

The convergent trajectories of bird communities along ecological successions in european forests

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Summary. There is much more variation in the composition of bird communities in the earlier open and semi-open seral stages of ecological successions in forested landscapes of Europe than later on in preforested and forested climactic stages. The demonstration of this trend is achieved from the study of four habitat gradients, two in the mediterranean region (Provence and Corsica) and two in central Europe (Burgundy, France and Poland). A multivariate analysis has been used to illustrate the dynamics of communities along these successions. Displays of the results in bivariate space as well as an illustration of the distributional profiles of some of the most characteristic species show that: i) there is a discrimination between the two mediterranean gradients and the two medioeuropean ones and ii) each succession starts with a very distinct set of species and then the four gradients regularly converge in the last climactic stage where there is almost no discrimination between communities. These results are discussed in the light of the history of European biotas during the Pleistocene. The reason why there is more variation in species composition in the earlier seral stages than in the later forested stages are discussed according to current theories on the role of habitat selection on speciation processes.

Key words: Ecological succession – Community dynamics – Historical biogeography – Speciation – Mediterranean

Previous studies on community ecology in the mediterranean region have shown that as vegetation gets higher and more complex as a result of ecological succession, the proportion of bird species of mediterranean origin, i.e. which evolved in this region, steadily decreases (Blondel 1981, 1986, 1987). In old mature forests dominated by such mediterranean evergreen tree species as the Holm oak, *Quercus ilex* and the Cork oak, *Q. suber*, there is hardly any species of bird of mediterranean origin although the mediterranean region has been recognized for a long time by biogeographers as a well-defined subregion of the Palearctic (Stegmann 1958; Darlington 1957; Voous 1960; Udvardy 1969). Bird communities in an old, mature stand of mediterranean tree species are not markedly different from those in a forest of similar structure in central Europe. Hence the hypothesis that the bird faunas of lowland forests in the western Palearctic are very homogeneous everywhere in Europe in-

cluding the southern mediterranean margins of the continent. Such a homogeneity is hypothesized to be due to a similar history of bird faunas in different parts of the continent.

The aim of this paper is i) to test quantitatively the hypothesis that there is an increasing similarity in the composition of bird communities along ecological successions located in different parts of Europe, and ii) to discuss on biogeographical as well as on historical grounds why and how the discrimination between communities is much more pronounced in the early stages of the successions than in the final forested stages.

Material and methods

Four ecological successions have been selected to carry out this study (Fig. 1). Two of them are located in the mediterranean region, one in Provence (southern France) and the other on the island of Corsica. They have been studied by J.B. and were the starting point of this study. We found in the literature two other studies where the experimental design was nearly identical to ours, one in Burgundy, Central France (Ferry and Frochot 1970) and the other in Poland (Głowacinski 1975). For these comparative purposes we had to select in the four successions only the seral stages which best match one another. This selection has been made using criteria of habitat structure. Six habitats have been chosen in each succession. Height of the vegetation and the number of layers (for the two mediterranean gradients only) are given on Table 1. The dominant plant species (bushes and trees) are evergreen in the two mediterranean gradients and deciduous in the two medioeuropean ones:

Provence: habitat 1: *Quercus coccifera*, *Ulex parviflorus*, 2: *Q. coccifera*, *Rosmarinus officinalis*, 3: *Q. coccifera*, *Q. ilex*, 4: *Q. ilex*, *Buxus sempervirens*, 5: *Q. ilex*, *Q. pubescens*, 6: *Q. ilex*.

Corsica: habitat 1: *Cistus monspeliensis*, 2, 3, 4: *Arbutus unedo*, *Erica multiflora*, 5: *Q. ilex*, *E. multiflora*, 6: *Q. ilex*.

Burgundy: habitat 1. *Molinia caerulea*, *Rubus* sp., 2: *Rubus* sp., *Quercus pedunculata*, *Carpinus betulus*, 3–6: *Q. pedunculata*, *C. betulus*, *Fagus sylvatica*. From habitat 3 onwards the floristic composition of the forest is rather homogeneous due to forestry management.

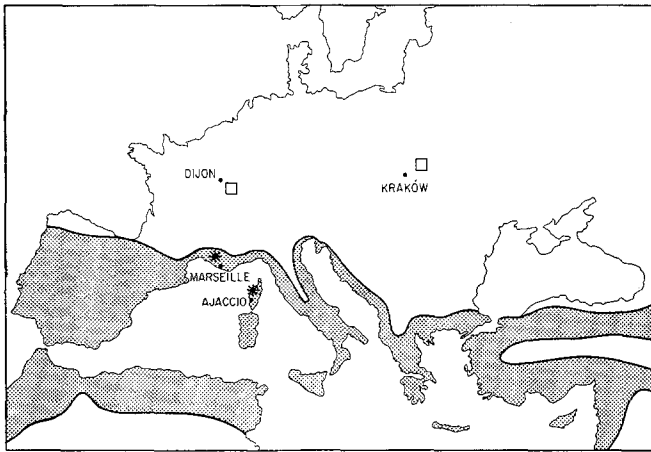


Fig. 1. Location of the study sites. The stippled area corresponds to the Mediterranean region

Table 1. Some characteristics of the habitats in the six stages of the four successions. Numbers of layers not available for Poland and Burgundy

	Habitat					
	1	2	3	4	5	6
Height of vegetation (m)						
Poland	0.6	2	8	12	20	30
Burgundy	1.0	1	2.5	5	20	27
Corsica	0.8	1	2	6	12	25
Provence	0.5	1	4	6	10	20
Number of layers						
Corsica	3	4	4	6	7	8
Provence	2	3	5	6	7	8

Poland: habitat 1: *Carex brizoides*, *Deschampsia caespitosa*, 2: *C. brizoides*, *Fraxinus excelsior*, *Quercus robur*, 3: *Solidago* sp., *Q. robur*, *F. excelsior*, 4: *Q. robur*, *Carpinus betulus*, *Tilia cordata*, 5–6: *Q. robur*, *C. betulus*.

There are some discrepancies between the gradients especially in the middle part of the successions. On the average the vegetation is taller, its structure is more complex and there are more plant species in the medioeuropean gradients than in the mediterranean ones. Moreover the former are structurally more diverse with patches of early stages present up to the last forested stage, especially in Poland. For this reason birds occupy on the average a larger spectrum of habitats in these gradients than in the Provencal one. By comparison with the other gradients, there is in Poland a slight shifting of the species from earlier to older stages. On the other hand since the gradient of Burgundy is managed for forestry, there is a tendency for birds to extend in earlier stages from coppices and old stands of forest. Birds occupy also a very large spectrum of habitats in Corsica, but for a different reason: they exhibit on the island a tremendous habitat-niche expansion due to a release in habitat selection patterns in insular environments (Blondel 1985a, 1986; Blondel et al. 1987). On the whole there is a more marked distinction between bushy and forest habitats in the mediterranean gradients than in their mid-

European counterparts as will be discussed later. On the other hand the structure of the forested stages is fairly similar in the four successions. These are dominated by old oaks of similar age (150 to 200 years) and similar height, either deciduous in Central Europe (*Quercus pedunculata* in Burgundy and *Q. robur* in Poland) or evergreen in the mediterranean (*Q. ilex* in Provence and in Corsica). As will be discussed later, these differences in vegetation structure and composition in the early stages of the successions are not only idiosyncratic, but they are an indication that mature forests in Europe are more similar than the successional stages from which they derive, whatever the initial disturbance either natural or produced by man.

Censuses of birds were achieved according to the recommendations of the International Bird Census Committee with the mapping method (IBCC 1977, Blondel et al. 1981) and a point count method (IBCC 1977, Blondel et al. 1981) in the three French study sites. Densities are expressed as numbers of breeding pairs/10 ha.

Analyses of community dynamics along gradients of vegetation have often been developed in the same direction as phytosociological studies (Sabo and Whittaker 1979). But the use of the classical tools of gradient analysis such as similarity indices among species in communities do not account for the nonmonotonic responses of species to habitat variation. Since the aim of the study was to test the hypothesis of an increasing similarity of bird communities among different ecological successions, the four data sets were pooled in a single matrix including 24 habitats (4 gradients times 6 habitats) and the 79 species found in the four gradients combined (see Table 4). Multivariate analysis proved to be an efficient tool to study the structure of such a complex data set because this technique looks for relationships among a series of samples and species (Gauch et al. 1977; Holmes et al. 1979; Prodon and Lebreton 1981; James and Wamer 1982; Chessel et al. 1982). Correspondence analysis (Benzécri 1973) also termed Reciprocal averaging (Hill 1973) provides several simultaneous ordinations of rows (i.e. species) and columns (i.e. samples). These ordinations, i.e. Correspondence analysis' factors have well known properties and can be used with different approaches (Greenacre 1984). Since the data sets of this study are species \times sample matrices resulting from a stratified sampling of passerine densities along similar environmental gradients in four regions which were hypothesized to differ in bird species composition, Correspondence analysis (further named CA) was thought to be the most appropriate technique to display differences between regional faunas or changes in species composition along environmental gradients. Moreover when species-specific densities are included in the matrix, CA is a sensitive technique to detect subtle differences in species composition (Lebreton and Yoccoz 1987). Properties of CA and recent refined graphical interpretations (Auda 1983; Auda et al. 1983) will allow us:

i) to display simultaneously the variation in species composition along the habitat gradient within each region as well as the changes or similarities in species composition between different regions. The best graphical tool for this is the sample typology and the species-specific typology provided by CA factors.

ii) to define and arrange in a logical way species \times sample groups which characterize a stage, a region or both, using the canonical graph (CA species ordination \times CA

sample ordination) or its approximation obtained by reorganizing the initial data matrix according to the order of species and samples over a CA factor. The first canonical graph (F1 samples \times F1 species) will be the best representation of the correspondence between species and samples. The value of this correspondence will be given by the canonical correlation 1.

iii) to display habitat niche breadth of the species from dispersion ellipses obtained by a visualization of the relative densities of the species on the sample typology plan (see Chessel et al. 1987).

Results

For semantic facility the two gradients belonging to the same biogeographical realm will be named "region", i.e. the mediterranean region includes the Provencal and the Corsican gradients and the medioeuropean region includes the gradients of Burgundy and Poland.

The numbers of species per habitat in each succession are shown on Table 2. The richest gradient is Burgundy with 45 species and the two poorest are Provence and Poland with 39 species each. On the average the number of species per gradient is fairly well balanced since there is no more than 13% difference between the extremes. This similarity in the numbers of species in secondary successions of forested environments in Europe is a general feature for all successions so far studied in European forested landscapes (see discussion). Out of the 79 species of the four gradients combined, 29 (36.7%) occur in only one gradient: 10 in Corsica, 10 in Provence, 4 in Burgundy and 5 in Poland (see Table 5). There are more unique species in the two mediterranean successions than in the two others. This is partly due to the occurrence of mediterranean endemic species (marked with a star on Table 4). In two cases a western species is replaced by an eastern vicariant species. These are the western *Hippolais polyglotta* replaced by the eastern *H. icterina* and the western *Locustella naevia* replaced by the eastern *L. fluviatilis*. These species are marked with an open circle on Table 4. From an ecological point of view these species can be regarded as equivalent, but they have been kept as separate species in the analyses.

Out of the 79 species of the four gradients combined, 28 have been found only in the mediterranean region, 24 only in the medioeuropean one and 27 in the two regions. Among the latter, ten species have been found in the four gradients (nine of them in the last forested stage) and 17 are partitioned in diverse combinations of gradients. These figures suggest that there is a biogeographical break between the mediterranean region and the medioeuropean one. This will be examined in further detail later. The increasing similarity of the composition of bird faunas as the vegetation becomes taller and more complex is illustrated on Fig. 2 where the proportion of species found in only one out of the four gradients decreases as the succession progresses towards its climax whereas the proportion of species found in two or more gradients increases, regardless of region. However, if we calculate for each stage of the gradients and for each gradient separately the proportion of those species which are present in only one habitat out of those which exist in the four habitats of similar rank (four gradients combined), the picture is more complex (Fig. 3). As expected the proportion of unique species steadily decreases along the succession in Corsica and in Bur-

Table 2. Numbers of species per habitat in each succession

Habitat	Po	Bu	Cu	Pr	Total
1	3	25	28	9	47
2	6	25	24	13	45
3	18	28	29	10	51
4	15	24	23	15	46
5	29	25	22	21	52
6	32	30	18	22	47
Total	39	45	40	39	79

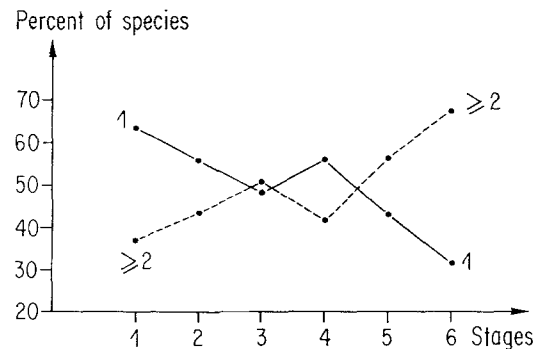


Fig. 2. Evolution along the habitat gradients of the proportions of the species found in only one habitat and in two or more habitats (four successions combined)

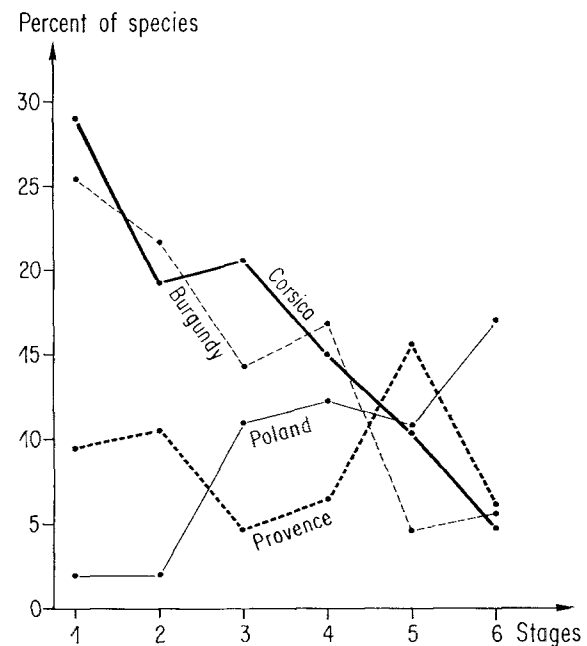


Fig. 3. Evolution along the habitat gradients of the proportion of the species present in only one stage in each succession out of the total number of species present in the four stages of similar rank. See text for further explanation

gundy. There is no conspicuous trend in Provence and in contrast with what would be expected this proportion increases in Poland. This is because, as stressed in the previous section, the Polish gradient is more heterogeneous than the three others, keeping in the last forested stage some habitat patches of early stages with such species as

Table 3. Eigenvalues, canonical correlations and inertia for the four first components of the correspondence analysis

Factor	Eigenvalue	Canonical correlation	% of inertia	Cumul. inertia
1	0.731	0.85	17.27	17.27
2	0.619	0.78	14.63	31.89
3	0.517	0.71	12.21	44.10
4	0.402	0.63	9.49	53.58

Emberiza citrinella, *Anthus trivialis*, *Sylvia borin*, *Streptopelia turtur* and *Locustella fluviatilis*. An interesting feature of this figure is the very similar number of unique species in the last stage for the three French gradients and the different trajectories of each of them, i.e. each gradient has a different proportion of unique species in the early and middle stages of the successions, but this number is fairly similar in the last forested stage except for the Polish gradient due to the idiosyncrasy just mentioned above. This is a nice illustration of the convergence in the composition of bird communities in the old mature forests.

In order to make the picture clearer and especially to take into account not only the specific composition of the communities, but also the species-specific densities, the next step was to process the data with a multivariate analysis. In this way the results can be displayed for the four gradients combined on one single representation. The whole data set has been processed by CA according to the procedure described in the section on Material and methods. Eigenvalues for the four first components are $\lambda_1=0.731$, $\lambda_2=0.619$, $\lambda_3=0.517$ and $\lambda_4=0.402$. These values correspond to very high canonical correlations (Table 3), which means a strong structuration of the initial matrix, but they totalize a rather low inertia (53.6%). This situation of high canonical correlations associated with a low inertia is typical for data sets with different levels of structure (Lebreton, unpublished work). In the present study there are two such levels: a between-region discrimination, i.e. the mediterranean region *vs* the medioeuropean region and a within-region discrimination of habitats.

The four axes of CA display three common features (Figs. 4, 5): i) a discrimination between the mediterranean region (positive part on F1) and the medioeuropean one (negative part), ii) the reconstitution of the sequence of habitats and species by this technique describes a nice ordination of the 6 habitats within each succession, which means that these gradients are really habitat gradients and iii) each succession starts from a different position in the multivariate space i.e. habitat 1 of any gradient is quite distant from the three other habitats 1 and then the four successions converge in the last forested stage. In other words the distance between the habitats which match one another, for instance between habitats 1, habitats 2 and so forth in the four successions steadily decreases from habitat 1 to habitat 6.

The display of the results in the bivariate space F1 \times F2 is shown on Fig. 4. The first axis F1 spreads out the habitats over the mediterranean gradients where the distinction between bushy habitats and forests is more marked than in the medioeuropean ones. This is especially true in Provence. The second axis F2 spreads out the habitats in the medioeuropean gradients and, more important, contrasts the

earlier stages from the later stages of the successions for three gradients out of the four (Corsica apart). There is no discrimination between the last forested stages of the different successions. They are pooled together and this picture is similar for the four components of CA. The typology of the species, which are located in the multivariate space at the barycenter of their distributional profiles, is parallel to that of habitats. Provence is best characterized by *Oenanthe hispanica*, *Emberiza hortulana*, *Anthus campestris* and *Sylvia conspicillata*, Corsica by *Miliaria calandra* and *Sylvia sarda*, Burgundy and Poland by *Sylvia communis* and *Motacilla alba*. Since the first stages of the two medioeuropean gradients are characterized by the same species, Burgundy and Poland are closer than the two mediterranean gradients where communities of the first stages are very distinct. On the other hand, the species which best characterize the discrimination between the mediterranean region and central Europe at the end of the gradients are those species which occur in one region, but not in the other: *Regulus ignicapillus* and *Parus ater* (mediterranean), *Phoenicurus phoenicurus* (central Europe), and the two vicariant *Certhia* species. However, all these species except one of the two *Certhia* and *Phoenicurus* which do not breed in Corsica could have been found in each gradient because they occur there at a regional scale. Species which are responsible for the ecological convergence of the trajectories of the four gradients are the nine species of the last forested stage which are found everywhere in European forests: *Columba palumbus*, *Picoides major*, *Parus major*, *P. caeruleus*, *Erithacus rubecula*, *Turdus merula*, *Sylvia atricapilla*, *Troglodytes troglodytes* and *Fringilla coelebs*. These species constitute what could be named the "background" of the sylvatic bird fauna all over Europe.

Finally the best visualization of the biogeographical and ecological convergence of bird communities in the forested stages of the successions is given by the display of the data on the bivariate space F1 \times F4 (Fig. 5). Indeed, as F1 spreads out the habitats over the two mediterranean gradients, F4 contrasts the two medioeuropean ones and mostly spreads the habitats over the Polish gradient. Thus the four gradients are nicely visualized since each of them starts from very distinct locations on this space and then converge towards the climax. The species which mostly characterize the two medioeuropean gradients on this representation are *Locustella naevia* and *Prunella modularis* in Burgundy and *Motacilla alba*, *Lanius collurio* and *Emberiza citrinella* in Poland. Actually there are no really unique species in Poland because the species which best characterize the axes on this gradient occur also in other gradients: *Lanius collurio* in Corsica, *Emberiza citrinella* and *Motacilla alba* in Burgundy. The species which characterize the pooling of the last forested stages in the four gradients are of course the same as on F1 \times F2. This is true also for the species of the first stages of Provence and Corsica.

These representations of the structure of the gradients emphasize from two different points of view i.e. within each of the two bivariate spaces (F1 \times F2 and F1 \times F4) as well as between them, the same phenomenon, namely the progressive similarity of the bird communities as far as the successions progress towards their climax.

Table 4 is a listing of the species-specific distributions of the 79 species arranged by an approximation of the first canonical graph. The canonical correlation is very high (0.85), which means a high correspondence between habi-

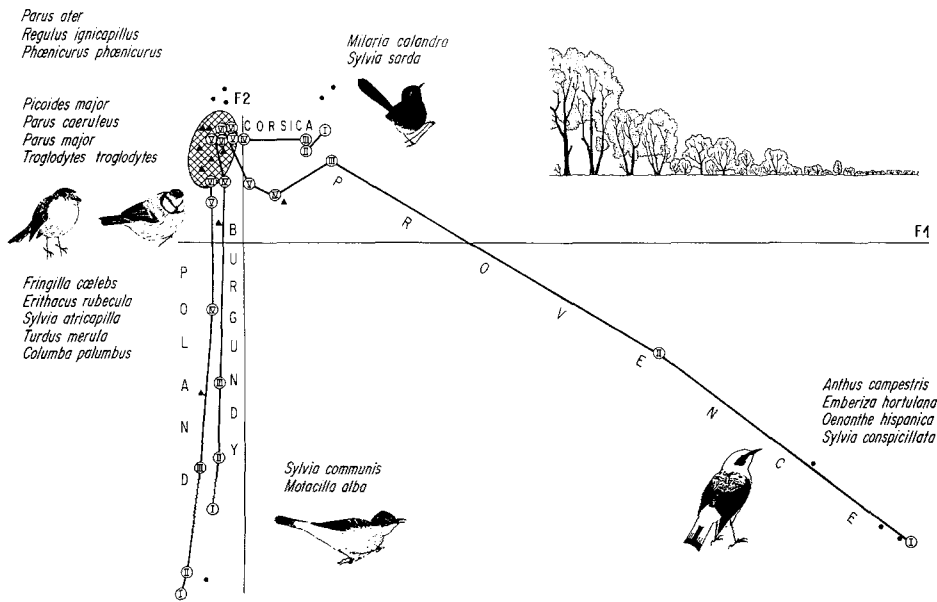


Fig. 4. Display of habitats (roman numbers) and of species (dots for species of early stages, triangles for forest species) on the bivariate space $F1 \times F2$ of correspondence analysis

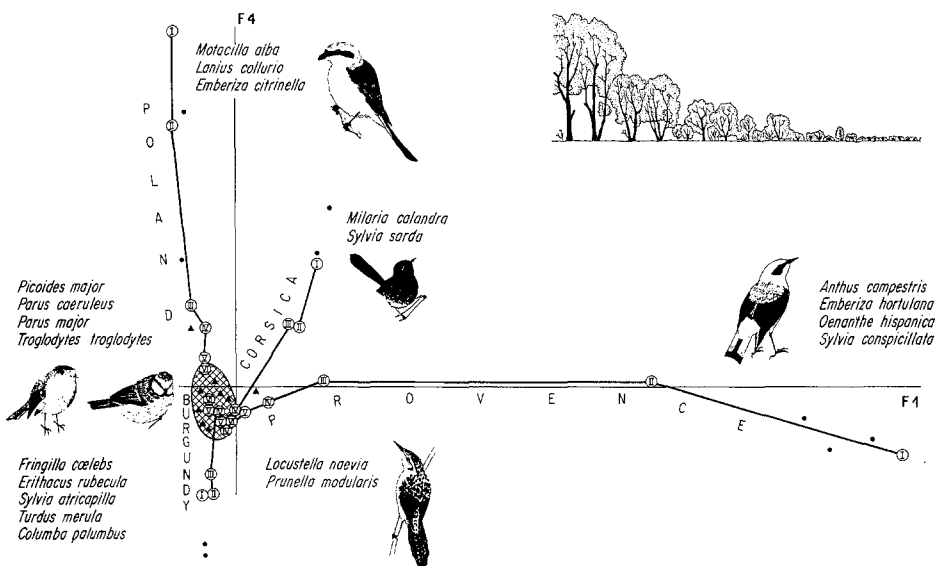


Fig. 5. Display of habitats and of species on the bivariate space $F1 \times F4$ of correspondence analysis. Same legend as in Fig. 4

tats and species. The arrangement of the species and of the habitats (four gradients combined) on this Table is that of their rank order on $F1$. This canonical representation strongly discriminates the medioeuropean region (top left of the Table) from the mediterranean one (bottom right). The species which are present in the four gradients, especially the species of forests, are in between. As expected such species do not allow any discrimination between the gradients. Moreover the convergence of ecological trajectories is expressed on this Table by the ordination of regions and habitats made by $F1$. On the average habitats tend to converge from Poland 1 to Poland 6 and from Burgundy 1 to Burgundy 6 from the left side of the Table to its center whereas Provence 1 to Provence 6 and Corsica 1 to Corsica 6 converge in the same way, but from the right side. As stressed earlier, habitats are closer in Burgundy and in Poland than in Provence and in Corsica because of a better discrimination of bushy *vs* preforested and forested habitats in the medioeuropean region than in the mediterranean one.

However, since the ordination of habitats in the medioeuropean region is achieved by $F2$, the arrangement of habitats in the $F1$ canonical graph of Table 4 cannot be perfect, hence some discrepancies in the ordination of these habitats along the medioeuropean gradients. On the other hand the ordination of habitats in Provence and in Corsica is nearly perfect. Notice that the break between the medioeuropean region and the mediterranean region is fully respected on this graph.

Such an ordination is useful to partition the different sets of communities. The two mediterranean successions combined share 28 species not found in the medioeuropean region. Among them ten are unique in Corsica and ten in Provence (Table 5). Many of them are endemic to the mediterranean region. There are four such species in Provence (*Sylvia hortensis*, *S. conspicillata*, *Clamator glandarius* and *Oenanthe hispanica*), 2 in Corsica (*S. sarda* and *Serinus citrinella*) and 4 in the two mediterranean gradients combined (*Alectoris rufa*, *S. melanocephala*, *S. cantillans*, and

Table 5. Numbers of “unique” species at the three biogeographical levels: I local (gradients), II regional, III continental = Western Eurasia. See text

I				II		III
Poland	Burgundy	Corsica	Provence	Medioeuropean region	Mediterranean region	Western Eurasia
<i>L. luscinia</i>	<i>L. naevia</i>	<i>C. coturnix</i>	<i>S. conspicillata</i>	<i>M. alba</i>	<i>S. undata</i>	<i>S. turtur</i>
<i>L. fluviatilis</i>	<i>P. modularis</i>	<i>L. senator</i>	<i>O. hispanica</i>	<i>E. citrinella</i>	<i>A. rufa</i>	<i>C. palumbus</i>
<i>H. icterina</i>	<i>P. pyrrhula</i>	<i>A. arvensis</i>	<i>A. campestris</i>	<i>A. trivialis</i>	<i>L. arborea</i>	<i>T. merula</i>
<i>D. martius</i>	<i>P. montanus</i>	<i>M. calandra</i>	<i>E. hortulana</i>	<i>S. borin</i>	<i>S. melanocephala</i>	<i>S. atricapilla</i>
<i>M. albicollis</i>		<i>E. cirrus</i>	<i>L. excubitor</i>	<i>C. coccothraustes</i>	<i>S. cantillans</i>	<i>E. rubecula</i>
		<i>S. sarda</i>	<i>C. glandarius</i>	<i>P. trochilus</i>	<i>C. canorus</i>	<i>F. coelebs</i>
		<i>S. rubetra</i>	<i>S. hortensis</i>	<i>P. sibilatrix</i>	<i>R. ignicapillus</i>	<i>T. troglodytes</i>
		<i>S. canaria</i>	<i>H. polyglotta</i>	<i>S. communis</i>	<i>P. ater</i>	<i>Pa. major</i>
		<i>S. citrinella</i>	<i>P. bonelli</i>	<i>T. philomelos</i>		<i>P. caeruleus</i>
		<i>C. cornix</i>	<i>P. cristatus</i>	<i>S. vulgaris</i>		<i>Pi. major</i>
				<i>C. oenas</i>		
				<i>P. medius</i>		
				<i>P. canus</i>		
				<i>P. phoenicurus</i>		
				<i>P. palustris</i>		

S. undata). *Serinus citrinella* is a particular case because this species of the mountains of south western Europe (Newton 1967) exhibits a very large niche expansion in Corsica where this bird is widespread in almost every type of terrestrial habitat from the sea level up to the timberline. On the whole no more than 10 species belong to a mediterranean endemic bird fauna the distributional limits of which do not go beyond the mediterranean region. This is especially true for the 6 species of the genus *Sylvia* which actively speciated in shrubland within the mediterranean region (Blondel 1986 and *in press*). The other species which are found in only one or in the two mediterranean successions exist at a regional scale in the medioeuropean region. Two reasons can explain their absence from the samples: i) they could have been missed from the censuses by chance only and ii) habitat selection patterns of some species are not the same in central Europe and in the mediterranean region. For instance *Parus cristatus*, *P. ater* and *Regulus ignicapillus* are mostly birds of conifers in central Europe, but they occupy broad-leaved stands in the mediterranean. The 8 other species which are unique at the scale of the mediterranean region are listed on Table 5. On the other hand the two medioeuropean gradients combined together share 24 species which have not been found in the mediterranean region (Table 5). Six of them (*C. oenas*, *Ph. phoenicurus*, *M. alba*, *S. communis*, *C. coccothraustes* and *St. vulgaris*) enter the mediterranean region where they are rather scarcely distributed. Among these 24 species, 12, that is nearly the same number as in the mediterranean region, have distributional limits which do not enter the mediterranean region (2 of them are unique to Poland). Notice that the private species of each region (marked on Table 4 with a star for the mediterranean region and with a triangle for the medioeuropean region) are located in their appropriate place in the listing of the species.

Most of the unique species are birds of the early or middle stages of the successions. Indeed 23 out of the 29 species listed in the four first columns of Table 5 have been found in the first three stages against 12 which have been found in the 4th stage and/or further on. On the other hand most of the species which have been found in the

two regions are birds of late or final forested stages. Among the ten species which occur in the four gradients (italics on Table 4) nine are found in the last sixth stage of the four successions. These are the nine species listed above which constitute the “background” of the sylvatic bird fauna all over Europe. From an ecological point of view the vicariant species *Certhia brachydactyla* (Burgundy, Provence) and *C. familiaris* (Poland, Corsica) should be added to this list.

To sum up these species lists show that the composition of bird faunas in these successions is more similar in the second part of the successions, i.e. preforested and forested stages than in the first half, i.e. bushy habitats and mediterranean shrubland.

An illustration of the distributional profiles of those species which are responsible for the overall structure of the gradients such as they are described by CA is given on Fig. 6 using a graphical technique described by Auda (1983). We chose the bivariate space F1 × F4 for this representation because it gives the best visualization of the four gradients. On this Figure the size of the squares is proportional to the densities of the species. The best examples for the early stages of the successions are *Oenanthe hispanica* and *Emberiza hortulana* in Provence, *Milvula calandra* and *Sylvia sarda* in Corsica, *Emberiza citrinella* and *Anthus trivialis* in Poland and *Locustella naevia* and *Prunella modularis* in Burgundy (Fig. 6A). Notice that in Poland the two selected species do not occur only in the first stages, but expand to a large extent later on in the succession. This is because, as already stressed, the Polish gradient is less defined and more heterogeneous than the three others due to the juxtaposition in its middle part of habitat structures which are characteristic of both early and late stages of the succession. Finally the profiles of four out of the nine species which make the background of the sylvatic bird fauna in Europe are illustrated on Fig. 6B: *Sylvia atricapilla*, *Erithacus rubecula*, *Fringilla coelebs*, and *Parus caeruleus*. The simultaneous occurrence of these species in the forested stages of the four gradients, that is at the intersection of F1 and F4, is clearly illustrated on this figure. Notice that these four species occur also in earlier stages in Corsica.

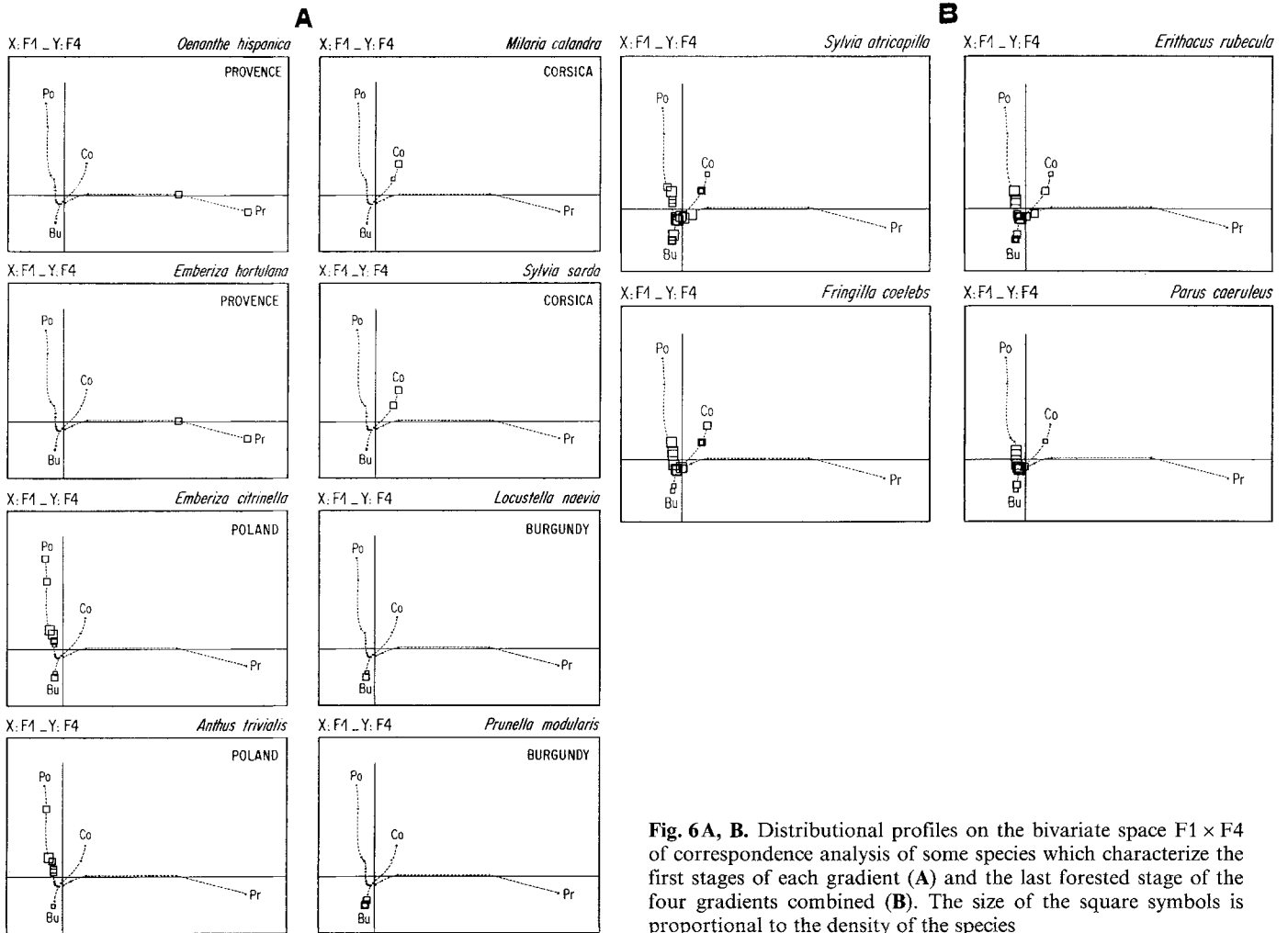


Fig. 6A, B. Distributional profiles on the bivariate space $F1 \times F4$ of correspondence analysis of some species which characterize the first stages of each gradient (A) and the last forested stage of the four gradients combined (B). The size of the square symbols is proportional to the density of the species

This is because of a tremendous habitat-niche expansion of the species of forests which invade coppices and shrubby habitats on the island (Blondel 1985, 1986; Blondel et al. in press, Martin 1982). This phenomenon occurs also in Burgundy for the reason explained in a previous section.

Discussion

The very similar number of species in the four successions in this study is a general feature in forested environments in Europe. Whatever the region, from Scandinavia to the mediterranean, the number of species of a successional pool is of the same order of magnitude: between 46 and 54 species for 7 case studies (Blondel 1986: 111). Moreover the results of this study show that the between regions discrimination of the bird faunas is stronger in the younger successional stages. This suggests that the composition of communities better reflects local or regional environmental conditions in the early stages of successions than in the final forested stages which, all things being equal, are very homogeneous over very large areas. As far as the differentiation of bird faunas in European forests is concerned, two points deserve discussion: i) the homogeneity of mature forests all over Europe, and ii) the strong differentiation in second growth habitats.

As to the first point, the history and development of forested biotas give interesting clues. The fauna of the cold,

temperate and warmer mediterranean regions of Europe which belong to Holarctic faunal types (Voous 1963) has taken part or has been subjected to the geographical and climatical history of the Eurasian continent, at least during the Pleistocene. This history greatly influenced the ecological characteristics and the geographical distribution of the fauna, especially the climatic vicissitudes of the Pleistocene which have been discussed by Steinbacher (1948) and by Moreau (1954). Recent paleobotanical, paleontological and archeological data allowed Blondel (1985b, 1986, 1987) to refine the arguments given by Moreau especially as far as the biogeographical and ecological relationships between the mediterranean and more northern parts of the western Palearctic are concerned. The main events can be briefly summarized as follows:

1. A series of alternating expansions and contractions of glacial and arctic conditions and consequent shifts of most ecological zones. This alternation is much more complicated than formerly believed. In particular the diversity of conditions of temperature and moisture within the mediterranean during a climatic phase (either interglacial or glacial), as well as the geotopographical diversity of the region allowed the coexistence, on a regional scale, of all the faunal types of Europe.

2. During the interglacial periods such as we enjoy at present, mediterranean forests of lowlands and mid altitudes were mostly dominated by broad-leaved trees (i.e.

Quercus pubescens), not evergreen trees (i.e. *Q. ilex*) as today. The dramatic extension of evergreen vegetation is a modern feature due to human impact (Pons 1981, 1984).

3. The mediterranean shrublands never disappeared from the region during the Pleistocene even during the most severe climatic conditions (Pons 1981). They persisted as patches locally distributed allowing the survival and the differentiation of the few species which are characteristic of this type of habitat.

4. Consequently during the most severe climatic phases all the forest types of Europe and their associated faunas were able to find refugia in the mediterranean region which was larger than it is at the present time due to a drop in sea level of 100 to 150 m.

5. The present extension of mediterranean shrublands is a secondary feature due to human deforestation since the early Neolithic (6000 BP). Before this impact, forests were much more widespread than today except in local patches where climatic, edaphic and topographical conditions allowed only a shrubby vegetation.

These events explain why, despite the fact that the mediterranean region extends over three continents (Europe, Asia, Africa) and despite its high geographical and topographical diversity (which is propitious for biological isolates) there has been so little speciation in this region. On several occasions during the Pleistocene all the faunal types of Europe have been concentrated in the mediterranean area. At each climatic improvement the faunal elements of central and northern Europe expanded northwards from their mediterranean refugia *without leaving the region* and retracted again at each climatic deterioration. Under these circumstances there has never been any kind of geographical isolation between the mediterranean forests and forests of central Europe, which is a prerequisite for allopatric speciation. From a biogeographical point of view the bird fauna of mediterranean forests cannot be different from the same general faunal stock of the western Palearctic forest block because these forests have never been fragmented during the Pleistocene. The bird faunas of mediterranean forests are not different, just impoverished because the mediterranean region is at the southwestern margin of Eurasia. This impoverishment is even more pronounced in the mediterranean islands. This history explains why out of the 343 species of birds which presently breed in the mediterranean region (Blondel 1986, 1987) no more than 47 (14%) belong to a mediterranean fauna *i.e.* which speciated within the geographical limits of this region. Among these species extremely few are species of forests. The most typical examples are the three endemic Nuthatches *Sitta whiteheadi*, *S. kruperi* and *S. ledanti* which are spatially restricted to stands of endemic conifers.

As far as the stronger discrimination of communities in second growth habitats than in forests is concerned, it must be pointed out that most cases of differentiation up to the species level in the mediterranean region refer to birds of open (15 out of the 47 species of mediterranean origin = 33%) or semi-open (21 species = 45%) habitats. Examples are the four species of *Alectoris* and, even more typical, the eleven species of the genus *Sylvia*. These species most probably speciated during the Pleistocene in localized patches of mediterranean shrubland which, as stressed above, were never absent from the mediterranean region even during the most severe climatic phases. Processes of isolation and subsequent re-contact have probably occurred

several times in relation to the spatio-temporal expansion and retraction of habitat patches generated by climatic oscillations.

The problem why species of early stages of successions differ so much between successions raises the question of the mechanisms of speciation in second growth habitats. This suggests that there are more isolating mechanisms in second growth habitats than in forests. Hesse et al. (1951) and Mayr (1963) discussed the different kinds of barriers that could be responsible for discontinuities between geographical isolates, which are prerequisites for speciation. Any area which is unsuitable for occupation by a species may serve as a distributional barrier (Mayr 1963). Thus large tracts of mature forest should act as barriers for birds of seral stages of successions. However, the survival of such species which occupy habitats which are by definition ephemeral because of successional processes implies an ability to disperse over areas which are unsuitable for them (i.e. deep forest) in order to find other patches of habitat produced by local disturbances. However, as pointed out by Mayr (1963) there should be no distinction between geographical and ecological barriers and distance should not be a criterion since many examples show that narrow belts of unsuitable habitat may act as isolating barriers.

Ecological conditions differ much more between regions in early stages than in mature forests because open or semi-open habitats are much more directly subjected to local environmental factors than forests where regional variation is largely buffered by the structure of the habitat. In this context the concept of adaptive peak of Wright (1932), extended by Simpson (1953) and by Dobzhansky et al. (1977), is especially useful because it explains the origin of discontinuities among contemporary species. Any environment is divided into habitats within which certain characteristic modes of adaptation are required. These habitats are separated by discontinuities that act as adaptive thresholds, and each habitat presents characteristic adaptive problems. Simpson (1953) considers a taxon together with the environmental characters that it inhabits to constitute an "adaptive zone". Boundaries between adaptive zones are found at environmental discontinuities within mosaic patches. Since environmental conditions differ more between regions in second growth habitats than in the deep forest, there should be more adaptive zones, hence a larger ecotypic selection in the former than in the latter. Since the model of adaptive zones heavily relies upon the interactions between organisms and their environment, ecological processes are largely implied in the process of regional differentiation. Besides the spatial discontinuities of seral stages which are extrinsic factors, intrinsic factors must play a role, especially physiological as well as behavioural properties which cause each species to react differently to barriers. Perhaps the most important of all the intrinsic factors for the localisation of populations and for a restriction of species to each species-specific habitat is the process of habitat selection, i.e. the process of occupying a habitat with a constellation of environmental factors which are necessary and sufficient for the realisation of each species-specific niche. This is the "niche-gestalt" of James (1971). This deliberate choosing of the proper habitat serves as a powerful reinforcement of geographical barriers (Miller 1942). Habitat selection is a conservative factor in speciation since it firmly ties a population to its appropriate habitat and reduces the probability that new isolates will be established beyond the present

species border. As Fretwell (1972) pointed out there are conservative mechanisms for the species to keep in their most appropriate habitats because their fitness will be optimized there. As equal fitness should discourage emigration in less favourable habitats, evolution would presumably proceed differently in different habitats and differentiation would correlate with habitat difference (ecotypic selection of Fretwell 1972, p. 189).

Since the rate of speciation largely depends on the degree of ecological diversity offering vacant niches (Mayr 1963; Pielou 1979) these differential ecological conditions together with the process of habitat selection in each appropriate niche-gestalt should explain the different rates of speciation observed. Although such a conceptual framework accounts for the observed pattern of biological diversity in different kinds of environments, it must be acknowledged that it is no more than speculative because data are lacking to detail the events underlying the different rates of speciation according to the variation of adaptive zones. In particular, what is unknown is the extent of area needed for such isolates to differentiate in this pattern of mosaic of seral stages which vary in space and in time according to the regime of disturbance which, for a given landscape, is a specific attribute determined by a complex set of factors including climatic, edaphic as well as botanical properties of the region (Pickett and Thompson 1978; Sousa 1984; Pickett and White 1985).

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