

# Vegetation and bird community dynamics in fragmented coppice forests

M. DECONCHAT AND G. BALENT

Institut National de la Recherche Agronomique (INRA), Unité de Recherche sur les Systèmes Agraires et le Développement (URSA), CNRS-UMR 5552 Ecologie Terrestre, BP 27, F-31326 Castanet Tolosan, France

## Summary

Richness and composition of plant and bird communities were used to evaluate the importance of seven within-forest factors on biodiversity in fragmented coppice forests in south-western France. Plants and birds were sampled on the same 98 plots. Plant abundance–dominance was measured on 400 m<sup>2</sup> plots. Birds were sampled using a 50-m fixed radius point-count method in the early and late periods of the breeding season. The selected factors were: years since logging (YSL), retention of standards (STANDARD), ownership (OWNER), distance to the nearest edge (EDGE), tree richness (TREE), density of vegetation in low (ST<sub>2</sub>) and high (ST<sub>16</sub>) strata. Paired comparisons of richness were carried out between YSL classes, according to other variables. The respective influence of each variable was evaluated using adapted CCA (canonical correspondence analysis) on plant and bird composition. Plant richness varied strongly between YSL classes, was independent of STANDARD, increased with TREE and was higher in collective owned forests. Bird richness seemed to be independent of YSL and was higher in low YSL plots with standards. Bird and plant richness was not correlated. Plant community composition was mainly explained by YSL/ST<sub>16</sub> on the first axis and by OWNER on the second axis. STANDARD and OWNER explained bird community composition. OWNER must be considered as a synthetic variable. This could be useful in adapting forestry practices for a better management of biodiversity, taking into account the very different taxonomic groups involved.

## Introduction

Management of biodiversity in forests requires dealing with different groups of species to embrace most of the ecological functions associated with biological diversity patterns (Franklin, 1993; Huston, 1994). It is only by a multi-group study that we can identify general rules which apply to different groups in particular environmental conditions, and which can help towards

manage the biodiversity more easily. Studies dealing with two or more groups of species at the same location, on the same scale, are necessary to compare how each is influenced by the same factors, under conditions considered as identical (Hansen *et al.*, 1991). Unfortunately such studies are not very frequent (Zuidema *et al.*, 1996), or do not place the different groups at the same level of analysis: the plant community is often sketchily described and used as an explanatory factor for

another group (for an example see Ambuel and Temple, 1983).

Plants and birds are probably the most frequently used groups for studying biodiversity in forests (Newton, 1995; Zuidema *et al.*, 1996). They give information about different aspects of biocoenosis functioning, according to their mobility, their scale of perception of the environment or their position in the trophic web (Huston, 1994). Factors that influence bird and plant diversity can be roughly classified according to their spatial level of action (Fuller and Warren, 1991; Deconchat and Balent, 1996). Within-wood factors are measured with a fine scale, at the plot level. Among them, factors associated with management and logging practices are of particular interest in the perspective of biodiversity management.

This paper presents the effects of seven within-wood factors evaluated at the plot level on plant and bird diversity. They have been selected to cover different critical aspects of coppice structure and dynamics, which is the main forestry system used in the area studied. Plants and birds were sampled on the same plots, which made it possible to compare characteristics of their communities and to assess what are the divergent and convergent patterns of diversity between them.

## Study area

The area studied (10 000 km<sup>2</sup>) lies between the Garonne and Gers rivers, in south-western France (43°N, 1°E). It is a hilly region (200–400 m a.s.l.), dissected by south–north valleys, having a subAtlantic climate with Mediterranean and mountain influences. The forests are fragmented and cover 15 per cent of the area (Balent and Courtiade, 1992). The most common silvicultural system is coppice (rotation ranging between 15 and 40 years), increasingly often with standard trees retained to produce high-quality wood for sawmills (Guyon *et al.*, 1996). Coppice is used for fuel and for pulp. Logging is often the major, if not the only, management activity in this type of forestry system based on rather short rotations.

Oaks (*Quercus robur* and *Q. sessiflora*), often in association with chestnut (*Castanea sativa*) in coppice, cherry (*Prunus avium*) and wild service

trees (*Sorbus torminalis*) are the main tree species in the area. The flora can be considered as medio-European, with Atlantic and Mediterranean components (Gonin, 1993). For birds, all the species present in the area studied are also found in other French plain regions (Joachim *et al.*, 1997).

## Method

### Sampling methods

**Vegetation** We listed all the vascular species observed in summer (June–August 1996) on a 400-m<sup>2</sup> circular plot. The nomenclature used was from the *Flora Europaea* (Tutin *et al.*, 1964). For each species we estimated visually its abundance–dominance on a six-point scale adapted from the typical Braun–Blanquet scale. For tree species, we recorded four levels of abundance–dominance for seedling trees ( $h < 0.50$  m), young trees (0.5–7 m), developed trees (7–20 m) and mature trees (>20 m), respectively (Gonin, 1993). In this paper, we use the maximum values recorded at these four levels (Table 1).

**Birds** We used a point-count method with a 50-m fixed radius (Hutto *et al.*, 1986; Frochot and Roché, 1990; Petty and Avery, 1990). For each plot, experienced observers recorded all bird species seen or heard during a 20-min period between sunrise and up to 4 h (maximum) after sunrise. A singer was registered as two individuals comprising a couple, and a bird only seen or only heard calling represented one individual. The census was performed twice, between 23 March and 10 April 1996 and between 13 May and 10 June 1996, in order to obtain data on sedentary birds, which are early singers, and migratory birds, which sing later in the season. For species encountered in both periods, we used the higher of the two counts recorded.

Species recorded at least once within a 50-m radius circle around the observer (estimated by eye) were used in our analysis. We assume that the species observed in a 50-m circle have a strong relationship with plot characteristics (Hutto *et al.*, 1986; Petty and Avery, 1990). This hypothesis is reasonable for passerine birds and small species (Table 2) (Fuller, 1992). Larger species

Table 1: List of the 71 plant species with a frequency of observation higher than or equal to 10 per cent (a total of 252 species were counted in 98 plots)

Scientific name	English name	Plots with species (max = 98)
<i>Rubus fruticosus</i> agg.	Blackberry	97
<i>Hedera helix</i>	Common ivy	90
<i>Lonicera periclymenum</i>	Common honeysuckle	89
<i>Prunus avium</i>	Gean	74
<i>Tamus communis</i>	Black bryony	73
<i>Crataegus monogyna</i>	Hawthorn	69
<i>Rubia peregrina</i>	Wild madder	67
<i>Quercus petraea</i>	Durmast oak	65
<i>Sorbus torminalis</i>	Wild service tree	63
<i>Ligustrum vulgare</i>	Common privet	63
<i>Corylus avellana</i>	Hazel	62
<i>Castanea sativa</i>	Spanish chestnut	62
<i>Quercus robur</i>	Common oak	61
<i>Cornus sanguinea</i>	Common dogwood	60
<i>Ruscus aculeatus</i>	Butcher's broom	58
<i>Rosa arvensis</i>	Field rose	56
<i>Quercus pubescens</i>	Pubescent oak	50
<i>Cytisus scoparius</i>	Common broom	48
<i>Carex flacca</i>	Glaucous sedge	47
<i>Prunus spinosa</i>	Sloe tree	46
<i>Pteridium aquilinum</i>	Bracken	41
<i>Teucrium scorodonia</i>	Wood sage	40
<i>Lonicera xylosteum</i>	Fly honeysuckle	39
<i>Viola</i> sp.	Violet	37
<i>Ranunculus nemorosus</i>		35
<i>Ilex aquifolium</i>	Common holly	31
<i>Pulmonaria affinis</i>		29
<i>Carpinus betulus</i>	Hornbeam	28
<i>Acer campestre</i>	Field maple	27
<i>Hypericum pulchrum</i>	Slender St John's-wort	26
<i>Brachypodium sylvaticum</i>	Slender false-brome	26
<i>Fraxinus excelsior</i>	Common ash	26
<i>Populus tremula</i>	Aspen	25
<i>Rosa canina</i>	Dog rose	21
<i>Fragaria vesca</i>	Wild strawberry	21
<i>Ulmus minor</i>	Smooth-leaved elm	20
<i>Juncus effusus</i>	Soft rush	20
<i>Eupatorium cannabinum</i>	Hemp agrimony	19
<i>Clematis vitalba</i>	Old man's beard	19
<i>Hypericum perforatum</i>	Common St John's-wort	19
<i>Arum italicum</i>	Large cuckoo pint	17
<i>Hypericum androsaemum</i>	Tutsan	17
<i>Solidago canadensis</i>	Canadian goldenrod	16
<i>Veronica officinalis</i>	Heath speedwell	16
<i>Juniperus communis</i>	Common juniper	15
<i>Cirsium arvense</i>	Creeping thistle	15
<i>Lotus uliginosus</i>	Marsh bird's-foot trefoil	15
<i>Molinia caerulea</i>	Purple moor-grass	15
<i>Holcus mollis</i>	Creeping soft-grass	15

Continued

Table 1: *Continued*

Scientific name	English name	Plots with species (max = 98)
<i>Ajuga reptans</i>	Bugle	15
<i>Fagus sylvatica</i>	Common beech	15
<i>Brachypodium pinnatum</i>	Chalk false-brome	14
<i>Agrostis capillaris</i>	Common bent	14
<i>Carex sylvatica</i>	Wood sedge	14
<i>Centaureum erythraea</i>	Common centaury	14
<i>Euonymus europaeus</i>	Spindle tree	14
<i>Melica uniflora</i>	Wood melick	14
<i>Galium aparine</i>	Goosegrass	14
<i>Stachys officinalis</i>	Betony	14
<i>Crataegus laevigata</i>	Midland hawthorn	14
<i>Hypericum hirsutum</i>	Hairy St John's-wort	13
<i>Cardamine pratensis</i>	Lady's smock	13
<i>Juncus conglomeratus</i>	Common rush	13
<i>Cirsium palustre</i>	Marsh thistle	12
<i>Taraxacum officinale</i>	Common dandelion	12
<i>Centaurea nigra</i>	Lesser knapweed	12
<i>Carex umbrosa</i>	Shady sedge	11
<i>Ulex europaeus</i>	Gorse	11
<i>Betula pendula</i>	Common birch	11
<i>Leucanthemum vulgare</i>	Ox-eye daisy	11
<i>Salix caprea</i>	Great sallow	11

(e.g. *Accipiter gentilis*, *Buteo buteo*, *Corvus corone*, *Columba palumbus*, *Falco tinunculus*, *Milvus migrans*, *Pernis apivorus*, *Picus viridis* and *Strix aluco*), were eliminated from our analysis (Ambuel and Temple, 1983; Freemark and Collins, 1992; Fuller, 1992). These were observed incidentally and were not strictly restricted to our sample unit.

#### *Variables studied*

*Time elapsed since the last logging operation* (years since logging; YSL) We used four classes of YSL: 0–3, 4–10, 11–20 and >20 years (Fuller and Moreton, 1987). This variable was either estimated on the plot by the development of the vegetation or by enquiring for the older plots.

*Retention of living standards on the logging site* (STANDARD) When the manager chooses to maintain standards, it strongly influences the structure of the vegetation and could therefore have an influence on diversity in the groups studied. It is a binary variable (with or without

standards). Effects of standard density were indirectly evaluated by a variable such as ST<sub>16</sub> (see below). This variable was estimated on the plots by the presence or absence of trees with a notably higher diameter than the majority or by evidence of retention on recent cuts.

*Ownership* (OWNER) This binary variable separates plots which are in a collective forest (owned mainly by communities), and those which are owned by private individuals. The French Office National des Forêts (ONF) manages collective forests homogeneously according to similar protection, maintenance and optimization objectives. These forests are large and have existed for a long time. The second group is very diverse, with many different objectives and management options. These forests are often fragmented and integrated into an agricultural landscape. Their long-term histories vary considerably and are not always known. This variable was obtained from cadastral registers.

*Distance to the nearest edge* (DEDGE) With this variable, we aimed to test the influence of

Table 2: The 40 bird species used in the analysis

Scientific name	English name	Plots with species (max = 98)
<i>Erithacus rubecula</i>	Robin	89
<i>Phylloscopus collybita</i>	Chiffchaff	81
<i>Sylvia atricapilla</i>	Blackcap	79
<i>Parus caeruleus</i>	Blue tit	75
<i>Troglodytes troglodytes</i>	Wren	75
<i>Turdus merula</i>	Blackbird	72
<i>Parus major</i>	Great tit	59
<i>Certhia brachydactyla</i>	Short-toed creeper	55
<i>Fringilla coelebs</i>	Chaffinch	45
<i>Dendrocopos major</i>	Greater spotted woodpecker	36
<i>Garrulus glandarius</i>	Jay	33
<i>Sitta europea</i>	Nuthatch	26
<i>Aegithalos caudatus</i>	Long-tailed tit	24
<i>Sturnus vulgaris</i>	Starling	19
<i>Emberiza citrinella</i>	Yellowhammer	14
<i>Turdus philomelos</i>	Song thrush	13
<i>Luscinia megarhynchos</i>	Nightingale	10
<i>Hippolais polyglotta</i>	Melodious warbler	7
<i>Oriolus oriolus</i>	Golden oriole	7
<i>Parus palustris</i>	Marsh tit	6
<i>Anthus trivialis</i>	Tree pipit	4
<i>Turdus viscivorus</i>	Mistle thrush	4
<i>Carduelis chloris</i>	Greenfinch	3
<i>Muscicapa striata</i>	Spotted flycatcher	3
<i>Phylloscopus bonelli</i>	Bonelli's warbler	3
<i>Sylvia communis</i>	Whitethroat	3
<i>Serinus serinus</i>	Serin	3
<i>Streptopelia turtur</i>	Turtle dove	3
<i>Alauda arvensis</i>	Skylark	2
<i>Acanthis cannabina</i>	Linnet	2
<i>Cuculus canorus</i>	Cuckoo	2
<i>Carduelis carduelis</i>	Goldfinch	2
<i>Coccothraustes coccothraustes</i>	Hawfinch	2
<i>Dendrocopos minor</i>	Lesser spotted woodpecker	2
<i>Hirundo rustica</i>	Swallow	2
<i>Passer domesticus</i>	House sparrow	2
<i>Regulus ignicapillus</i>	Firecrest	2
<i>Sylvia borin</i>	Garden warbler	2
<i>Lanius collurio</i>	Red-backed shrike	1
<i>Saxicola torquata</i>	Stonechat	1

non-forest elements on forest plots. This variable was normalized with a square root function.

*Richness of tree species (TREE)* The richness of tree species is an indicator of management practices and ecological conditions, which favour some species to the detriment of others. This richness could influence the diversity of the groups

studied by modifying the litter composition or by offering fruits with varying nutritive value. This variable was extracted from the vegetation data.

*Vegetation density in low strata (ST2)* This variable represents the percentage of area covered by the vertical projection of all the vegetation in the strata between 1 m and 2 m. This variable was

estimated visually (Small, 1989). It gives information on the structure of the bush vegetation in the plot.

*Vegetation density in high strata (ST<sub>16</sub>)* The definition is the same as ST<sub>2</sub>, but with the strata between 8 m and 16 m. The variable could be linked with the canopy structure, which is partly influenced by management and logging practices.

YSL is a variable related to the temporal dynamics of the ecological system, STANDARD and OWNER are variables which summarize the main management options, DEDGE is a spatial variable which summarizes some aspect of the ecological context, TREE, ST<sub>2</sub> and ST<sub>16</sub> are structural variables which describe the present situation. This set of variables covers a broad range of main factors which could be expected to influence bird and plant diversity at the plot level. The trophic status of soil is a factor that could influence vegetation composition. Previous unpublished work indicates that this factor presents little variability in our data set and that the selected variables are more influential.

### Sample

We sampled both vegetation and birds in 98 plots located in typical forests of the study area, with oaks and diverse species managed by coppice with or without standards. The first level of structure in our sample was YSL, with 46, 18, 19 and 15 plots in each YSL class, respectively. The second level was Standard, where logging without standard was less common (20 plots) than with standards (78). The last level was ownership: plots in collective forests were less numerous (29) than plots in private forests (69). It was not possible to find all the combinations of these first three variables; in particular, we did not find collective forest without standards. Main features for variables in YSL classes are shown in Table 3.

### Analysis

We first analysed the relationships between the richness of the groups studied and other variables. Richness is one of the most commonly used indicators of diversity (Huston, 1994). Our plots

Table 3: Main statistical characteristics of quantitative variables

	YSL	DEEDGE	TREE	ST <sub>2</sub>	ST <sub>16</sub>
Mean	13.2 ± 2.7	10.1 ± 0.9	5.5 ± 0.3	32.3 ± 4.3	31.5 ± 5.4
Min-max	[3-40]	[3.5-30.4]	[2-12]	[0-80]	[0-90]
0-3 years		10.3 ± 1.4	5.7 ± 0.5	30.3 ± 5.5	14.8 ± 4.6
		[1.6-30.4]	[2-12]	[0-80]	[0-70]
4-10 years		9.9 ± 3	5.3 ± 0.9	47.8 ± 12.4	29.6 ± 13
		[3.5-21.8]	[2-8]	[10-80]	[0-80]
11-20 years		9.5 ± 2.3	5.6 ± 0.6	20.5 ± 5.4	55.3 ± 9.5
		[3.5-18.7]	[3-8]	[5-40]	[20-80]
>20 years		10.1 ± 3.1	4.7 ± 0.9	34.7 ± 7.4	55 ± 14.5
		[3.5-21.8]	[2-7]	[10-0]	[5-90]
Correlations					
DEEDGE	-0.02				
TREE	-0.17	-0.08			
ST <sub>2</sub>	-0.02	-0.04	-0.01		
ST <sub>16</sub>	0.59	-0.01	0.04	-0.15	
	$P < 0.001$				

For the whole sample and for each YSL class, the first line is the mean value of the variable in the column, with its confidence interval ( $P = 0.95$ ), the second line is the range of variation. The bottom of the table contains Pearson's coefficient of correlation between quantitative variables, with the probability of significance when necessary.

were of equal surface area, therefore richness comparisons could be used without the bias of a sampling area effect.

The effect of YSL on plot richness was tested with Mann–Whitney statistics because of the very unequal number of plots in each class. The effects of other variables were tested for whole sample and in each YSL class. We compared qualitative variables (STANDARD and OWNER), with the Mann–Whitney test. For the >20 YSL class, we did not always have enough data to compare means for STANDARD. For the relationships between richness and quantitative variables, we tested the Pearson correlation with Bonferroni correction of the probability of significance (SYSTAT, 1996).

Next we analysed the relationships between the composition of the groups studied and variables using canonical correspondence analysis (CCA). We used an adaptation of CCA to fit with our variables, which were both quantitative and qualitative. The method has been described by Hill and Smith (1976) and is implemented in ADE-4 software (Thioulouse *et al.*, 1997). Qualitative variables were transformed by multiple correspondence analysis and quantitative ones by principal component analysis. The Hill and Smith method combines both and gives the same weight to qualitative and quantitative variables, whatever the number of their modalities. Transformed variables were used, as the constraint applied to taxonomic data treated by correspondence analysis (CA) (Thioulouse *et al.*, 1997).

The contribution of a variable to the definition of the main CCA axis helped to explain the structure observed in the plots. Correlation and mean comparisons were tested with Bonferroni probabilities and *t* tests to underline the main features shown by CCA. Groups of plots were defined according to the structure observed; for each of them, we gave an indicative list of species which were strongly linked with plot groups.

## Results

### *Evolution of the richness by plot*

**Vegetation** The highest mean richness per plot ( $32.7 \pm 4$ ) was observed in the YSL = 3 class. Richness decreased drastically after this period to

$20.9 \pm 2.5$  species per plot (Table 4). Richness seemed to increase from YSL = 10 to YSL >20 but remained lower than the first phase richness. We also noticed that the greatest variations in richness were observed in the YSL = 3 class, with the minimum and maximum richness of all plots.

**Birds** The mean bird richness of plots did not vary much after logging. No significant differences between YSL classes were demonstrated. We noticed that there were large variations of richness between plots in a YSL class.

### *Relationships between variables and plot richness*

**Vegetation** Plant richness decreased with the density of vegetation in the 8–16 m stratum, mainly in the YSL = 3 class (Table 4). However, we cannot demonstrate an effect of the retention of standards. These two results are not contradictory if we remember that a density of standards could be associated with different canopy developments related to the tree age. Thus, the presence of standards is not sufficient to reduce plant richness; a high density of canopy strata is required.

Plant richness increased with the richness of tree species, mainly in YSL >10 classes (Table 4). This relationship could be an artefact: tree richness could be related to plant species because tree species are also included in plant richness and represent a high proportion in the YSL = 20 and YSL >20 classes (25 and 19 per cent, respectively). However, the low correlation in the YSL = 10 class is not compatible with this hypothesis because its plant richness was the lowest (20.9) and its proportion of trees was the highest (25 per cent). Thus, we suggest that tree richness has a positive relationship with plant richness in the oldest YSL classes.

The plots owned by private individuals had significantly lower plant richness (6.5 fewer species), in the YSL = 10 class than collective plots (Table 4). This difference (26 per cent) was high because this class had the lowest richness.

**Birds** Bird richness was significantly lower in plots of the first YSL class (0–3 years) without standards than plots where standards were kept (Table 4). No difference between the other YSL

Table 4: Mean richness of plant and bird per plot according to YSL and qualitative variables (STANDARD and OWNER)

	Global	YSL			
		0–3 years	4–10 years	11–20 years	>20 years
<b>PLANT</b>					
<i>Mean richness</i>					
Richness/plot		32.7 ± 4 <sup>a</sup>	20.9 ± 2.5 <sup>b</sup>	22.3 ± 4.2 <sup>b</sup>	24.7 ± 2.8 <sup>a,b</sup>
Min–max		[10–70]	[16–32]	[10–39]	[14–31]
Richness with vs without standard	28.0 vs 24.2	33.1 vs 30.5	21.4 vs 19.8	22.6 vs 21.6	Not enough data
Richness with private vs collective owner	26.1 vs 30.0	31.0 vs 36.9	18.7 vs 25.2 ( <i>P</i> < 0.05)	22.6 vs 21.0	23.8 vs 26.0
<i>Correlation of variables with richness (Pearson's coefficient)</i>					
DEDGE	–0.06	–0.24	0.63 ( <i>P</i> < 0.05)	–0.27	0.23
ST <sub>2</sub>	–0.08	–0.13	0.34	0.29	–0.18
ST <sub>16</sub>	–0.34 ( <i>P</i> < 0.01)	–0.34	–0.07	0.03	–0.02
TREE	0.32 ( <i>P</i> < 0.01)	0.29	0.14	0.53*	0.59*
<b>BIRD</b>					
<i>Mean richness</i>					
Richness/plot		8.8 ± 0.7	8.2 ± 1.2	9.3 ± 1.2	9.5 ± 1.5
Min–max		[4–13]	[3–11]	[5–16]	[6–15]
Richness with vs without standard	9.1 vs 8.3	9.1 vs 7.2,	8.5 vs 7.6 ( <i>P</i> < 0.05)	9.3 vs 9.4	Not enough data
Richness with private vs collective owner	9.0 vs 8.7	8.6 vs 9.2	8.2 vs 8.3	7.7 vs 9.7	8.7 vs 10.1
<i>Correlation of variables with richness (Pearson's coefficient)</i>					
DEDGE	–0.25	–0.18	–0.06	–0.40	–0.53
ST <sub>2</sub>	–0.11	–0.23	0.36	0.00	–0.23
ST <sub>16</sub>	0.10	0.24	–0.32	0.11	–0.03
TREE	–0.08	–0.07	–0.17	0.18	–0.20
Plant richness	0.13	0.18	0.16	0.40	–0.40

Differences between richness were tested using Mann–Whitney *U* test statistics. Superscripts indicate significant differences between YSL classes (*P* < 0.01). Correlations between richness and quantitative variables with significance according to Pearson's coefficient.

\* Coefficient close to significant probability, TREE is significantly correlated with the richness of YSL = 20 and YSL >20 pooled together.

classes was noted. The richness of plots without standard seemed to increase after logging and reached the level of richness of plots with standards. This effect of standard retention was not visible in the correlation between richness and the density of vegetation in canopy strata (ST<sub>16</sub>). We suggest that standards have an effect on their own, for example by providing nesting sites or foraging areas, whatever their density or the canopy density.

Richness was not significantly related to any other variables. In particular, we note that there

was no correlation between bird and plant richness.

#### *Multivariate analysis of plot composition*

**Vegetation** The variables explained 11 per cent of the total variance of the data set (variance of CA on vegetation: 5.7; variance of CCA: 0.65). Nevertheless, the first two axes explained 74 and 69 per cent of the first and second axes of unconstrained CA on vegetation data, respectively.

The botanical composition of plots was most



influenced by time since last logging, which is represented by the first axis ( $F_1$ ) (Figure 1). The negative side represents young YSL classes and the positive side old YSL classes (between  $F_1$  and YSL,  $r = 0.8$ ,  $P < 0.001$ ). It was also strongly correlated with  $ST_{16}$  ( $r = 0.87$ ,  $P < 0.001$ ) which was correlated with YSL (Table 3). YSL classes were very well separated on the  $F_1$  axis, for private and collective plots.

The botanical composition separated ( $P < 0.001$ ) two groups of plots highly significantly along the second axis ( $F_2$ ): private and collective plots (Figure 1). For each YSL class, the comparison on  $F_2$  gave a significant difference ( $P < 0.01$ ) between private and collective plots.

Low-YSL privately owned plots (bottom left corner of Figure 1) were associated with *Centaureum erythraea*, *Cirsium vulgare*, *Cirsium tubero-*

*sum*, *Salix atrocinerea*, *Salix cinerea* and *Juncus inflexus*. Low-YSL collective plots (top left corner of Figure 1) were associated with *Taraxacum officinale*, *Veronica chamaedrys*, *Peucedanum cervaria* and *Lactuca seriola*. High-YSL collective plots (top right corner of Figure 1) were associated with *Polygonatum verticillatum*, *Gallium odoratum*, *Gallium uliginosum*, *Helleborus foetidus* and *Ulmus glabra*. High-YSL privately owned plots (bottom right corner of Figure 1) were associated with *Crataegus laevigata*, *Mespilus germanica* and *Anemone nemorosa*. We noticed that annual species and Compositae species were associated with low YSL plots, probably because of their capacity to colonize by anemochory and to use perturbed soils. On the other hand, species associated with high-YSL plots were perennial and ligneous. In privately

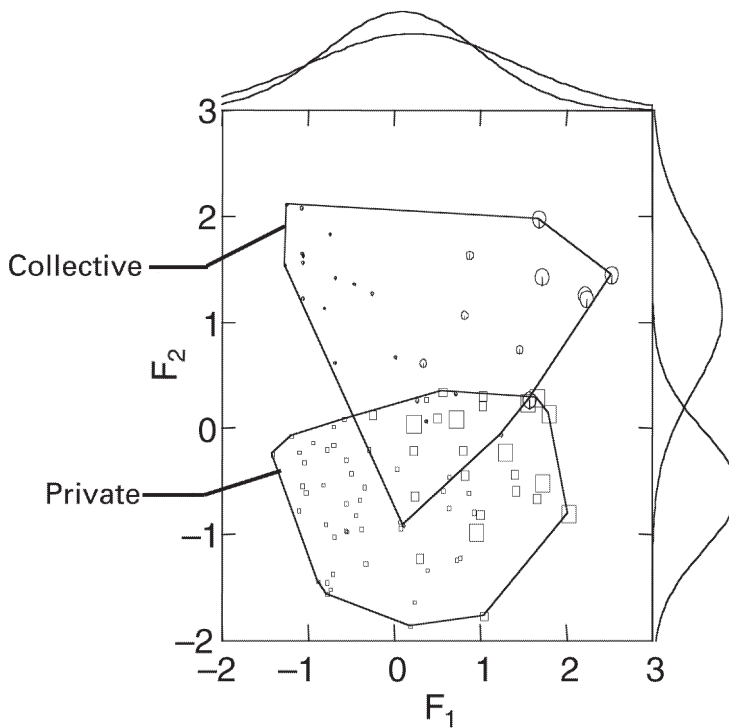


Figure 1. Plot position in the first factorial plan obtained by CCA on vegetation abundance–dominance and the seven selected variables. The symbol size is proportional to YSL (3–40 years);  $F_1$  is correlated with YSL ( $r = 0.8$ ,  $P < 0.001$ ). Two groups (hulls) are separated on  $F_2$  with a high significance level ( $P < 0.001$ ); their distribution curves are represented on the top and right-hand sides of the graph.

owned plots, there were more heliophyte species than in collective plots, probably because of a more open and heterogeneous canopy.

*Birds* The main characteristics of the CCA on bird data showed that the selected variables explained 9.7 per cent of the total variance (variance of CA on bird abundances: 3.5; variance of CCA: 0.34). The first axis of CCA explained 61 per cent of the first axis of unconstrained CA on bird abundances.

On the first axis ( $F_1$ ), bird composition separated plots without standards on the positive side (Figure 2), privately owned plots with standards in the middle and collective plots with standards on the negative side, with highly significant differences ( $P < 0.001$ ).  $ST_2$  contributed to  $F_1$

with a very good correlation ( $r = 0.5$ ,  $P < 0.001$ ) for all plots and a better one in each group ( $r = 0.8$ ,  $P < 0.001$  for 'without standards, private';  $r = 0.8$ ,  $P < 0.001$  for 'with standards, private';  $r = 0.7$ ,  $P < 0.001$  for 'with standards, collective'). The second axis, which was smaller, was characterized by a gradient of  $ST_{16}$  and DEDGE toward negative values and also by notable contributions of  $ST_2$  and STANDARD.

The group of plots without standards was characterized by reports of *Luscinia megarhynchos*, *Turdus philomelos* and *Aegithalos caudatus* representing the most common species (global frequency  $>10$  per cent) and *Alauda arvensis*, *Streptopelia turtur* and *Hippolais polyglotta* the less common species. These species are generally associated with open habitats or mixed

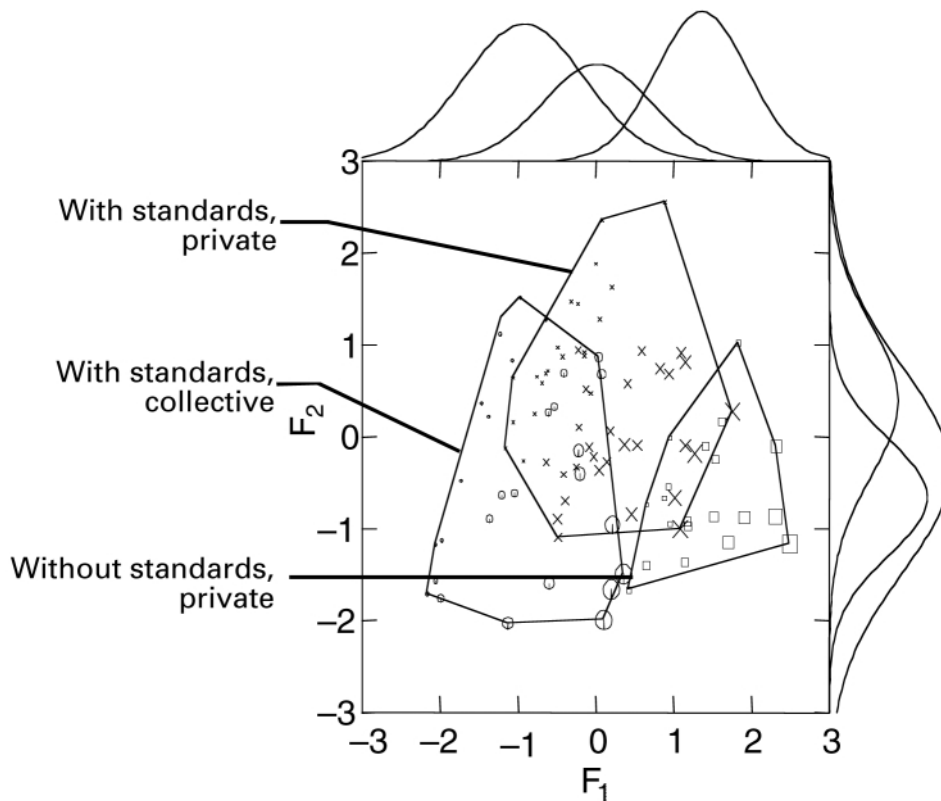


Figure 2. Position of the 98 plots in the first factorial plan obtained by CCA on bird abundance and the seven selected variables. Three groups of plots (hulls) are separated on the  $F_1$  axis with a high level of significance ( $P < 0.001$ ). Their distribution curves are represented on the top and right-hand sides of the graph. The size of plot symbols is proportional to  $ST_2$ .

open/forest habitats. The group of collective plots with standards was characterized by *Sitta europaea*, *Dendrocopos major* and *Certhia brachydactyla* representing the most common species and also *Regulus ignicapillus*, *Turdus viscivorus*, *Dendrocopos minor* and *Cuculus canorus*. These species are generally associated strictly with forest conditions, large areas and long silvicultural rotations. The final group contained almost all the other species and was less precise.

## Discussion

### Vegetation

*Initial effect and long-term effects of logging perturbation* For plants, time since last logging operation (YSL) has a major effect on both species richness and composition (Halpern and Spies, 1995; Roberts and Gilliam, 1995). Plant richness increased strongly just after logging operations, due to the development of numerous ruderal species. It decreased severely during the next phase, to increase slowly in the mature phase (Table 4). This trend is consistent with the pattern of changes proposed for secondary forest successions (Gilliam *et al.*, 1995). This trajectory of diversity could be explained considering two broad kinds of disturbance effects associated with logging (Halpern and Spies, 1995). The first one is a long-term effect and is related to competition and stand development. In particular, the evolution of light availability could explain long-term trends of botanical diversity. The second is an initial effect and is related to species dispersion and fine scale modifications of habitat conditions. Soil disturbances caused by logging activities could be an important source of fine scale spatial heterogeneity (Barkham, 1992) which could explain the higher diversity just after logging (Deconchat and Balent, 2001).

A major aspect of the modification caused by logging perturbation on botanical composition is the invasion of non-forest species. Many weed species can grow in forests just after the logging operation. They seem to disappear again very rapidly. Because the forest was very fragmented, agricultural areas and weed sources of colonization are close to any point in the forest. Most of

these species are anemochorous and they were able to travel easily over a small tract of high forest to reach any logging site. However, we did not find an effect of the distance to the nearest edge that could explain the different levels of contamination by non-forest species. This effect could be masked by others and needs to be further studied. Another hypothesis is that forests were so fragmented that they were completely submerged by a homogeneous seed-rain. Seed dispersion by mud on machines and other human activities could be also an important transport factor (Usher *et al.*, 1992). These ruderal species could have potentially strong influence on ecological system properties and functions. From the point of view of the forester, some of these species could create problems for regenerating, for example by allelopathic antagonism (Jobidon, 1992). However, at the same time, Leguminosae could be of primary importance in maintaining soil fertility by fixing atmospheric nitrogen. The effects of management and logging practices on botanical composition need to be studied in detail in order to increase positive effects and limit negative ones.

### Birds

*Effect of standards on birds* Bird community composition, and even its richness, was influenced by the retention of standards and vegetation density in low layers. Standards can be used by birds as nesting sites, especially for woodpeckers, tits and short-toe creepers, which live in holes in logs. On clear-felled sites, the bird community is characterized by the presence of open-habitat species during the first years after logging. Lower richness in the 4–10 years YSL class could be explained by the complete closure of coppice canopies, which creates a very uniform vegetation layer. Standards could be seen as a way of maintaining more forest-like conditions just after cutting and of creating heterogeneity in the coppice layer later. The low effect of ST<sub>16</sub> could indicate that the density of retained standards is not a factor of primary importance for birds: the effect of standards seems to be a binary effect.

*Birds and succession stage* The literature indicates that there is often a strong relationship between bird community composition and the

succession stage of the forest (Fuller and Moreton, 1987; Bersier and Meyer, 1994; Schieck *et al.*, 1995). We did not find such a relationship. We propose three main explanations.

First, bird community composition is strongly influenced by the structure of the vegetation (Bersier and Meyer, 1994). In our region, the diversity of management, with retention of a varying number of standards for instance, creates a wide diversity in the vegetation structure and its evolution. Thus, the time spent since the last logging operation is not correlated with the vegetation structure: for the same YSL, we found two very different structures, as demonstrated by the low correlation between YSL and structural variables (Table 3).

Second, edges have important effects on bird communities (Fuller, 1991; Bellamy *et al.*, 1996). In our region, forests are very fragmented and many plots are not very far from forest edges or from interior edges between two different management units. These edges could have major, but complex, effects on birds (DeGraaf, 1992; Paton, 1994). However, the distance to the nearest edge seems to have little influence on bird community composition, probably because this variable does not integrate all complex interactions between forests and interior edges very well.

Third, the census methodology used in this study might have introduced some bias into the results. In fragmented woodlots, the distribution of bird species, especially migrant ones, can present large yearly variations, caused by external factors, such as population dynamics in wintering regions and the influence of agricultural practices, or stochasticity (Haila *et al.*, 1993). A multi-annual census could decrease the sensitivity of bird data to these factors and could allow diachronic pre- and post-logging comparisons (Baker and Lacki, 1997).

#### *Vegetation and bird comparisons*

*Logging: temporary ruderalization of plant and bird communities* In our study, for both birds and plants, forest logging introduces non-forest species in previous exclusively forest communities. This invasion is probably facilitated by forest fragmentation. From a conservation point of view, forest communities are more vulnerable and particular attention should be paid to them to

maintain their integrity. Thus, controlling ruderalization by human intervention is necessary. For bird communities, the conservation of some standards is sufficient to reduce ruderalization and to maintain most of the forest-associated species (Norton and Hannon, 1997). For plants, ruderalization is dependent on light availability, which is difficult to modify without a complete change in silvicultural practices. Nevertheless, it is probably possible to influence botanical composition through a better management of logging. New studies are needed to determine the effects of logging practices.

*Ownership effects* The effect of ownership on bird and plant community compositions, which was unexpected, needs to be discussed. In fact, ownership could be considered as a synthetic variable, which integrates different aspects (Maltamo *et al.*, 1997). Private forests are mainly small, fragmented forests, with small management units, each with different objectives and silvicultural practices (Balent, 1996). The history and the management of these forests are not well known and often chaotic. Collective forests are larger, often more compact and are managed by the same organization (ONF), with clear production objectives, on large management units, with more uniform silvicultural practices. Their history is older and more continuous. More precise analyses are needed to separate all these components. We are considering using partial canonical correspondence analysis to extract the effects of each of these components (Bersier and Meyer, 1995).

Nevertheless, at this stage of the analysis, these simple results may be very useful in decision-making. It is easier for logging enterprises, who do not have the resources to perform a complete ecological analysis, to obtain information about ownership status than about area, history, and management, without which they are dealing with uncertainty (McCarthy and Burgman, 1995). With this simple information, they could adapt their practices in two broad separate ways. In privately owned forests, they should probably not find bird or plant species strictly associated with forest conditions and which could be endangered at the regional level. In collective forests, however, this is possible and it would be preferable to check that no rare species will be affected

by logging. To provide new forest habitats for associated species, loggers should maintain as many standards as possible in private forests for birds, and reduce soil perturbations to limit the invasion of ruderal plant species. In collective forests, whole communities are resistant to ruderalization and they need less attention. Attention should be concentrated on identified heritage species.

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