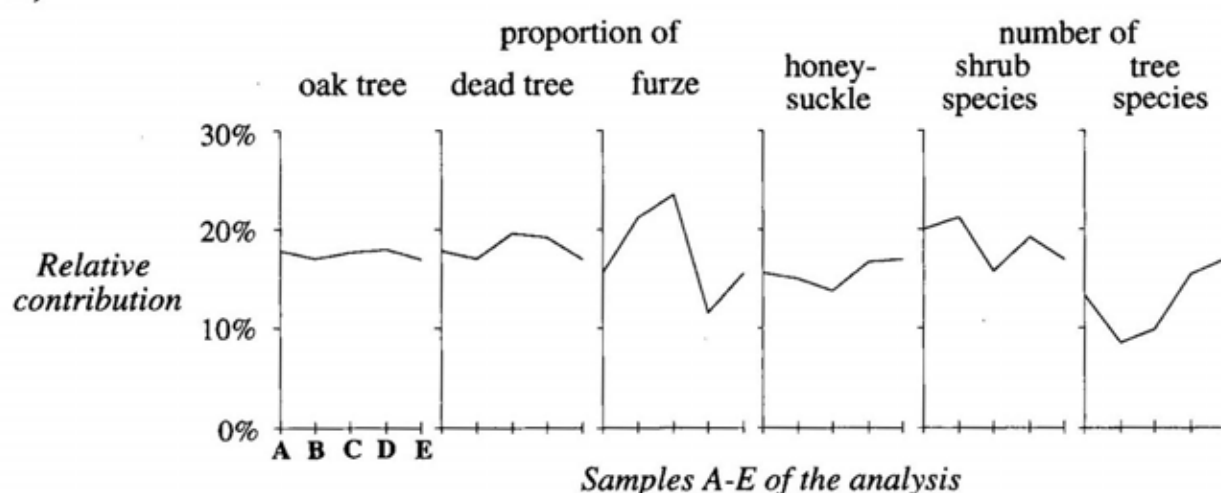


FIG. 4. – a) Evolution along the successional stages of the total amount of variation explained by the floristics and the vegetation structure. b) Evolution of the relative contributions of the three fractions (fraction of variation due exclusively to the floristics, to the structure, and in common to the floristics and the structure) that compose the total amount of the explained variation.

DISCUSSION

The overall results of canonical ordinations show that the vegetation variables best correlated with the bird assemblages are those related to plant succession (arrows in fig. 3a and b). This agrees with the results of numerous studies on forest

a)



b)

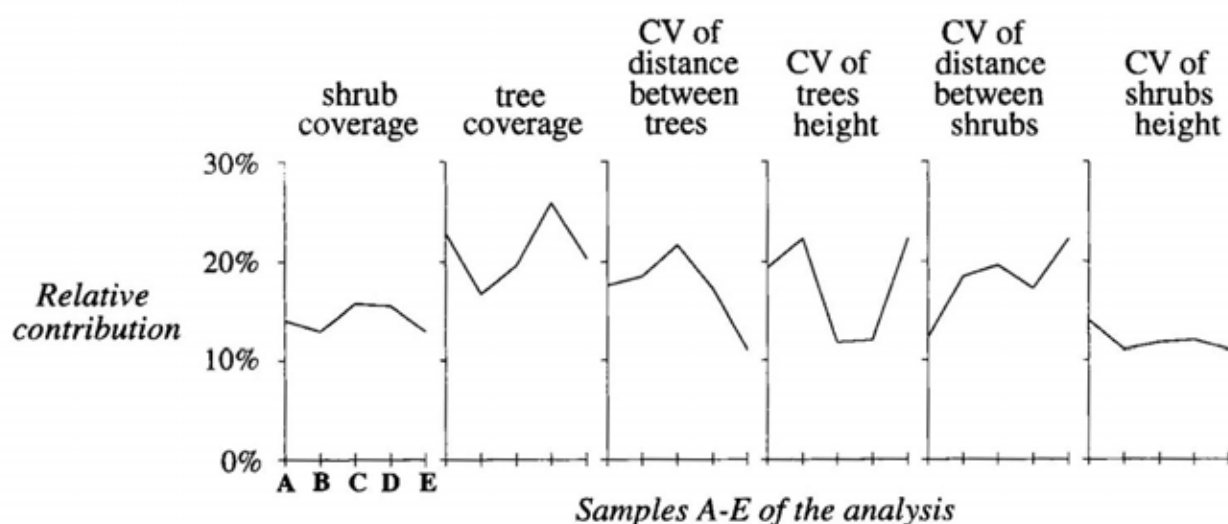


FIG. 5. – Evolution of the relative contributions of each variable of a) the floristics, and b) the vegetation structure in the fraction of variation explained exclusively by each set of variables.

birds (e. g. RØV, 1975; MULLER, 1985; HOLMES & SHERRY, 1988; MOSKAT & SZEKELY, 1989; BLONDEL, 1991). Both analyses with the plant taxonomic composition and with the structure of the vegetation ordinate the bird species according to the successional gradient.

The pattern of evolution of percentages of variation due to floristics and vegetation structure is in accordance with the hypothesis of ROTENBERRY (1985). The variables describing the structure of the vegetation are best correlated with the bird data matrix when the whole succession is analysed. The variables describing plant taxonomic composition best explain the variation in the bird data matrix in small-scale homogeneous samples. To our knowledge, this is the first report for forest birds of this scale-specific difference in the importance of floristics and structure. The differences of contribution of floristics and structure reported by ROTENBERRY (1985) for bird assemblages in steppes were large. In our case, the differences are small, but significant. One possible explanation for that discrepancy

is that the "large-scale" in our analysis is the entire range of the forest succession in a small region (see fig. 1). In contrast, what ROTENBERRY (1985) considered "large-scale" is the range of North America.

Why are floristics more important at small-scale? One possible explanation is that the taxonomic composition is a finer descriptor of the vegetation structure at small scale than the variables of the vegetation structure themselves. This artifact is more likely to be found if one compares bird assemblages at a very small scale with those at a very large scale, which is not the case in our study. Moreover, we used the same set of vegetation variables to describe the small-scale and the large-scale samples. According to ROTENBERRY (1985), the mechanism responsible for the strong correlation between birds and floristics at small scale is related to food and foraging behaviour. The insectivorous bird species may respond to particular groups of plant species. A habitat with more plant species will provide more different categories of food items (SOUTHWOOD *et al.*, 1979; REED, 1982; NILSSON *et al.*, 1988; BROWN & OPLER, 1990; GASTON, 1992), thus enabling more bird species to coexist. This is most likely the strongest effect that plant taxonomic composition can have on the whole bird assemblage. Indeed, our analysis shows that the relative increase in the importance of the floristics in comparison with the structure is due to the high increase of the contribution of the richness of tree species. This result gives additional support to the hypothesized process.

A difficult problem in disentangling the relative contribution of vegetation structure and of plant taxonomic composition is that both are related: a furze is structurally a shrub, an aged oak is structurally a tree. This relatedness is expressed by the common contribution of both sets of variables (fraction b), which is, in our case, always higher than the individual contributions. A clear answer as to the relative importance that one or the other element of this fraction has for the birds cannot be given by partial CCA. A complete path analysis (e.g. LEGENDRE & TROUSSELIER, 1988) is beyond the scope of this paper.

In this study, we analysed the contributions of the floristics and of the physiognomy of the vegetation for the distribution of birds, and we decomposed these two components in their constituent variables. The importance of these variables, and thus the generality of the observed patterns, should be confirmed at other locations. However, the comparison will be meaningful only if the variables are approximately similar, and if plant species have approximately the same habitus.

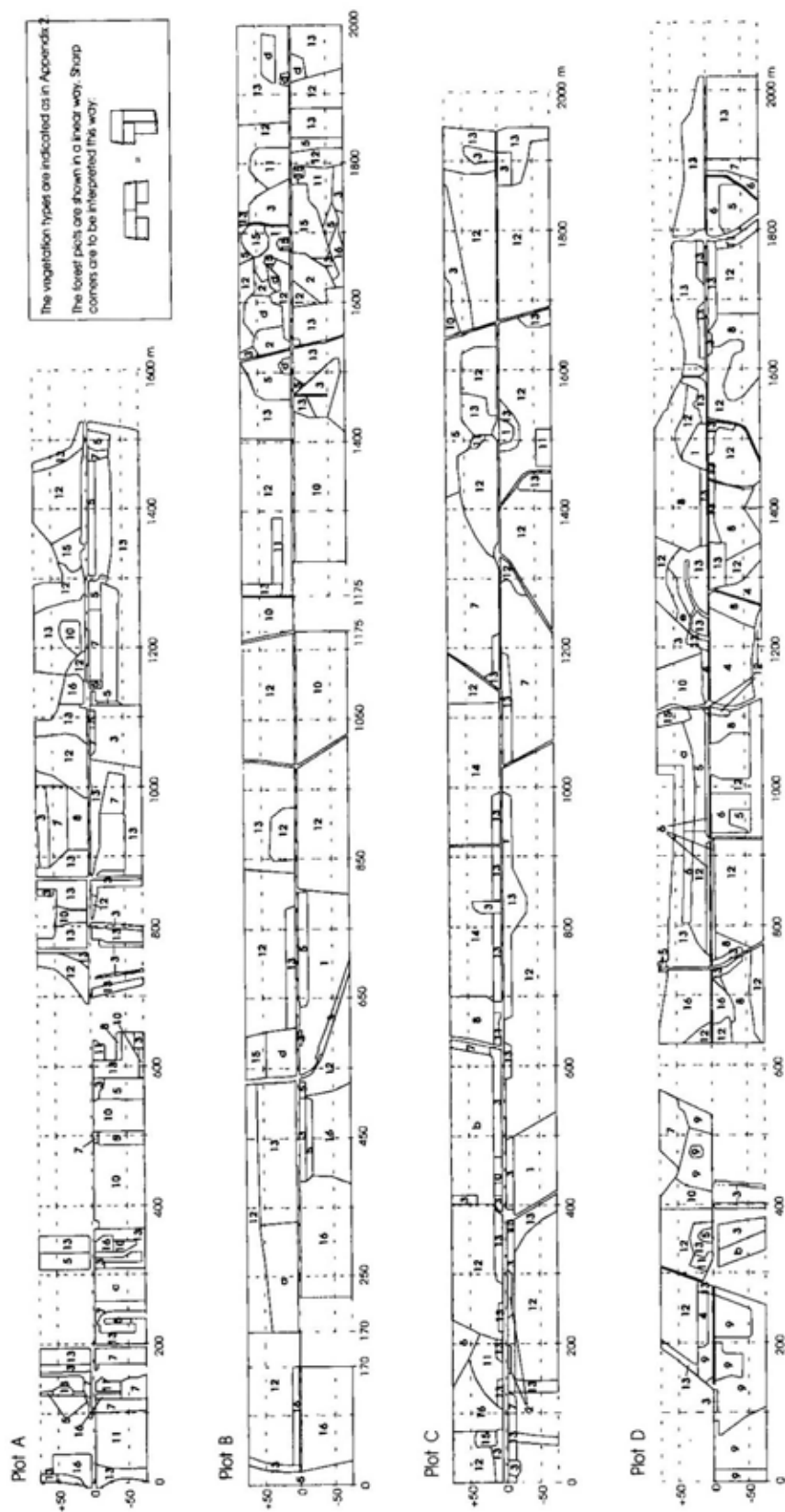
Although our results support the hypothesis of ROTENBERRY (1985), other processes are important for the selection of the habitat as well (e.g. CODY, 1985a; WIENS, 1989). Especially in these heterogeneous forests, the structure of the mosaic has implications for the pattern of distribution of birds (BERSIER *et al.*, in prep.). A hint that other factors than those of the vegetation are important is given by the high proportion of unexplained variation in the bird data matrix (fig. 4a). Vegetational variables are nevertheless important in shaping bird assemblages. The formulation of a model for the assembly of bird communities requires precise knowledge about the influence of such variables, and about the scale at which their effects are the strongest.

ACKNOWLEDGEMENTS

We are grateful to Philippe BLAISE who developed GEOBASE according to our needs, to Claude COLLET who helped with geographic information systems. Daniel BORCARD helped with ordination

- LOVEJOY T. E., 1974. – Bird diversity and abundance in Amazon forest communities. *Living Bird*, **13**, 127-191.
- MCARTHUR R. H. & MCARTHUR J. W., 1961. – On bird species diversity. *Ecology*, **42**, 594-598.
- MAGURRAN A. E., 1988. – *Ecological diversity and its measurement*. Croom Helm, London.
- MARION L. & MARION P., 1975. – Contribution à l'étude écologique du Lac de Grand-Lieu. *Bull. Soc. Sc. Nat. Ouest France*, special issue, 1-611.
- MEYER D. R., 1993. – Dynamik, strukturelle Heterogenität und biologische Diversität von Wald-Ökosystemen. In: DAPHINOFF D. & MARSCH E., eds., *Der Wald*. Éditions universitaires, Fribourg.
- MOSKAT C. & SZEKELY T., 1989. – Habitat distribution of breeding birds in relation to forest succession. *Folia Zool.*, **38**, 363-376.
- MULLER Y., 1985. – L'avifaune forestière nicheuse des Vosges du Nord, sa place dans le contexte médio-européen. PhD thesis, Université de Dijon, France.
- NILSSON S. G., BENGTTSSON J. & AS S., 1988. – Habitat diversity or area *per se*? Species richness of woody plants, carabid beetles and land snails on islands. *J. Anim. Ecol.*, **57**, 685-704.
- POWER D. M., 1975. – Similarity among avifaunas of the Galapagos Islands. *Ecology*, **56**, 616-626.
- REED T. M., 1982. – The number of butterfly species on British islands. *Proceedings of the 3rd Congress of European Lepidopterists*. Cambridge, 146-152.
- REMMERT H., ed., 1991. – *The Mosaic-Cycle Concept of Ecosystems*. Springer Verlag, Berlin.
- ROTEBERRY J. T., 1985. – The role of habitat in avian community composition: physiognomy or floristics. *Öecologia*, **67**, 213-217.
- ROTEBERRY J. T. & WIENS J. A., 1980. – Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. *Ecology*, **61**, 1228-1250.
- ROTH R., 1976. – Spatial heterogeneity and bird species diversity. *Ecology*, **57**, 773-782.
- ROTHSTEIN S. J., 1971. – High nest density and nonrandom nest placement in the Cedar Waxwing. *Condor*, **73**, 483-485.
- RØV N., 1975. – Breeding bird community structure and species diversity along an ecological gradient in deciduous forest in western Norway. *Ornis Scand.*, **6**, 1-14.
- SMITH K. G., 1977. – Distribution of summer birds along a forest moisture gradient in an Ozark watershed. *Ecology*, **58**, 810-819.
- SNOW B. K. & SNOW D. W., 1971. – The feeding ecology of tanagers and honeycreepers in Trinidad. *Auk*, **88**, 291-322.
- SNOW B. K. & SNOW D. W., 1980. – Relationships between hummingbirds and flowers in the Andes of Columbia. *Bull. Br. Mus. (Nat. Hist) Zool.*, **38**, 105-139.
- SOUTHWOOD T. R. E., BROWN V. K. & READER P. M., 1979. – The relationship of plant and insect diversities in succession. *Biol. J. Linn. Soc.*, **12**, 327-348.
- TER BRAAK C. J. F., 1986. – Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, **67**, 1167-1179.
- TER BRAAK C. J. F., 1988a. – Partial canonical correspondence analysis. In: BOCK H. H., ed., *Classification and related methods of data analysis*. North-Holland Press, Amsterdam.
- TER BRAAK C. J. F., 1988b. – *CANOCO – a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis*. GLW, Wageningen NL.
- TOMOFF C. W., 1974. – Avian species diversity in desert scrub. *Ecology*, **55**, 396-403.
- VERNER J., 1985. – Assessment of counting techniques. In: JOHNSTON R., ed., *Current Ornithology*, **2**, Plenum Press, New York.
- WIENS J. A., 1969. – An approach to the study of ecological relationships among grasslands birds. *Ornithol. Monogr.*, **8**, 1-93.
- WIENS J. A., 1989. – *Ecology of Bird Communities*. Vol. 2. Cambridge University Press, Cambridge.
- WIENS J. A. & ROTEBERRY J. T., 1981. – Habitat associations and community structure of birds in shrubsteppe environments. *Ecol. Monogr.*, **51**, 21-41.
- WILLSON M. F., 1974. – Avian community organization and habitat structure. *Ecology*, **55**, 1017-1029.

APPENDIX 1



APPENDIX. 1. – Map of the vegetation in the 4 forest plots.

APPENDIX 3

abbrev.	area [ha]	Vegetation type																Forest plots			
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	A	B	C	D
		2	1	2	1	3	1	3	2	2	2	19	13	4	2	1	3	9	19	18	16
col pal	<i>Columba palumbus</i>	-	-	1.4	-	2.9	8.4	1.7	5.8	4.3	3.8	3.3	7.7	4.9	4.9	13.2	2.0	3.8	3.6	3.1	6.6
str tur	<i>Streptopelia turtur</i>	-	-	-	-	1.7	-	-	-	-	-	0.3	0.4	1.2	-	-	-	1.1	-	-	0.6
pic vir	<i>Picus viridis</i>	-	-	-	-	-	-	0.8	-	1.7	-	0.6	0.8	1.4	1.6	-	1.5	1.1	0.5	0.6	0.6
den maj	<i>Dendrocopos major</i>	-	-	-	1.7	-	-	2.3	3.1	-	1.6	3.0	2.5	3.3	1.2	10.4	4.6	4.3	2.1	2.5	1.6
den min	<i>Dendrocopos minor</i>	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-	-	-	-	0.3	-
tro tro	<i>Troglodytes trogl.</i>	7.3	18.9	21.0	-	25.2	28.1	7.3	6.9	5.0	22.4	22.9	28.8	26.4	36.3	33.6	18.3	35.7	22.3	21.5	12.5
pru mod	<i>Prunella modularis</i>	-	-	5.0	-	3.5	-	1.1	0.8	-	2.6	0.4	3.2	3.6	3.1	-	1.0	7.6	0.3	1.7	-
eri rub	<i>Erithacus rubecula</i>	2.5	9.8	2.7	14.1	23.8	17.3	12.2	16.1	20.9	8.2	14.3	18.9	13.6	4.7	3.1	12.1	16.8	13.9	11.0	18.8
lus meg	<i>Luscinia megarhyn.</i>	-	-	-	-	-	-	1.6	-	-	-	-	-	-	-	-	-	-	-	0.3	-
tur mer	<i>Turdus merula</i>	-	-	7.1	13.1	11.6	8.5	12.2	4.3	7.5	8.4	7.3	15.0	9.2	6.8	6.2	4.4	17.8	5.6	7.9	9.4
tur phi	<i>Turdus philomelos</i>	-	-	2.1	-	1.9	-	1.8	0.7	-	1.1	1.0	3.6	3.8	9.9	-	-	4.9	0.8	3.1	-
tur vis	<i>Turdus viscivorus</i>	-	-	-	-	-	-	-	-	0.8	2.2	0.4	0.6	0.9	-	-	-	0.5	0.8	-	0.6
cet cet	<i>Cettia cetti</i>	-	-	3.7	-	4.8	-	0.4	-	-	-	0.6	0.7	2.7	-	-	0.4	5.4	0.3	-	-
hip pol	<i>Hippolais polyglotta</i>	-	-	10.6	-	-	-	-	-	-	-	-	-	-	-	-	-	1.1	-	0.6	0.3
syl com	<i>Sylvia communis</i>	-	-	4.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.6
syl bor	<i>Sylvia borin</i>	-	-	27.8	-	21.9	-	7.9	1.7	1.0	3.8	1.1	3.7	26.8	4.6	3.1	-	8.7	6.9	5.4	2.2
syl atr	<i>Sylvia atricapilla</i>	5.4	24.6	28.9	14.1	60.2	24.0	41.1	9.0	17.4	14.2	15.7	37.2	44.8	42.7	7.7	11.2	49.2	19.5	26.1	20.7
phy col	<i>Phylloscopus collyb.</i>	1.7	25.2	26.2	10.1	41.0	36.6	48.3	9.5	29.9	24.9	31.0	57.6	52.1	71.5	52.5	27.7	57.3	34.4	39.9	29.8
reg reg	<i>Regulus regulus</i>	-	-	-	-	-	4.0	-	-	-	-	-	0.2	-	-	-	-	-	-	-	0.6
reg ign	<i>Regulus ignicapillus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.8	-	-
mus str	<i>Muscicapa striata</i>	-	-	-	-	1.2	-	-	-	-	5.4	0.1	0.1	1.8	-	-	0.8	2.2	0.3	-	-
aeg cau	<i>Aegithalos caudatus</i>	-	-	4.3	-	8.1	-	4.6	1.0	-	3.9	2.1	5.1	2.4	1.6	9.6	2.0	4.9	3.6	2.5	1.9
par pal	<i>Parus palustris</i>	-	-	-	-	1.5	-	0.7	-	8.0	7.6	1.7	2.0	2.4	-	2.5	4.1	2.2	2.8	1.7	1.3
par cri	<i>Parus cristatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5	-	-
par car	<i>Parus caeruleus</i>	-	6.6	5.7	6.4	15.9	8.5	8.8	8.2	16.3	11.6	12.9	19.0	11.1	14.8	24.6	14.5	16.2	10.8	13.3	13.5
par maj	<i>Parus major</i>	1.2	-	4.3	14.1	6.4	5.3	6.5	4.1	10.0	10.5	8.7	7.4	5.3	3.3	2.5	5.9	8.1	3.9	7.1	9.1
sit eur	<i>Sitta europaea</i>	-	-	-	-	0.9	-	1.3	-	-	1.6	1.5	1.3	2.2	-	2.1	-	1.1	1.0	1.4	0.6
cer bra	<i>Certhia brachydact.</i>	-	-	2.3	-	3.6	-	4.0	3.8	1.3	20.0	10.7	14.0	11.4	11.4	23.3	13.0	12.4	11.6	8.8	5.6
ori ori	<i>Oriolus oriolus</i>	-	-	-	-	-	-	-	-	-	3.3	-	-	0.7	-	-	-	1.1	-	-	-
gar gla	<i>Garrulus glandarius</i>	-	-	0.4	6.2	1.3	-	0.8	3.4	3.0	1.6	3.0	3.0	5.2	1.6	2.1	1.7	1.6	2.8	2.0	3.8
pic pic	<i>Pica pica</i>	-	-	0.7	-	-	-	-	-	-	-	-	0.4	0.9	-	-	-	1.1	-	-	-
stu vul	<i>Sturnus vulgaris</i>	-	-	1.1	-	2.2	-	0.8	-	-	-	1.4	4.1	3.7	1.6	9.4	1.0	5.4	1.5	1.1	1.3
fri coe	<i>Fringilla coelebs</i>	-	6.6	9.5	13.2	9.6	16.7	11.4	17.6	23.8	25.6	16.9	26.4	14.4	17.7	33.7	17.6	28.7	12.1	15.0	21.3
car chl	<i>Carduelis chloris</i>	-	-	-	-	-	-	-	-	-	1.6	-	-	0.7	-	-	-	0.5	-	-	-
pyr pyr	<i>Pyrrhula pyrrhula</i>	-	-	-	-	-	-	0.8	-	-	1.6	0.2	0.8	3.2	-	-	-	1.6	0.3	0.6	-
coc coc	<i>C. coccythraustes</i>	-	-	-	-	-	-	-	-	-	1.3	0.2	0.3	-	-	-	-	-	-	0.6	-
emb cit	<i>Emberiza citrinella</i>	-	-	2.8	-	-	-	-	-	-	-	-	-	0.9	-	-	-	-	-	-	0.6

APPENDIX. 3. – Densities (number of territories/10 ha) of birds in the 16 most widespread vegetation types and in the four forest plots. The vegetation types are indicated as in Appendix 2, the forest plots as in figure 1 and Appendix 1.

APPENDIX 2

16 most widespread vegetation types

- 1 Early-successional zones with dense grass layer and sparse shrubs
- 2 Early-successional zones with dense fern *Pteridium aquilinum* layer and sparse shrubs
- 3 Early-successional zones with dense grass layer and numerous shrubs
- 4 Plantation of young chestnut *Castanea sativa*
- 5 Dense bushes
- 6 Young plantation of conifers
- 7 Young oak forest *Quercus robur* with dense shrub layer
- 8 Plantation of adolescent chestnut *Castanea sativa*

- 9 Temporarily flooded oak forest with medium undergrowth
- 10 Dense bushes with sparse trees
- 11 Old-growth oak forest with sparse undergrowth
- 12 Old-growth oak forest with medium undergrowth
- 13 Old-growth oak forest with dense undergrowth
- 14 Thin old-growth oak forest with dense undergrowth
- 15 Old plantation of Pines *Pinus pinaster* with sparse undergrowth and understory of oaks
- 16 Old-growth oak forest with cleared undergrowth

5 remaining vegetation types

- a Plantation of young conifers invaded by shrubs and young trees.
- b Plantation of young poplars *Populus sp.*
- c Old plantation of poplars
- d Plantation of young robinia *Robinia pseudoacacia*
- e Old plantation of spruces *Picea abies*

Vegetation type	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Total surface area [ha]	2	1	2	1	3	1	3	2	4	2	19	13	2	1	3	
Man-made perturbation	no	no	no	plant.	no	plant.	no	plant.	no	no	no	no	no	no	no	clear.
Age-class	1	1	1	2	2	3	3	3	4	4	5	5	5	5	5	5
Percentage cover																
0.05 - 0.25 m	100	100	100	69	100	92	100	100	99	100	100	100	100	96	85	93
0.25 - 0.5 m	92	100	100	46	100	77	96	77	87	100	68	88	100	96	74	79
0.5 - 1 m	77	100	100	46	100	38	96	54	62	100	32	84	96	92	51	50
1 - 2 m	46	76	95	69	100	38	87	77	48	92	28	64	88	40	20	22
2 - 4 m	0	0	13	77	56	92	91	46	53	62	24	68	68	32	26	29
4 - 8 m	0	0	0	69	4	85	49	31	63	8	32	60	76	12	54	14
8 - 16 m	0	0	0	54	0	15	8	100	61	38	92	80	88	52	62	86
16 - 32 m	0	0	0	0	0	0	0	0	11	8	64	72	48	68	84	24
Mean distance betw. trees [m]	-	-	-	1.6	3.5	2.1	2.4	2.1	2.6	8.1	3.4	3.1	2.7	5.4	3.2	3.7
Standard deviation	-	-	-	1.2	2.0	1.1	1.2	0.8	1.2	6.0	1.7	1.4	1.2	2.8	1.7	1.9
Mean dbh [cm]	-	-	-	6.6	9.0	11.5	9.6	11.2	15.6	29.3	23.6	20.5	20.6	30.3	32.2	20.6
Standard deviation	-	-	-	2.8	3.4	6.3	5.0	5.5	8.9	25.1	13.6	14.1	15.7	18.5	22.7	12.2
Mean distance betw. shrubs [m]	2.3	2.7	1.7	1.8	1.4	2.0	1.5	1.4	1.6	1.5	2.0	1.4	1.3	0.9	1.5	1.6
Standard deviation	2.2	1.8	1.1	1.0	1.2	1.1	1.3	0.8	1.4	1.2	1.5	1.0	1.0	0.7	1.2	1.0
Number of ligneous species	4	3	8	5	14	8	11	6	7	12	14	20	18	14	12	10
Dominant tree species (≥ 10 %)																
<i>Alnus sp.</i>	-	-	-	-	40	-	-	-	-	-	-	-	-	-	-	-
<i>Betula pendula</i>	-	-	-	-	-	-	20	-	-	-	-	-	-	-	-	-
<i>Castanea sativa</i>	-	-	-	100	-	40	20	100	-	40	-	20	30	-	-	-
<i>Quercus robur</i>	-	-	-	-	50	-	60	-	100	40	80	60	50	80	60	90
<i>Carpinus betulus</i>	-	-	-	-	-	-	-	-	-	-	10	-	20	-	-	-
<i>Abies alba</i>	-	-	-	-	-	50	-	-	-	-	-	-	-	-	-	-
<i>Prunus padus</i>	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-
<i>Pinus pinaster</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	40	-
<i>Robinia pseudoacacia</i>	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-
Dead trees	-	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-
Dominant shrub species (≥ 10 %)																
<i>Ulex europaeus</i>	40	-	10	-	20	-	10	-	-	20	-	-	10	-	-	-
<i>Crataegus sp.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	20	-	-
<i>Alnus sp.</i>	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Betula pendula</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10
<i>Castanea sativa</i>	-	20	-	50	10	70	10	70	-	10	10	20	10	10	10	20
<i>Quercus robur</i>	30	60	30	-	20	10	30	-	30	-	10	10	10	-	20	20
<i>Acer pseudoplatanus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	-
<i>Fraxinus excelsior</i>	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-
<i>Genista tinctoria</i>	-	-	-	-	-	-	-	-	10	10	-	-	-	-	-	-
<i>Ilex aquifolium</i>	-	-	-	-	-	-	-	-	-	-	-	20	-	-	10	10
<i>Ulmus minor</i>	-	-	-	-	-	-	-	-	-	-	-	-	20	-	-	-
<i>Ruscus aculeatus</i>	-	-	-	-	-	10	-	-	-	-	-	20	-	-	10	-
<i>Pinus sylvestris</i>	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pyrus pyrastrer</i>	-	-	-	10	-	-	-	20	-	-	-	-	-	-	-	-
<i>Populus sp.</i>	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	20
<i>Robinia pseudoacacia</i>	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rubus fruticosus</i>	-	-	20	-	20	-	40	10	40	40	20	10	40	50	30	-
<i>Salix sp.</i>	10	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-
Dead shrubs	-	-	-	40	-	-	-	-	10	-	20	-	-	-	10	10

APPENDIX. 2. – Description of the 21 vegetation types. The measurements are given for the 16 most widespread types only.