

RELATIONSHIPS BETWEEN BIRD ASSEMBLAGES, VEGETATION STRUCTURE, AND FLORISTIC COMPOSITION OF MOSAIC PATCHES IN RIPARIAN FORESTS

Louis-Félix BERSIER* & Dietrich R. MEYER**

INTRODUCTION

We are still far from explaining and predicting actual species assemblages of any community by a set of rules. Ecological and evolutionary theory has improved our understanding of assembly rules in some fields : the empirical species-area function first described by Arrhenius (1921) and the log-normal distribution of species-abundances (Preston, 1962) have found a theoretical basis (Sugihara, 1980 ; Wissel & Maier, 1992). The models of ecosystem energetics can only predict species richness, species succession and the effect of disturbances in very general terms ; the hypotheses still await formal testing (Lotka, 1925 ; Odum, 1990 ; Schindler, 1990). Similarly, the many observations on food-web structures have not yet led to a unified hypothesis as regard to the species composition and the number of individuals (see Pimm *et al.*, 1991 for a review). More recently, the recognition of the importance of historical and regional effects (e.g. Drake *et al.*, 1993 ; Ricklefs and Schluter, 1993) and of environmental variability and disturbance (e.g. Chesson & Huntly, 1989 ; Lavorel *et al.*, 1994) gave a more nuanced view of determinism in the structure of communities. A community can evolve following different trajectories, and tend to alternative states (Kauffman, 1993 ; Law & Morton, 1993).

There are, however, many empirically established relations between environmental factors and individual species. Plants in a given ecosystem form structures that are important to animals. Biotic processes inside a given assemblage, for example past and present intraspecific and interspecific competition, immigration and local extinction, are presumably shaping that assemblage (e.g. Diamond, 1975 ; Ricklefs, 1975 ; Schoener, 1983 ; Gilpin & Hanski, 1991 ; Bock *et al.* 1992 ; Danielson, 1992 for reviews). Some species might attract or repel other species (in the case of birds see Monkkonen *et al.*, 1990). These environmental and biotic factors act at various spatial and temporal scales (Wiens, 1986, 1989 ; Cornell & Lawton, 1992). Whole bird assemblages are presumed to be influenced from outside the ecosystem through neighbourhood effects (see Danielson, 1992 ;

* Present address : Scripps Institution of Oceanography-0202, UCSD, San Diego CA 92093, USA

** Institut de Zoologie, Université, Bd. de Pérolles, CH-1700 Fribourg, Switzerland

Dunning *et al.*, 1992 ; Hansson, 1992) or edge effects (for a review see Ranney, 1981). Large-scale and small-scale structural heterogeneities in an ecosystem are also thought to influence the animal assemblages (e.g. Freemark & Merriam, 1986 ; Urban & Smith, 1989 ; Sugihara & May, 1990 ; Rolstad, 1991 ; Hansson, 1992).

In this paper, we concentrate on the correlations between woody plant structures and the plant taxonomic compositions with the nesting bird assemblage in riparian (bottomland) forest patches. Several authors have studied bird assemblages in riparian forests before, but from other viewpoints (e.g. Barbieri & Fasola, 1975 ; Rice *et al.*, 1986 ; Finch, 1991 ; Bock *et al.*, 1992 ; Douglas *et al.*, 1992). Efforts to correlate either plant structures or plant taxonomic compositions with bird assemblages have been made before (e.g. MacArthur & MacArthur, 1961 ; Blondel *et al.*, 1973 ; James & Wamer, 1982 ; Blondel, 1986 ; Thiollay, 1990), but these have generally focused on homogeneous environments. These studies revealed general organisational patterns of the bird assemblages in relation to their habitat. In contrast, we shall consider forests that are mosaics of patches of different vegetation types. The mosaic structures of forests are natural as well as man-made (Blondel, 1986 ; Remmert, 1991 ; Hansson, 1992 ; Meyer, 1993), and these structures influence the distribution of birds (Bersier *et al.*, submitted). Do the bird assemblages in such mosaic forests show the same general patterns of organisation in relation to the vegetation ? To shed some light on this question, two ways to investigate the relations between plant structure or plant taxonomic composition and the bird assemblage are used here. The first brings together the various plant parameters with some synthetic value of the bird assemblage like the diversity index or the number of species (analysis of correlation or regression). The second compares the plant parameters with the whole bird matrix (ordinations).

METHODS

STUDY AREA, VEGETATION

The choice of the two taxonomic groups, ligneous plants and birds, for our study is justified as follows. Both are well known ecologically and systematically (for birds see Swift *et al.*, 1984 ; Cody, 1985 ; Blondel, 1986 ; Wiens, 1989 ; Finch, 1991 ; for forests see Ellenberg, 1982 ; Gehu, 1984 ; Koop, 1989 ; Remmert, 1991). The choice of riparian forests at the site of lake Grand Lieu has been made because they are particularly species-rich and are thus presumed to yield general species assembly rules more easily (see Magurran, 1988 for discussion). Their recent histories have been described (Marion & Marion, 1975).

In our four study plots (Fig. 1), 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 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 « stratiscope » (Blondel & Cuvillier, 1977) and the « point centred quarter » method of Cottam & Curtis (1956). At least 50 measurements with the stratiscope and 25 with the point

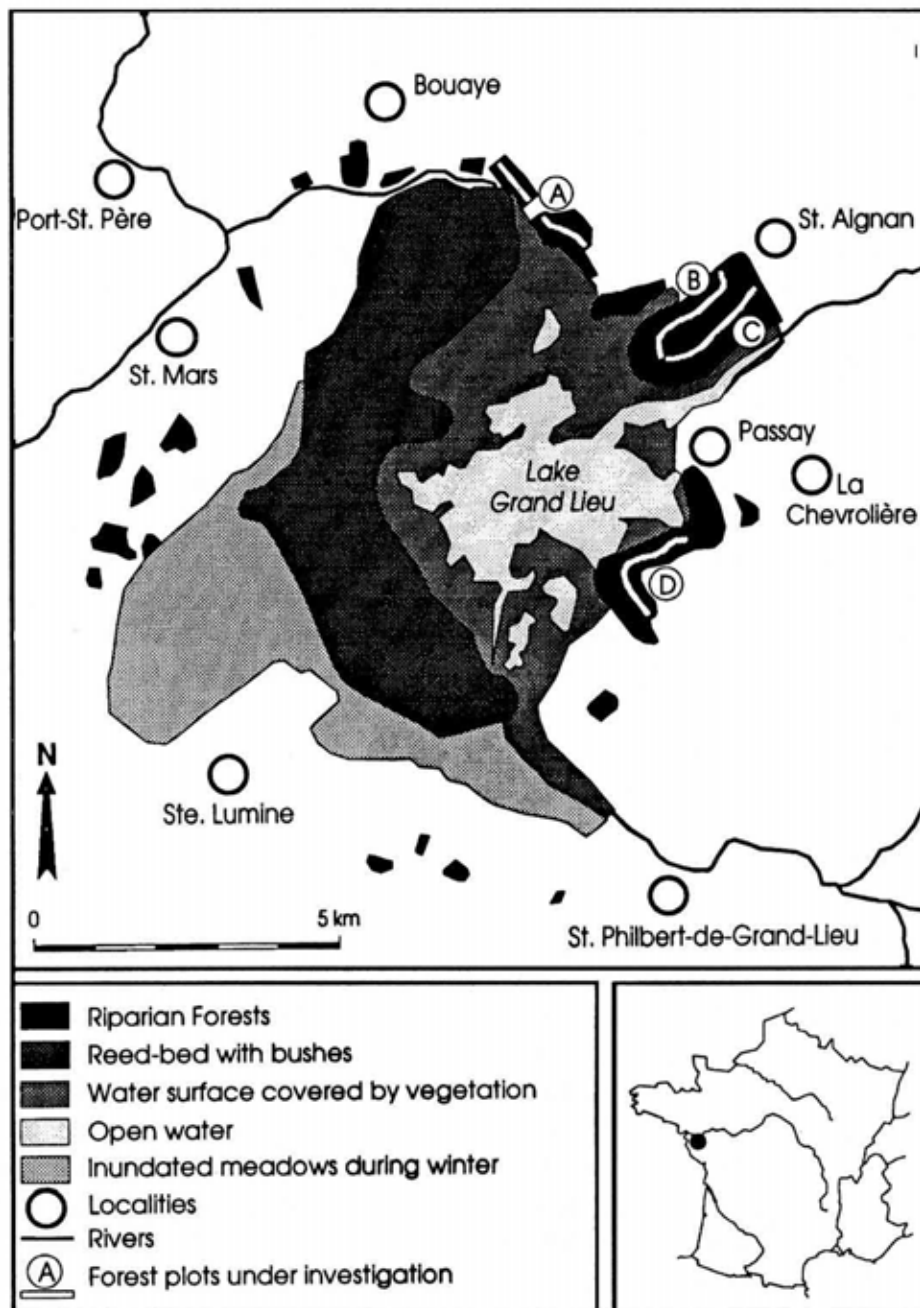


Figure 1. — Geographic situation of the four forest plots at Lake Grand Lieu, near Nantes, France.

centred quarter method were made for each vegetation type following a transect, with measurements separated by 4 and 8 meters respectively. The measurements using a stratiscope 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 centred 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 (0-3, 4-6, 7-15, 16-30, 31-60 years, more than 60 years old), based on the growth form of the vegetation. The

degree of man-made disturbances (forestry) was estimated to be of class 0, 1 or 2. The class 0 indicates that the vegetation is not influenced by forestry. The class 1 indicates that the perturbation is small : the intervention by forestry was performed in the past and is now attenuated. The class 2 is given in the case of recent intervention (plantation or undergrowth clearing).

The 31 vegetation types were analysed using the coefficient of Gower and intermediate linkage clustering (Legendre & Legendre, 1983). The most similar types were combined in one. This led to the establishment of 21 different types.

From the raw vegetation data we calculated several composite indices to condense the information into a small set of variables : the strata diversity (foliage height diversity, MacArthur & MacArthur, 1961) ; the herb layer percent coverage, the shrub coverage, the tree coverage, the coefficient of variation (CV) for the distances between trees and between shrubs (horizontal heterogeneity, 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 co-ordinates were performed with the geographical information system software GEOBASE (Blaise & Gessler, 1992) and IDRISI (Eastman, 1992) on a personal computer.

BIRD COUNTING

Bird counting was based on the spot mapping method (Blondel, 1969 ; Verner, 1985). The 4 forest plots, indicated in figure 1, are strips that are 100 m wide by 1 600-2 000 m long. 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 if they were outside the limits of the plots. The maps were 25 m broader on each side for that purpose. This was done to correctly assess the 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.

STATISTICAL ANALYSIS

Because we concentrate here on the general relationships between the vegetation and the bird community, patches of the same type were lumped together. Control measurements retained only the vegetation types for which the

species-area curve (Williams, 1943) reached a near-plateau, indicating an approximately complete set of bird species. We excluded 5 vegetation types, and only the 16 remaining types were subjected to the analyses.

We performed a cluster analysis on the bird data matrix, using the coefficient of Bray-Curtis and the intermediate linkage clustering (Legendre & Legendre, 1983). We performed analyses of regression with the variables of the vegetation and those of the bird assemblages (number of species, Shannon diversity). We used as dependent variables the various descriptors of vegetation and the indices described above. In one specific case (Fig. 3), we compared two regressions using a test for equality of slopes followed by an analysis of covariance (Sokal & Rohlf, 1981). In cases where we computed simultaneous regressions, we corrected the level of type I error using the Bonferroni method (Sokal & Rohlf, 1987 ; Krauth, 1988).

We studied the effects of vegetation on the whole bird assemblage using simple and partial canonical correspondence analysis (Ter Braak, 1986, 1988a ; Jongman *et al.*, 1987), using the software CANOCO (Ter Braak, 1988b). Because our sample size is small ($n = 16$), we performed a step-by-step procedure of selection of the environmental variables, retaining only the variables that explained most of the variance. Partial correspondence analysis was needed to distinguish between the effects of vegetation structure and those of the plant taxonomic composition. To do this we used the Borcard *et al.* (1992) variation partitioning method. The total variation in the bird data matrix (vegetation types x bird species table) can be decomposed in four fractions : the fraction of variation explained 1) exclusively by the vegetation structure, 2) exclusively by the plant taxonomic composition, 3) in common by the vegetation structure and by the taxonomic composition, and 4) an unexplained fraction (see Borcard & Legendre, 1993). In all ordinations we used the logarithms of the bird species abundances for the construction of the bird assemblage matrix.

RESULTS

The description of the 16 types of vegetation patches are presented in Table I and Appendix 1. The basic results of the bird mapping for the whole forest strips and for the various vegetation patch types are given in Appendix 2. The number of nesting bird species is high (37), not including large and rare birds. A cluster analysis on the bird data matrix reveals considerable similarity of data among the four forest strips and, in contrast to that, a differential bird assemblage structure in the different patch types (Fig. 2). The vegetation types are compared with the whole forest plots in this cluster analysis. The bird assemblages of complete forest plots most resemble those of late-successional and undisturbed patch types.

Table II shows the results of regression analysis between the vegetation variables and the variables for the bird assemblage in all forest patch types. The first group of variables deals with the physical structure of the vegetation ; here, the natural logarithm of age class showed the strongest correlation with both bird species richness and diversity. The diversity of stratification corresponds to the foliage height diversity of MacArthur & MacArthur (1961) ; it correlates with bird species diversity. The second group of variables in Table II deals with the plant taxonomic composition. Here the diversity of shrub species correlates best with

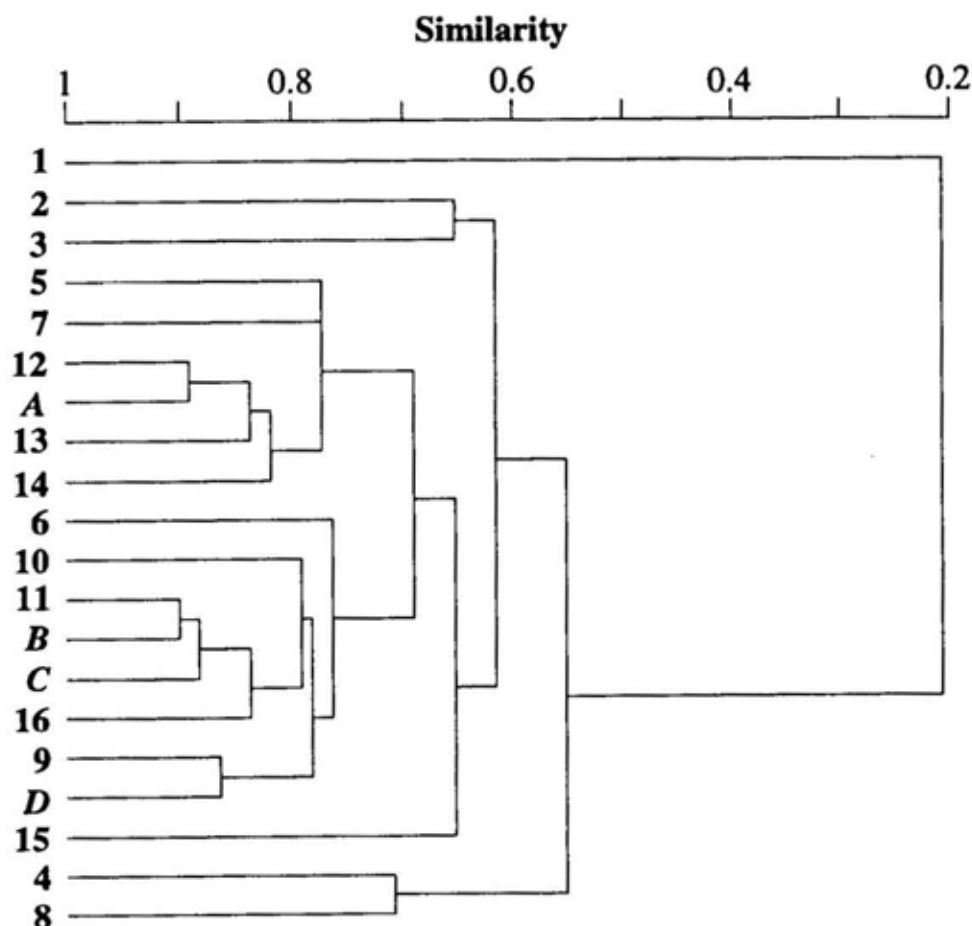


Figure 2. — Dendrogram based on similarities of bird assemblages in the 16 vegetation types and in the 4 forest plots. Names are abbreviated as in figure 1 and Table I.

bird species richness and diversity. The natural logarithms of the tree age types and the species numbers of ligneous plants correlate positively (product-moment correlation coefficient $r = 0.72$, $p < 0.01$).

In figure 3 the vegetation data set has been divided into two groups, namely forest patches that had not been disturbed by forestry (disturbance class 0) and the disturbed ones (disturbance classes 1 and 2). The disturbed forest patches have lower values of natural logarithms of bird species numbers than the non-disturbed patches. Separate regressions for disturbed and non-disturbed forest patches lead to two nearly-parallel regression lines that both are statistically significant (in both cases $p < 0.01$). No significant difference between the slopes could be detected ($p = 0.72$, test for equality of slopes), but the two adjusted means differ ($p < 0.025$, analysis of covariance). The relation between the logarithm of age class and species richness is not thought to be log-log linear (e.g. Ferry & Frochot, 1970 ; Dierschke, 1973 ; Glowacinski, 1975 ; Harris, 1984 ; Muller, 1985 ; Urban & Smith, 1989). Log-log linear regression was however used as it fits well with our data, probably because the successional time at lake Grand Lieu is quite short (60 to 200 years), and as it allows us to perform a simple covariance test. The natural logarithms of the age classes are not correlated with the disturbance level ($r = 0.08$). The simple regression of the independent variable « disturbance class » and the natural logarithm of bird species number shows no relation at all.

TABLE I

Description of main vegetation types in forests at lake Grand Lieu. A = age class, p = degree of perturbation, S = number of bushes and trees species, n = number of patches. X-axis of the profiles is percentage cover (0-100 %), Y-axis is height (0-42 m).

Vegetation type				profile	Vegetation type				profile
1	Early-successional zones with dense grass layer and sparse scrubs	A	0 - 3 y.		9	Temporarily flooded oak forest with medium undergrowth	A	31-60 y.	
		p	0				p	0	
		S	3				S	7	
		n	7				n	9	
2	Early-successional zones with dense fern <i>Pteridium aquilinum</i> layer and sparse scrubs	A	0 - 3 y.		10	Old-growth oak forest with sparse undergrowth	A	> 60 y.	
		p	0				p	0	
		S	3				S	14	
		n	6				n	11	
3	Early-successional zones with dense grass layer and numerous bushes	A	4 - 6 y.		11	Old-growth oak forest with medium undergrowth	A	> 60 y.	
		p	0				p	0	
		S	8				S	20	
		n	27				n	47	
4	Plantation of young chestnut <i>Castanea sativa</i>	A	4 - 6 y.		12	Old-growth oak forest with dense undergrowth	A	> 60 y.	
		p	2				p	0	
		S	5				S	18	
		n	4				n	80	
5	Dense bushes	A	7 - 15 y.		13	Dense bushes with sparse trees	A	> 60 y.	
		p	0				p	0	
		S	14				S	12	
		n	25				n	12	
6	Plantation of conifers	A	7 - 15 y.		14	Thin old-growth oak forest with dense undergrowth	A	> 60 y.	
		p	2				p	1	
		S	8				S	14	
		n	5				n	2	
7	Young oak forest <i>Quercus robur</i> with dense bush layer	A	16 - 30 y.		15	Old plantation of Pines <i>Pinus pinaster</i> with sparse undergrowth and understory of oaks	A	> 60 y.	
		p	0				p	1	
		S	11				S	12	
		n	17				n	8	
8	Plantation of adolescent chestnut <i>Castanea sativa</i>	A	16 - 30 y.		16	Old-growth oak forest with cleared undergrowth	A	> 60 y.	
		p	2				p	2	
		S	6				S	10	
		n	10				n	11	

Ordination is more explicit in presenting the relative importance of several variables to the bird assemblage composition. It takes the whole bird assemblage matrix into account and not just a synthetic index. The complete bird data set was subjected to canonical correspondence analysis, first with the variables of plant structure, then with the variables of plant taxonomic composition as explanatory variables for the bird matrix (Figs. 4a and b). In both cases, we found three plant variables that significantly explain the variation in the bird data. For plant structures they were: tree diameter heterogeneity, ($p = 0.005$, 999 permutations),

TABLE II

Analysis of regressions between plant variables and bird variables of all forest patch types. The upper group of values are those obtained with variables of plant structures, the lower group was obtained with variables of plant taxonomic associations. Values in bold indicate significant relation at the Bonferroni corrected level of 5 % ($\alpha' = 0.05/22 = 0.0023$).

Variables of vegetation	Bird species richness				Bird species diversity			
	n	r ² adj.	coeff	p	n	r ² adj.	coeff	p
Diversity of strata (FHD)	16	0.22	20.19	0.0372	16	0.46	1.27	0.0023
Horizontal heterogeneity of shrubs	16	-0.03	13.21	0.4538	16	-0.05	-0.41	0.6270
Horizontal heterogeneity of trees	13	-0.08	-6.03	0.7369	13	-0.06	-0.29	0.6039
CV of shrubs' height	16	-0.07	2.21	0.8636	16	0.02	0.66	0.2661
CV of trees' height	13	0.28	16.16	0.0377	13	0.17	0.42	0.0922
CV of trees' diameters (dbh)	13	0.32	29.43	0.0264	13	0.18	0.75	0.0836
log of age class	16	0.54	9.04	0.0007	16	0.64	0.46	0.0001
degree of disturbance	16	0.07	-3.15	0.1591	16	-0.07	-0.02	0.8632
Tree species diversity	16	0.47	10.09	0.0021	16	0.18	0.33	0.0565
Shrub species diversity	16	0.65	12.39	0.0001	16	0.51	0.53	0.0011
Ligneous plant diversity	16	0.66	12.06	0.0001	16	0.33	0.43	0.0112

percentage coverage by shrubs ($p = 0.045$) and age class ($p = 0.016$). The first ordination axis separates early-successional stages with high percentage cover of shrubs from other vegetation types that show a high heterogeneity of trunks' diameters. The second axis is best correlated with the age of the vegetation (Fig. 4a). The first two ordination axes explain 19 % and 12.4 % of the variance in the bird data. For these axes, the bird-plant structure relationship is significant ($p = 0.005$ and $p = 0.035$). For the plant taxonomic composition, the three significant variables are : proportion of *Quercus pedunculata* ($p = 0.002$), proportion of chestnut bushes *Castanea sativa* ($p = 0.006$) and Shannon diversity of ligneous plant species ($p = 0.014$). The first ordination axis shows a gradient reflecting the succession by the importance of oak trees and of chestnut shrubs. The second axis distinguishes disturbed from undisturbed vegetation types by the richness of ligneous plants (Fig. 4b). The first two axes of ordination explain 22.2 % and 11.5 % respectively of the variance in the bird data, both values being statistically significant with $p = 0.006$ and $p = 0.047$. The sum of all unconstrained eigenvalues (the trace of the covariance matrix of bird data) equals 0.586 for both ordinations.

To gain insight into the relative importance of plant structure variables and of plant taxonomic composition variables in structuring the bird community, we subjected the data to partial canonical correspondence analysis. The analysis was restricted to the three variables in each set of plant data explaining most of the variance in the bird data, the ones indicated above. The results are presented in Table III and figure 5a. The individual contributions due to the vegetation structure

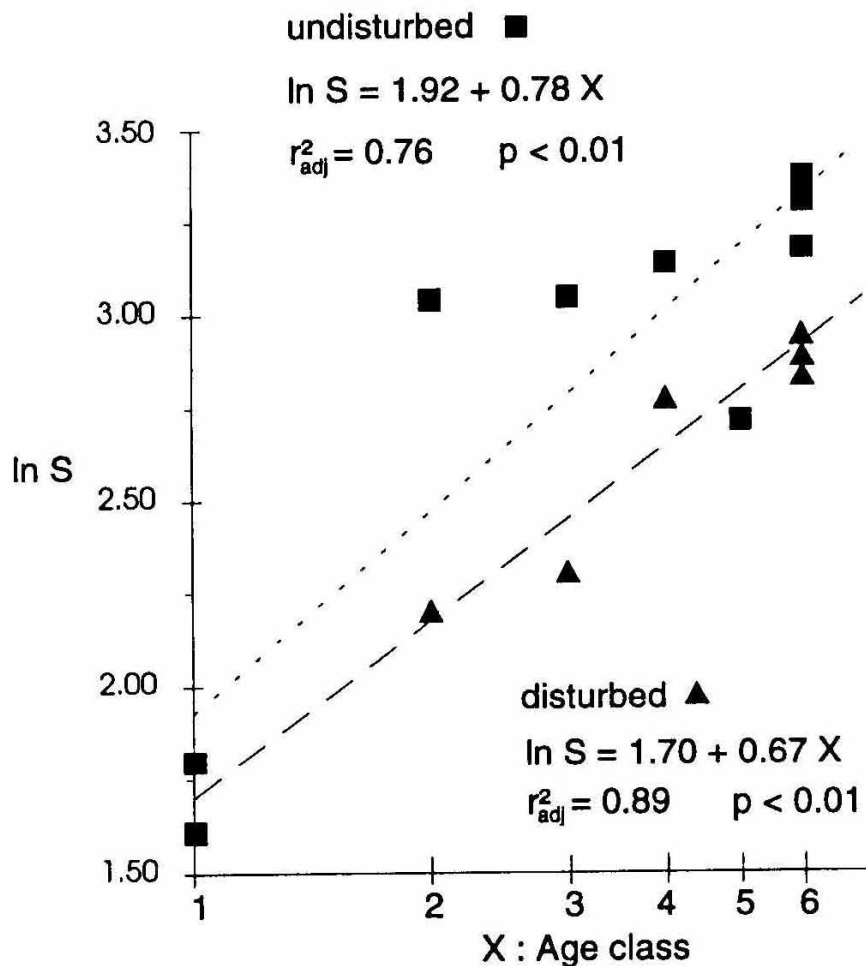


Figure 3. — Regression analyses with the logarithms of bird species number S as dependent variable, and the logarithm of the age class of the vegetation as dependent variable. The wood patch types are divided into two groups, those disturbed by forestry (triangles) and those not disturbed (squares).

and to the plant composition are similar (17 %). Their common contribution is high (21 %). Rotenberry (1985) proposed that birds may differentiate between gross habitat types on the basis of physiognomy, and within the proper habitat type on the basis of plant taxonomic composition. Thus the relative influence of floristics on the bird assemblage should increase as the range of habitat types diminishes. We have tested this hypothesis by removing the 3 early-successional vegetation types 1, 2 and 3. Indeed, Table III and figure 5b show that the taxonomic composition gains in importance over the plant structure variables as the range of habitat types is reduced.

DISCUSSION

We have shown that the distribution of nesting birds in a riparian forest varies in the mosaic patches in relation to the vegetation (Table II). The Shannon diversity of birds increases locally with the structural diversity of the plants, as demonstrated before, but on a whole-forest scale (e.g. MacArthur & MacArthur, 1961 ; Recher, 1969 ; Blondel *et al.*, 1973 ; Wilson, 1974 ; Røv, 1975 ; Erdelen,

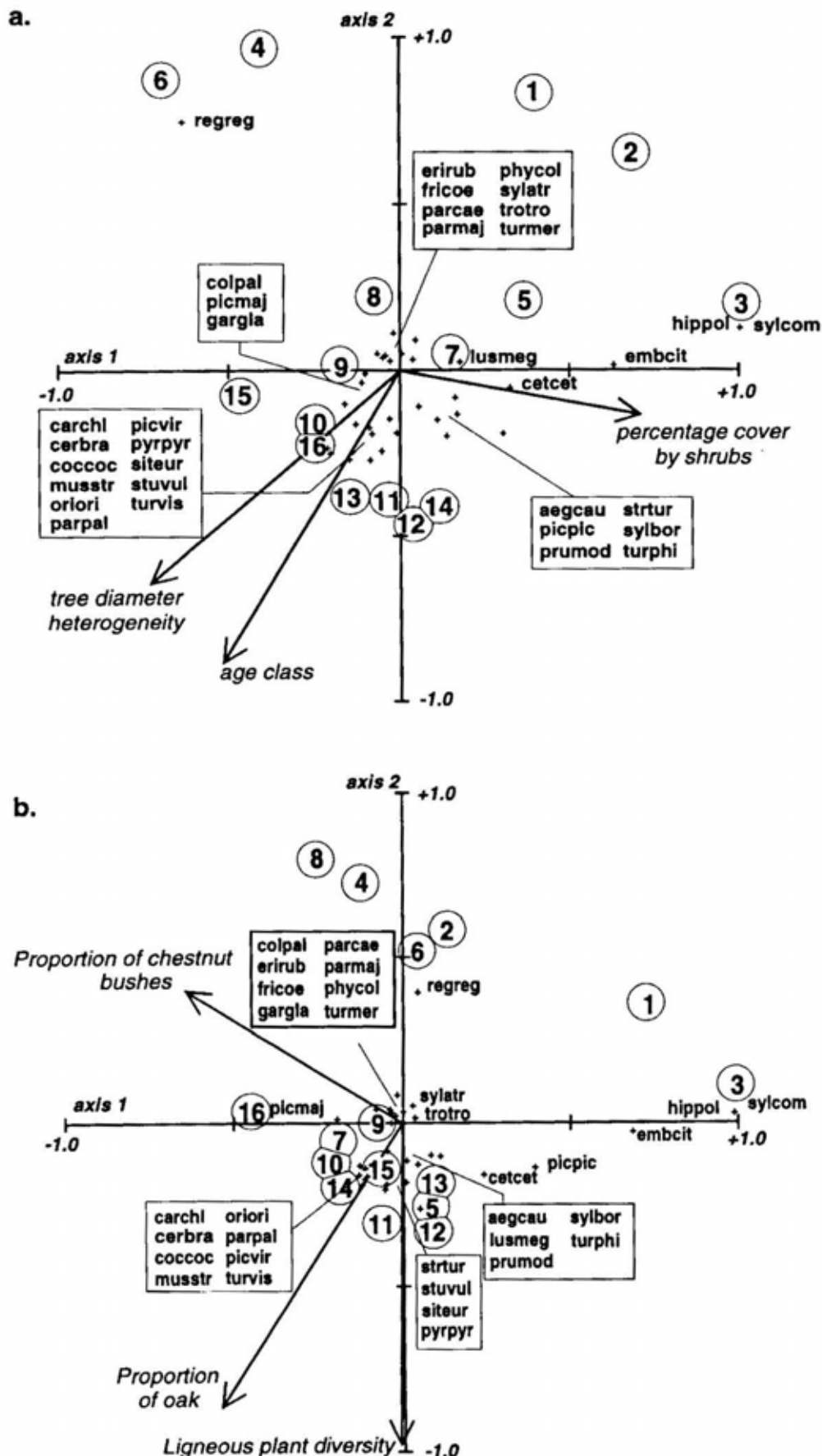


Figure 4. — Ordination diagrams of the canonical correspondence analyses of the bird community matrix with : a) the variables of plant structure ; b) the variables for plant taxonomic composition. Arrows : significant variables explaining the bird variation ; crosses : bird species ; circled numbers : vegetation types, abbreviations as in Table I. The abbreviations for bird names are explained in appendix 2. The degree of association of bird abundance with forest types is indicated by the neighbourhood of the crosses to forest patch types.

TABLE III

Partitioning of the variation in the bird data matrix explained by the variables of the vegetation structure and of the plant taxonomic composition. The sums of eigenvalues are given with their corresponding percentages of variation. The ordination methods used are : CA = correspondence analysis, CCA = canonical CA, pCCA = partial CCA. For the analyses without the early-successional types, the percentage variation due exclusively to the structure is 15 %, due exclusively to the taxonomic composition is 23 %, due in common to the structure and to the taxonomic composition is 36 % - 15 % = 44 % - 23 % = 21 %. The total explained variation is 36 % + 23 % = 44 % + 15 % = 59 %.

Method		For all the vegetation types (n = 16)		Without the early-successional vegetation (n = 13)	
CA	Sum of all unconstrained eigenvalues	0.586	(100 %)	0.501	(100 %)
CCA	Sum of eigenvalues, constrained by the variables of vegetation structure	0.223	(38 %)	0.181	(36 %)
CCA	Sum of eigenvalues, constrained by the variables of plant taxonomic composition	0.221	(38 %)	0.219	(44 %)
pCCA	Sum of eigenvalues constrained by the variables of vegetation structure, after removing the effect of plant taxonomy	0.101	(17 %)	0.076	(15 %)
pCCA	Sum of eigenvalues, constrained by the variables of plant composition, after removing the effect of vegetation structure	0.099	(17 %)	0.114	(23 %)

1984 ; Swift, 1984). In contrast to the findings of Roth (1976) the horizontal structural heterogeneity inside a forest patch type does not appear to be important for bird diversity in our case. It is biologically meaningful that the age classes correlate best with species richness in birds ; this structural variable is related to succession as are other plant structural descriptors to a lesser degree. The floristic variables correlate well with the indices of bird assemblages. They are also to be interpreted in the context of plant succession.

That forestry influences the bird assemblage has been postulated in more general studies (Harris, 1984 ; Blondel, 1986 ; Virkkala, 1987 ; Saxon, 1990 ; Thiollay, 1992). Our findings indicate that even on a small scale, and with forestry methods other than clearcuts (undergrowth clearing, plantation), the bird assemblage reacts as if disturbances were of high amplitude. The effect (lower species number) is independent of forest age and it is not known whether it will last over several years.

As in the regression analysis, the results of canonical correspondence analysis show that vegetation variables best correlated with the bird assemblage variance (arrows in Figs. 4a and b) are those related to plant succession. The effect of disturbance by forestry is less apparent here than with regression analysis. This

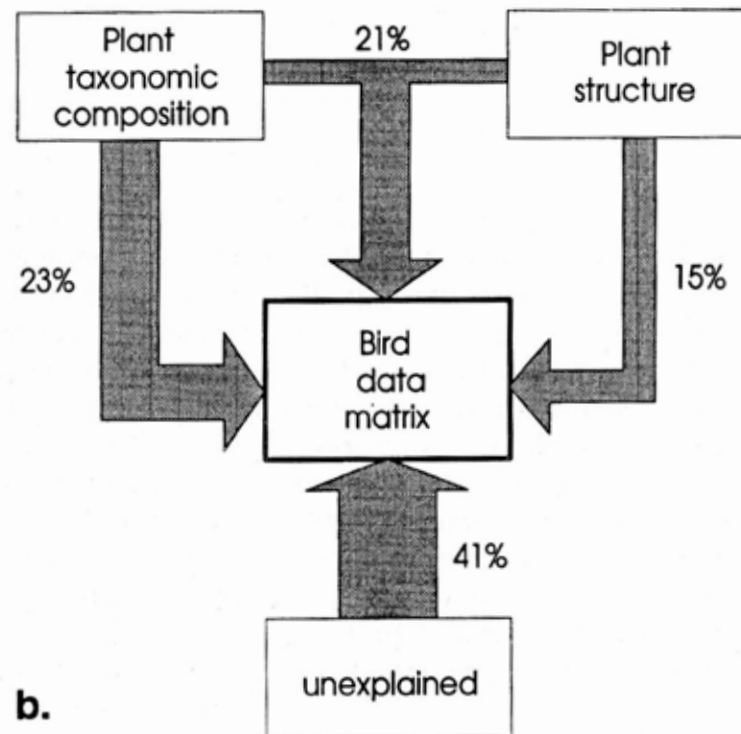
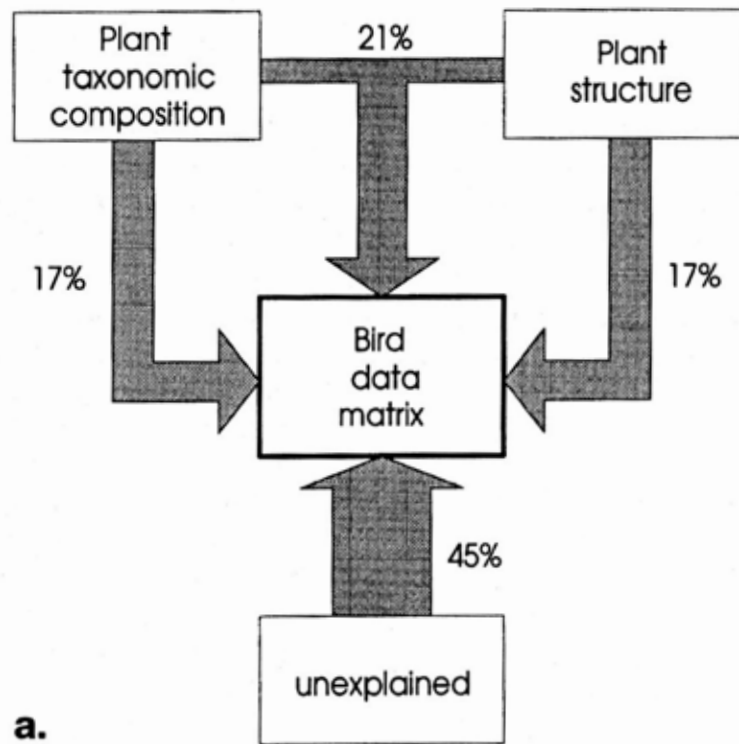


Figure 5. — a) The result of partial canonical correspondence analysis based on the first three variables of plant structure or of plant taxonomic composition as they explain the variation in the bird data matrix. This variation is explained exclusively and jointly by the two groups of variables. b) The results with the same data except that the data from early-successional forest patch types (1 to 3) were excluded.

indicates that the disturbance lowers the total number of bird species but does not eliminate any particular species from the assemblage (see however Rolstad, 1991).

The value of the trace of the covariance matrix is low (Jongman *et al.*, 1987). This indicates that the total dispersion of the bird matrix is low. This is unexpected because a wide range of forest successional stages had been sampled. Neighbourhood effects that are not taken into account here increase the homogeneity of the bird assemblage (Bersier *et al.*, submitted).

An equal amount of variation in the bird data is explained either by the variables of vegetation structure or of plant taxonomic composition. Plant structure as well as taxonomic variables are important for the bird assemblages. The common effect of both components is 21 %, indicating that both sets of vegetation variables are mutually dependent. This was pointed out before (e.g. Wiens & Rotenberry, 1981 ; Hino, 1985), and is not a surprise : particular plant species have particular physiognomy. If we restrict our analysis to forest vegetation types without early-successional types, the importance of plant taxonomic composition increases. This is consistent with the hypothesis of Rotenberry (1985). Vegetation structure is more important for birds on a larger scale, taxonomic composition more so on a smaller scale. A detailed study of this scale-dependent habitat selection is presented elsewhere (Bersier & Meyer, in press).

The bird assemblage of a riparian forest is tied to the successional stage of the forest. The diversity of the plant stratification as well as the low-scale floristic composition appear to have some value for predicting bird species diversity. The bird assemblage differentiates however only to some extent with these environmental variables, thus the action of the vegetation variables is partially obscured by the mosaic pattern of vegetation patches. Based on correlation patterns that are biologically meaningful, a hypothesis for causes and effects on the bird assemblage is to be formulated and tested at other biogeographic locations.

SUMMARY

The vegetation structure and the plant taxonomic composition of riparian forests, together with the birds, were mapped and analysed. The forest plots were 100 m wide and 1 600 to 2 000 m long, and were located near lake Grand Lieu, Brittany, France. The plots were not homogeneous, but a mosaic of different vegetation types. The patches of the same vegetation type were combined. We recognized 21 vegetation types, but we retained only 16 that were of sufficient size to neutralize species-area effects. Variables of vegetation structure as well as variables of plant taxonomic composition associated with plant succession showed the strongest correlations with the variables of bird community. Disturbances caused by forestry is correlated with reduced bird species richness in forest patches of all ages. Canonical correspondence analyses of the bird data constrained by the vegetation data allowed us to identify that variables that explain most of the variance in bird data are those related strongly to succession. Partial CCA revealed the relative influence of plant structure versus floristic variables as well as their combined influence on bird community structure (17, 17, 21 % respectively). When the same analysis is applied after removal of early-successional vegetation types, the importance of floristic variables increased.

RÉSUMÉ

Nous avons analysé et reporté sur plan la structure et la composition en espèces de la végétation, ainsi que des oiseaux nicheurs des forêts riveraines du lac de Grand Lieu, en Bretagne (France). Les parcelles d'études sont des bandes de 100 m de large et de 1 600 à 2 000 m de long. Les parcelles ne sont pas homogènes, mais constituent une mosaïque de différents types de végétation. Nous avons combiné les zones de même type de végétation. Nous n'avons retenu que les types de végétation pour lesquels la relation nombre d'espèces d'oiseaux-surface atteignait un plateau. Les descripteurs de la structure de la végétation et de la floristique associés à la succession forestière sont les mieux corrélés avec les paramètres de structure de l'assemblage en espèces d'oiseaux. Les perturbations causées par la sylviculture sont inversement corrélées avec la richesse en espèces d'oiseaux dans les types de végétation de tout âge. Nous avons effectué des analyses canoniques des correspondances simples et partielles, contraintes par les variables de la structure de la végétation et de la composition floristique. Les résultats confirment que les variables expliquant le plus de variation dans la distribution des oiseaux sont celles liées à la succession forestière. L'analyse des correspondances partielle révèle les influences individuelles de la structure de la végétation et de la floristique, ainsi que leur influence commune (respectivement 17, 17 et 21 %). Nous avons effectué la même analyse après avoir éliminé les types de végétation des premiers stades de la succession. Le résultat montre que l'influence de la floristique augmente lorsque l'on diminue ainsi l'échelle d'étude.

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 techniques and greatly improved an earlier draft of the manuscript. Loïc Marion and Patrice Boret introduced us to the lake of Grand Lieu. Jacques Blondel, Gregory Hart, Jean-Dominique Lebreton, Francis Saucy and George Sugihara provided valuable comments on this manuscript. We are indebted to IBM Switzerland who offered advanced computing equipment for this work ; we thank Jakob Vogel and Georges Duperrut for support. This research was supported by a grant from the « Société vaudoise des sciences naturelles », by the committee for travel grants of the Swiss Academy of Science and by ONR N00014-92-5-4068.

APPENDIX 1

Description of the 16 vegetation types. The vegetation types are indicated as in Table 1.

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	2	13	4	2	19	2	1	3
Man-made perturbation	0	0	0	2	0	2	0	2	0	0	0	0	0	1	1	2
Age-class	1	1	2	2	3	3	4	4	5	6	6	6	6	6	6	6
Percentage cover																
0 - 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	100	68	88	96	74	79
0.5 - 1 m	77	100	100	46	100	38	96	54	62	96	100	32	84	92	51	50
1 - 2 m	46	76	95	69	100	38	87	77	48	88	92	28	64	40	20	22
2 - 4 m	0	0	13	77	56	92	91	46	53	68	62	24	68	32	26	29
4 - 8 m	0	0	0	69	4	85	49	31	63	76	8	32	60	12	54	14
8 - 16 m	0	0	0	54	0	15	8	100	61	88	38	92	80	52	62	86
16 - 32 m	0	0	0	0	0	0	0	0	11	48	8	64	72	68	84	24
Mean distance betw. trees [m]	-	-	-	1.6	3.5	2.1	2.4	2.1	2.6	2.7	8.1	3.4	3.1	5.4	3.2	3.7
Standard deviation	-	-	-	1.2	2.0	1.1	1.2	0.8	1.2	1.2	6.0	1.7	1.4	2.8	1.7	1.9
Mean trees' height	-	-	-	8.1	8.3	11.3	9.1	11.7	14.4	21.3	18.9	18.3	22.4	25.2	26	18.8
Standard deviation	-	-	-	2.1	1.9	4.4	2.6	2.9	6.3	9.7	11.2	13.2	22.7	12.5	19.4	8.6
Mean dbh [cm]	-	-	-	6.6	9.0	11.5	9.6	11.2	15.6	20.6	29.3	23.6	20.5	30.3	32.2	20.6
Standard deviation	-	-	-	2.8	3.4	6.3	5.0	5.5	8.9	15.7	25.1	13.6	14.1	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	1.3	1.5	2.0	1.4	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	1.0	1.2	1.5	1.0	0.7	1.2	1.0
Mean shrubs' height	1.3	1.6	2.1	1.9	2.4	2.3	2.5	1.6	2.0	1.6	2.0	2.0	2.4	1.3	1.6	1.6
Standard deviation	0.6	0.3	0.7	1.1	0.7	1.1	1.0	1.2	1.1	1.2	1.1	0.9	0.8	0.6	1.2	1.1
Number of ligneous species	4	3	8	5	14	8	11	6	7	18	12	14	20	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	-	30	40	-	20	-	-	-
<i>Quercus robur</i>	-	-	-	-	50	-	60	-	100	50	40	80	60	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	-	-	10	20	-	-	-	-	-
<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	10	20	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 pyraeaster</i>	-	-	-	10	-	-	-	20	-	-	-	-	-	-	-	-
<i>Populus sp.</i>	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	20
<i>Robinia pseudoacacia</i>	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rubus fruticosus</i>	-	-	20	-	20	-	40	10	40	40	40	20	10	50	30	-
<i>Salix sp.</i>	10	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-
Dead shrubs	-	-	-	40	-	-	-	-	10	-	-	20	-	-	10	10

APPENDIX 2

Densities of nesting bird species in the 16 vegetation types and in the four forest plots.
Densities are calculated for 10 ha.

abbrev.	area [ha]	Vegetation type																Survey strip			
		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
colpal	<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
stturt	<i>Streptopelia turtur</i>	-	-	-	-	1.7	-	-	-	-	-	0.3	0.4	1.2	-	-	-	1.1	-	-	0.6
picvir	<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
picmaj	<i>Picoides 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
picmin	<i>Picoides minor</i>	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-	-	-	-	0.3	-
trotro	<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
prumod	<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	-
erirub	<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
lusemeg	<i>Luscinia megarhyn.</i>	-	-	-	-	-	-	1.6	-	-	-	-	-	-	-	-	-	-	-	0.3	-
turmer	<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
turphi	<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	-
turvis	<i>Turdus viscivorus</i>	-	-	-	-	-	-	-	-	0.8	2.2	0.4	0.6	0.9	-	-	-	0.5	0.8	-	0.6
cetoet	<i>Cettia cetti</i>	-	-	3.7	-	4.8	-	0.4	-	-	-	0.6	0.7	2.7	-	-	0.4	5.4	0.3	-	-
hippol	<i>Hippolais polyglotta</i>	-	-	10.6	-	-	-	-	-	-	-	-	-	-	-	-	-	1.1	-	0.6	0.3
syloom	<i>Sylvia communis</i>	-	-	4.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.6
sylbor	<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
sylatr	<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
phycol	<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
regreg	<i>Regulus regulus</i>	-	-	-	-	-	4.0	-	-	-	-	-	0.2	-	-	-	-	-	-	-	0.6
regign	<i>Regulus ignicapillus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.8	-	-
musstr	<i>Muscicapa striata</i>	-	-	-	-	1.2	-	-	-	-	5.4	0.1	0.1	1.8	-	-	0.8	2.2	0.3	-	-
aegcau	<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
parpal	<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
parcri	<i>Parus cristatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5	-	-
parcae	<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
parmaj	<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
siteur	<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
cerbra	<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
oriori	<i>Oriolus oriolus</i>	-	-	-	-	-	-	-	-	-	3.3	-	-	0.7	-	-	-	1.1	-	-	-
gargla	<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
picpic	<i>Pica pica</i>	-	-	0.7	-	-	-	-	-	-	-	-	0.4	0.9	-	-	-	1.1	-	-	-
stuvul	<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
fricoe	<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
carchl	<i>Carduelis chloris</i>	-	-	-	-	-	-	-	-	-	1.6	-	-	0.7	-	-	-	0.5	-	-	-
pytpyr	<i>Pyrrhula pyrrhula</i>	-	-	-	-	-	-	0.8	-	-	1.6	0.2	0.8	3.2	-	-	-	1.6	0.3	0.6	-
coccoc	<i>C. coccythraustes</i>	-	-	-	-	-	-	-	-	-	1.3	0.2	0.3	-	-	-	-	-	-	0.6	-
embcit	<i>Emberiza citrinella</i>	-	-	2.8	-	-	-	-	-	-	-	-	-	0.9	-	-	-	-	-	-	0.6

REFERENCES

- ARRHENIUS, O. (1921). — Species and area. *J. Ecol.*, 9 : 95-99.
- BARBIERI, F. & FASOLA, M. (1975). — Censimento della popolazione di uccelli nidificanti in un bosco ripariale del Ticino. *Riv. Ital. Ornitol.*, 45 : 28-41.
- BERSIER, L.F. & MEYER, D.R. (in press). — Bird assemblages in mosaic forests : the relative importance of vegetation structure and floristic composition along the successional gradient. *Acta Oecol.*
- BERSIER, L.F., BORCARD, D., MARTHE, C. & MEYER, D.R. (submitted). — Bird assemblages and patch mosaic structure of forests : the importance of neighbourhood effects.
- BERTHOLD, P. (1976). — Methoden der Bestandeserfassung in der Ornithologie : Übersicht und kritische Betrachtung. *J. Ornithol.*, 117 : 1-69.
- BLAISE, P. & GESSLER, C. (1990). — *GEOBASE, version 2.0 (beta)*. Institut für Phytomedizin ETH, Zürich CH.
- BLONDEL, J. (1969). — Méthodes de dénombrement des populations d'oiseaux. In : *Problèmes d'écologie : l'échantillonnage des peuplements animaux des milieux terrestres*. M. Lamotte & F. Bourlière (eds). Masson, Paris : 97-151.
- BLONDEL, J. (1986). — *Biogéographie évolutive*. Masson, Paris.
- BLONDEL, J. & CUVILLIER, R. (1977). — Une méthode simple et rapide pour décrire les habitants d'oiseaux : le stratiscope. *Oikos*, 29 : 326-331.
- BLONDEL, J., FERRY, C. & FROCHOT, B. (1973). — Avifaune et végétation, essai d'analyse de la diversité. *Alauda*, 41 : 63-84.
- BOCK, C.E., CRUZ, A., GRANT, M.C., AID, C.S. & STRONG, T.R. (1992). — Field experimental evidence for diffuse competition among Southwestern riparian birds. *Am. Nat.*, 140 : 815-828.
- BORCARD, D., LEGENDRE, P. & DRAPEAU, P. (1992). — Partialling out the spatial component of ecological variation. *Ecology*, 73 : 1045-1055.
- BORCARD, D. & LEGENDRE, P. (1993). — Environmental control and spatial structure in ecological communities, with an example on Oribatid mites (Acari, Oribatei). *J. Envir. Stat.*, 1 : 55-76.
- CHESSON, P. & HUNTLY, N. (1989). — Short-term instabilities and long-term community dynamics. *Trends Ecol. Evol.*, 4 : 293-298.
- CODY, M.L. (ed) (1985). — *Habitat Selection in Birds*. Academic Press, New York.
- CORNELL, H.V. & LAWTON, J.H. (1992). — Species interactions, local and regional processes, and limits to the richness of ecological communities : a theoretical perspective. *J. Anim. Ecol.*, 61 : 1-12.
- COTTAM, G. & CURTIS, J. (1956). — The use of distance measures in phytosociological sampling. *Ecology*, 37 : 451-460.
- DANIELSON, B.J. (1992). — Habitat selection, interspecific interactions, landscape composition. *Evol. Ecol.*, 6 : 399-460.
- DIAMOND, J.M. (1975). — Assembly of species communities. In : *Ecology and evolution of communities*. M.L. Cody & J.M. Diamond (eds). Harvard University Press, Cambridge MA : 342-444.
- DIERSCHKE, F. (1973). — Die Sommervogelbestände nordwestdeutscher Kiefernforsten. *Vogelwelt*, 94 : 201-225.
- DOUGLAS, D.C., RATTI, J.T., BLACK, R.A. & ALLDREDGE, J.R. (1992). — Avian habitat associations in riparian zones of Idaho's Centennial Mountains. *Wilson Bull.*, 104 : 485-500.
- DRAKE, J.A., FLUM, T.E., WITTEMAN, G.J., VOSKUIL, T., HOYLMAN, A.M., CRESO, C., KENNY, D.A., HUXEL, G.R., LARUE, C.S. & DUNCAN, J.R. (1993). — The construction and assembly of an ecological landscape. *J. Anim. Ecol.*, 62 : 117-130.
- DUNNING, J.B., DANIELSON, B.J. & PULLIAM, H. (1992). — Ecological processes that affect populations in complex landscapes. *Oikos*, 65 : 169-175.
- ELLENBERG, H. (1982). — *Vegetation Mitteleuropas mit den Alpen*. Ulmer Verlag, Stuttgart.
- ERDELEN, M. (1984). — Bird communities and vegetation structure : I. Correlations and comparisons of simple and diversity indices. *Oecologia*, 61 : 277-284.
- EASTMAN, J.R. (1992). — *IDRISI Version 4.0*. Clark University, Graduate School of Geography, Worcester, Ma USA.
- FERRY, C. & FROCHOT, B. (1970). — L'avifaune nidificatrice d'une forêt de chênes pédonculés en Bourgogne : étude de deux successions écologiques. *Terre Vie*, 24 : 153-250.
- FINCH, D.M. (1991). — Positive associations among riparian bird species correspond to elevational changes in plant communities. *Can. J. Zool.*, 69 : 951-963.
- FREEMARK, K.E. & MERRIAM, H.G. (1986). — Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. *Biol. Conserv.*, 31 : 95-105.

- GEHU, J.M. (ed.) (1984). — *La végétation des forêts alluviales*. Colloques phytosociologiques. Cramer Verlag, Vaduz FL.
- GILPIN, M. & HANSKI, I. (eds) (1991). — *Metapopulation dynamics : empirical and theoretical investigations*. Academic Press, New York.
- GLOWACINSKI, Z. (1975). — Succession of bird communities in the Niepolomice forest (Southern Poland). *Ekol. Polska.*, 23 : 231-263.
- HANSSON, L. (1992). — Landscape Ecology of Boreal Forests. *Trends Ecol. Evol.*, 7 : 299-302.
- HARRIS, L. (1984). — *The fragmented forest : island biogeography theory and the preservation of biotic diversity*. University of Chicago Press, Chicago.
- HINO, T. (1985). — Relationships between bird community and habitat structure in shelterbelts of Hokkaido, Japan. *Oecologia*, 65 : 442-448.
- JAMES, F.C. & WAMER, N.D. (1982). — Relationships between temperature forest bird communities and vegetation structure. *Ecology*, 63 : 159-171.
- JONGMAN, R.H.G., TER BRAAK, C.J.F. & VAN TONGEREN, O.F.R. (eds) (1987). — *Data analysis in community and landscape ecology*. Pudoc, Wageningen NL.
- KOOP, H. (1989). — *Forest Dynamics SILVI-STAR : A Comprehensive Monitoring System*. Springer Verlag, Berlin.
- KAUFMANN, S.A. (1993). — *The origins of order - Self-organization and selection in evolution*. Oxford University Press, New York.
- KRAUTH, J. (1988). — *Distribution-free statistics : an application-oriented approach*. Elsevier, Amsterdam.
- LAVOREL, S., LEPART, J., DEBUSSCHE, M., LEBRETON, J.D. & BEFFY, J.L. (1994). — Small scale disturbances and the maintenance of species diversity in Mediterranean old fields. *Oikos*, 70 : 455-473.
- LAW, R. & MORTON, R.D. (1993). — Alternative permanent states of ecological communities. *Ecology*, 74 : 1347-1361.
- LEGENDRE, L. & LEGENDRE, P. (1983). — *Numerical ecology*. Developments in environmental modelling. 3. Elsevier, Amsterdam.
- LOTKA, A. (1925). — *Elements in physical biology*. Williams and Wilkins Co, Baltimore, USA.
- MACARTHUR, R.H. & MACARTHUR, 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*, spécial issue : 1-611.
- MEYER, D.R. (1993). — Dynamik, strukturelle Heterogenität und biologische Diversität von Wald-Ökosystemen. In *Der Wald*. D. Daphinoff & E. Marsch (eds). Editions universitaires, Fribourg CH : 23-47.
- MONKKONEN, M., HELLE, P. & SOPPELA, K. (1990). — Numerical and behavioural responses of migrant Passerines to experimental manipulation of resident tits (*Parus spp.*). - Heterospecific attraction in Northern breeding bird communities. *Oecologia*, 85 : 218-225.
- MÜLLER, Y. (1985). — *L'avifaune forestière nicheuse des Vosges du Nord, sa place dans le contexte médio-européen*. PhD Thesis, University of Dijon F.
- ODUM, E. (1990). — Field experimental tests of ecosystem-level hypotheses. *Trends Ecol. Evol.*, 5 : 204-205.
- PIMM, S.L., LAWTON, J. & COHEN, J. (1991). — Food web patterns and their consequences. *Nature*, 350 : 669-674.
- PRESTON, F. (1962). — The canonical distribution of commonness and rarity. *Ecology*, 43 : 185-215.
- RANNEY, J.W. (1981). — The importance of edge in the structure and dynamics of forest islands. In : *Forest island dynamics in man-dominated landscapes*. R.L. Burgess & D. Sharpe (eds). Springer, New York : 67-95.
- RECHER, F. (1969). — Bird species diversity and habitat diversity in Australia and North America. *Am. Nat.*, 103 : 75-80.
- REMMERT, H. (ed) (1991). — *The Mosaic-Cycle Concept of Ecosystems*. Springer Verlag, Berlin.
- RICE, J.C., OHMART, R.D. & ANDERSON, B.W. (1986). — Limits in a data-rich model : modeling experience with habitat management on the Colorado river. In : *Wildlife 2000. Modeling Habitat Relationships of Terrestrial Vertebrates*. J. Verner, M. Morrison & C. Ralph (eds). University of Wisconsin Press, Madison : 79-86.
- RICKLEFS, R.E. (1975). — Competition and the structure of bird communities. *Evolution*, 29 : 581-585.
- RICKLEFS, R.E. & SCHLUTER, D. (eds) (1993). — *Species Diversity in Ecological Communities. Historical and Geographical Perspectives*. University of Chicago Press, Chicago.
- ROLSTAD, J. (1991). — Consequences of forest fragmentation for the dynamics of bird populations : conceptual issues and the evidence. *Biol. J. Linn. Soc.*, 42 : 149-163.

- ROTEBERRY, J.T. (1985). — The role of habitat in avian community composition : physiognomy or floristics. *Oecologia*, 67 : 213-217.
- ROTH, R. (1976). — Spatial heterogeneity and bird species diversity. *Ecology*, 57 : 773-782.
- 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.
- SAXON, E.C. (1990). — Disturbance regimes in North Queensland rainforests - a reevaluation of their relationship to species richness and diversity. *Aust. J. Ecol.*, 15 : 241-244.
- SCHINDLER, D.W. (1990). — Experimental perturbations of whole lakes as tests of hypotheses concerning ecosystem structure and function. *Oikos*, 57 : 25-41.
- SCHOENER, T.W. (1983). — Field experiments on interspecific competition. *Am. Nat.*, 122 : 240-285.
- SOKAL, R. & ROHLF, J. (1981). — *Biometry*. Second edition. Freeman and Co, New York.
- SOKAL, R. & ROHLF, J. (1987). — *Introduction to biostatistics*, Second edition. Freeman and Co, New York.
- SUGIHARA, G. (1980). — Minimal community structure : an explanation of species abundance patterns. *Am. Nat.*, 116 : 770-787.
- SUGIHARA, G. & MAY, R.M. (1990). — Applications of fractals in ecology. *Trends Ecol. Evol.*, 5 : 79-86.
- SWIFT, B., LARSON, J. & DEGRAAF, R. (1984). — Relationship of breeding bird density and diversity to habitat variables in forested wetlands. *Wilson Bull.*, 96 : 48-59.
- 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 : *Classification and related methods of data analysis*. H.H. Bock, (ed). North-Holland Press, Amsterdam : 551-558.
- 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.
- THIOLLAY, J.M. (1990). — Comparative diversity of temperate and tropical forest bird communities. The influence of habitat heterogeneity. *Acta Oecol.*, 11 : 887-911.
- THIOLLAY, J.M. (1992). — Influence of Selective Logging on Bird Species Diversity in a Guianan Rain Forest. *Conserv. Biol.*, 6 : 47-63.
- URBAN, D.L. & SMITH, T.M. (1989). — Microhabitat pattern and the structure of forest bird communities. *Am. Nat.*, 133 : 811-829.
- VERNER, J. (1985). — Assessment of counting techniques. In : *Current Ornithology*. (Vol. 2). R. Johnston (ed). Plenum Press, New York : 247-302.
- VIRKKALA, R. (1987). — Effects of forest management on birds breeding in northern Finland. *Ann. Zool. Fenn.*, 24 : 281-294.
- WIENS, J.A. (1986). — Spatial scale and temporal variation in studies of shrubsteppe birds. In : *Community ecology*. J.M. Diamond & T.J. Case (eds). Harper & Row, New York : 154-172.
- WIENS, J.A. (1989). — *Ecology of Bird Communities*. (Vol. 1). Cambridge Univ. Press, Cambridge GB.
- WIENS, J.A. & ROTENBERRY, J.T. (1981). — Habitat associations and community structure of birds in shrubsteppe environments. *Ecol. Monogr.*, 51 : 21-41.
- WILLIAMS, C. (1943). — Area and the number of species. *Nature*, 152 : 264-267.
- WILLSON, M.F. (1974). — Avian community organization and habitat structure. *Ecology*, 55 : 1017-1029.
- WISSEL, C. & MAIER, B.A. (1992). — Stochastic model for the species-area relationship. *J. Biogeogr.*, 19 : 355-362.