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ORIGINAL PAPER

# Impact of four silvicultural systems on birds in the Belgian Ardenne: implications for biodiversity in plantation forests

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**Abstract** Uneven-aged management of conifer plantations is proposed as a way to increase the value of these forests for the conservation of bird diversity. To test this assumption, we compared the impact of four common silvicultural systems on bird communities, defined by cutblock size (large in even-aged silvicultural systems/smaller in uneven-aged silvicultural systems) and tree species composition (spruce/beech) in the Belgian Ardenne where beech forests have been replaced by spruce plantations. The abundances of bird species were surveyed in young, medium-aged and mature stands in 3–5 forests per silvicultural system (66 plots in all). The effect of silvicultural systems on bird species richness, abundance and composition were analysed both at the plot and at the silvicultural system levels. In plots of a given age, beech stands were richer in species. The composition of bird species at the plot level was explained by stand age and tree composition, but weakly so by stand evenness. For the silvicultural systems, bird species richness was significantly higher in even-aged and in beech forests, and bird species composition depended on the silvicultural system. This study emphasises the importance of maintaining native beech stands for birds and suggests that uneven-aged management of conifer plantations does not provide a valuable improvement of bird diversity comparatively with even-aged systems.

**Keywords** Silvicultural system · Biodiversity · Bird communities · Silvicultural cycle · Coniferous plantation

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## Introduction

The replacement of native broadleaf stands by uniform conifer plantations is a matter of concern for biodiversity conservation (Lack 1933, 1939; Ledant et al. 1983; Laiolo et al. 2004) and this question needs detailed analysis. Bird species composition is affected by tree species composition (e.g. Moss 1978; Müller 1987; Bersier and Meyer 1994, 1995; Hansen 1995) with few species associated with conifers while some are more associated with broadleaf species. Bird species composition is also influenced by vertical and horizontal vegetation structure that is determined by tree growth in the stand (Wigley and Roberts 1997; Lertzmann and Fall 1998) and the silviculture (Bellamy et al. 1996; Jokimäki and Huhta 1996; Drapeau et al. 2000). The size of the disturbance created by harvesting operations (cutbock size) defines different silvicultural systems and is known to influence biodiversity (Attiwill 1994; Chesson and Pantastico-Caldas 1994; Schnitzer and Carson 2001). In most of the cases, planted conifers are managed with large cutblocks (>2 ha) that are considered as unfavorable for bird diversity conservation (Ledant et al. 1983).

To improve the value of planted conifer forests for bird diversity, alternative silvicultural systems based on varying the areas where mature trees are harvested have been proposed (Kerr 1999). To test this idea, the differences in bird diversity between cutblock sizes in planted conifer forests have to be compared to similar differences in the original broadleaf forests. The Belgian Ardenne has the particularity of containing within a restricted region, four main silvicultural systems, including conifer plantations and broadleaf forest, and both forests managed by small and large cutblocks. In the forest manager's terminology, the large cutblock sizes are typical of the "even-aged" silvicultural system, while smaller cutblock sizes are typical of the "uneven-aged" silvicultural system used in this part of Europe (Kerr 1999).

Silvicultural systems have to be characterized by considering the whole silvicultural cycle. Moreover, as biodiversity can be influenced considerably by stand age, the effect of silvicultural systems can only be understood by considering the whole cycle (du Bus de Warnaffe 2002). Yet the age of the stand should be seen as a stage rather than an absolute age, since the effect of the absolute age on birds depends on the composition of the stand. Three stages can be identified in managed forests: a short one just after logging when low vegetation is dominant, a medium-aged stage when trees grow rapidly and induce a closed canopy, a long mature stage when trees have commercial dimensions and induce a high canopy with an overstorey (du Bus de Warnaffe and Lebrun 2004). An over-mature stage with collapsing and senescent trees can be identified in forests where harvesting does not occur (Fuller and Moreton 1987). Different silvicultural systems can be compared for each stage, or by gathering the stages over space, using a space-for-time substitution. Two spatial levels must therefore be considered: the plot, which only considers one stage, and a larger spatial and temporal scale integrating the complete silvicultural cycle of a silvicultural system (Huston 1999).

The hypothesis tested in this paper is that uneven-aged conifer planted forests have a higher value for bird conservation than even-aged conifer planted forests. This difference was tested with a sampling design including several stages of forest development and was compared with the same design in natural beech forests. These comparisons help to identify the impacts on biodiversity of the silvicultural systems applied to a large part of the forests in Europe and may provide guidance to mitigate their consequences on biodiversity conservation.

## Materials and methods

### Study region

The study was conducted in the Belgian Ardenne, between Namur and Luxembourg (Fig. 1). The historical land-use types in this region are pastures and broadleaf woodlands, which now account for 20 and 40% of the region (Paquet et al. 2006). They have been partly transformed into commercial conifer plantations (30% of the area) over the last 150 years (Devillez and Delhaise 1991). The elevation of our study plots ranged from 320 to 560 m, mean annual rainfall from 1,050 to 1,200 mm $yr^{-1}$ and mean annual temperatures from 7.3 to 7.8°C (Weissen et al. 1994). All study plots comprised plantations established on *Luzulo-Fagetum* or *Luzulo-Quercetum* vegetation types, according to Noirfalise (1984) and Rameau et al. (2000) phytosociological systems, on flat or very gently sloping ground with acid and moderately dry soils (*Dystric cambisol*) (FAO 1990). The main tree species are native, mostly Norway spruce (*Picea abies* (L.) Karst), beech (*Fagus sylvatica* L.) and oaks (*Quercus petraea* (Mattme.) Liebl. and *Quercus robur* L.), with few introduced species, mostly Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco). Rotation length is typically 60–80 years for spruce, which is usually planted, and 120–150 years for beech, which is usually natural. Logging is done by clearcut on cutblocks with sizes ranging from 0.1 ha to more than 2 ha.

In even-aged systems, all the tree of a stand (>1 ha) are of the same age at a given time. In this system, logging is applied on large areas (cutblocks) by clearcutting. Even-aged systems result from planted forests for conifer tree and for beech tree from naturally regenerated forests managed to produce timber wood. In uneven-aged systems, the trees of different ages are mixed on smaller areas (<0.5 ha), logging is done by cutting mature trees on small cutblocks, as younger trees remain we do not be considered it as a clearcut. Uneven-aged conifer silvicultural system has developed from even-aged planted forests where small logging areas have been used rather than the large typical clearcuts. Forest managers consider it as a way to improve the sustainability of planted conifer forests.

### Sampling design

The study compared four important silvicultural systems in the Belgian Ardenne:

(1) Even-aged conifer (EC): planted forests with greater than 80% cover of Norway spruce logged by clearcut on large cutblocks (>2 ha);

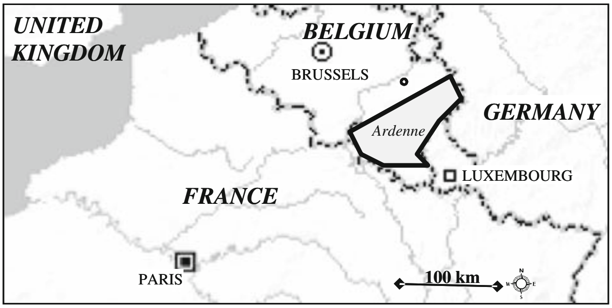


**Fig. 1** Study area: ecological limits of the Belgian Ardenne (gray area with solid lines)

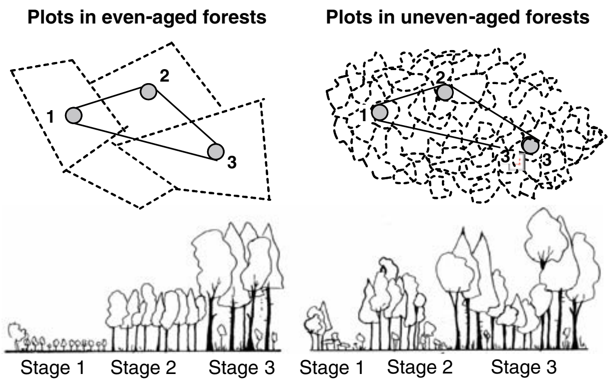


**Fig. 2** Scheme of the location of the plots in even-aged and uneven-aged forest areas, in aerial and field views. Broken lines define stands of different ages and/or tree composition, circles represent bird counting zones in plots (25 m circle) and solid line convex hulls define the silvicultural system (about 15 ha)

(2) Even-aged Beech (EB): naturally regenerated forests with greater than 80% cover of Beech logged by clearcut on large cutblocks (>2 ha);
(3) Uneven-aged conifer (UC): planted forests with greater than 80% cover of Norway spruce logged on small cutblocks (<0.5 ha) producing a mix of trees of different ages;
(4) Uneven-aged Beech (UB): naturally regenerated forests with greater than 80% of Beech logged by small cutblocks (<0.5 ha).

We selected three to six forests per silvicultural system, these forests comprised at least 15 ha corresponding to the silvicultural system as defined above and managed for at least two rotations with the same system (du Bus de Warnaffe and Dufrêne 2004). The size of the cutblocks and the composition of each forest were determined by GIS analysis of 1/10,000 aerial photographs, and checked on site.

Plots were selected in three non-overlapping stages covering the silvicultural cycles of each silvicultural system (Fuller and Moreton 1987; Hansen 1995; Lertzmann and Fall 1998): regeneration stage (stage 1: trees 3–10 years old), medium-aged stage (stage 2: 20–40 years old for conifer, 30–60 years old for beech), and mature stage (stage 3: 50–80 years old for conifer, 80–140 years old for beech). The stage in uneven-aged systems was defined according to the time since the last logging, it is similar to the age of the oldest trees at a given time. The plots were separated by at least 200 m. A set of three plots belonging to these three stages in the same forest and the same silvicultural system defined a silvicultual cycle since it included the tree stages (Fig. 2).

The sampling was thus characterized by 54 plots belonging to 18 silvicultural systems (Tables 1, 2).

## Bird data

The bird survey method was based on point counts (Bibby et al. 1985; Frochot and Roché 1990; Petty and Avery 1990) within a maximum 25 m fixed radius visually estimated. Singing birds were surveyed by trained observers over 20 min periods in each plot, twice during the breeding season (April and early June 2000), to record both sedentary and migrant species, and to reduce the bias associated with differences in detectability. The data were collected in the first 4 h after dawn, avoiding rainy and windy days. According to the

**Table 1** Number of plots

| Silvicultural system | EC | EB | UC | UB | Total |
|---|---|---|---|---|---|
| Number of plots | | | | | |
| In stage 1 | 4 | 3 | 6 | 5 | 18 |
| In stage 2 | 4 | 3 | 6 | 5 | 18 |
| In stage 3 | 4 | 3 | 6 | 5 | 18 |
| Total number of plots | 12 | 9 | 18 | 15 | 54 |

Silvicultural systems are defined by cutblock size and tree species composition of the forest: EC, even-aged conifer; EB, even-aged beech; UC, uneven-aged conifer; UB, uneven-aged beech. Each silvicultural system contains three stages. See text and Fig. 2 for details

**Table 2** Major characteristics of plots in each class (see Table 1 for codes)

| Silvicultural system | Stage | Tree species | Altitude (m) | Mean dbh (cm) | Basal area ($m^2$/ha) | Cutblock size (ha) |
|---|---|---|---|---|---|---|
| EC | 1 | PA | 380–520 | 2–7 | 1–7 | 4–12 |
| | 2 | PA, PM | 320–490 | 20–27 | 34–41 | – |
| | 3 | PA, PM | 320–520 | 43–50 | 47–53 | – |
| EB | 1 | FS | 410–540 | 2–6 | 1–5 | 3–6 |
| | 2 | FS | 380–540 | 28–44 | 21–31 | – |
| | 3 | FS | 380–460 | 43–59 | 22–28 | – |
| UC | 1 | PA, PM | 420–580 | 2–8 | 18–27 | 0.02–0.45 |
| | 2 | PA, PM | 420–580 | 22–36 | 32–40 | – |
| | 3 | PA, PM | 420–580 | 41–52 | 31–42 | – |
| UB | 1 | FS, QP, QR | 410–500 | 1–8 | 11–20 | 0.03–0.25 |
| | 2 | FS | 350–500 | 23–33 | 17–28 | – |
| | 3 | FS, QP, QR | 350–500 | 34–52 | 21–29 | – |

All plots were situated on flat or very slightly sloping ground, on acid brown and moderately dry soils. Dbh (diameter at breast height) and basal area were measured on 0.20 ha. Cutblock size was measured for stage 1. Tree species: PA, *Picea abies*; PM, *Pseudotsuga menziesii*; FS, *Fagus sylvatica*; QP, *Quercus petraea*; QR, *Quercus robur*

territorial behavior of most of the bird species in spring, the fixed radius of the plots and the experience of the surveyors, we assumed to have comparable lists, but not necessarily exhaustive, of the bird species living in the plots (Buckland et al. 2001; Kery and Schmid 2004). All recorded species were used for the analyses, except over-flying birds, such as raptors and corvids, which were discarded. The abundance was estimated as two individuals (a pair) for each bird heard singing and one individual for each bird that was only seen or heard calling (not singing). The highest abundance recorded on the two dates was used as abundance index (Frochot and Roché 1990). For silvicultural systems, abundance of each species was the sum of the abundance index in the three plots (stages 1, 2 and 3).

## Data analysis

ANOVA was used to test for differences in species richness and abundance between the datasets defined by the silvicultural systems and the stages: three-way ANOVA for the plot analysis (cutblock size, tree species composition, growth stage) and two-way ANOVA for the analysis of silvicultural systems (cutblock size, tree species composition) (Sokal and Rohlf 2000). Interactions between factors were included in the model and post-hoc tests, after Bonferonni correction, were used to identify significant differences between the means.

We used a linear ordination [Correspondence Analysis (Hill 1974)] to reduce the bird community data (in presence–absence) to a smaller set of dimensions, allowing us “to describe the strongest patterns in species composition” (McCune and Grace 2002). The result is an ordination of the species and the samples along axes computed as the solution of linear equations linking (1) the species space, where each sample is a coordinate, and (2) the sample space, where each species is a coordinate. Correspondence analysis can be interpreted as a summary of the departure of the observed contingency table (species by sample) from a null hypothesis of independence between species and samples, estimated by the $\chi^2$ distance (Couteron et al. 2003). Several orthogonal axes can be computed and can be interpreted as follow: the closer the species on the axes, the more similar their distributions in samples; the closer the samples, the more similar their bird species composition. The higher values along the axes indicate samples or species with composition or distribution, respectively, more different from the mean composition or distribution of the whole sample (Balent and Courtiade 1992). Samples and species ordinations can be displayed on the same plan: the closer a species and a sample, the higher the probability, estimated from $\chi^2$ distance, to have this species observed in this sample (Pelissier et al. 2003). This ordination of the samples, based on the covariations and associations among the species, was constrained by the silvicultural system classes to measure their influence on the bird species communities. This so called “between-group analysis” can be seen as a discriminant analysis adapted to species survey data and is a special case of the Canonical Correspondence Analysis (CCA) with only one explaining qualitative factor. It allows us to test the influence of qualitative variables on the structure of a species community (McCune and Grace 2002). The results are displayed as factorial plans where the separation of the sample classes is maximized according to their species composition (Thioulouse et al. 1997). A permutation test measured the departure of the observed structure from a random distribution of the species and gave a significance level of the difference between groups. All calculations were performed with R software (R development core team 2006) and with ade4 package (Chessel et al. 2004).

## Results

A total of 44 species were found but 10 were recorded only once. The most abundant species were Chaffinch (*Fringilla coelebs*), Robin (*Erithacus rubecula*), Wren (*Troglodytes troglodytes*), and Wood pigeon (*Columba palumbus*) (Table 3).

### Species richness and abundance

#### *Plot analysis (each stage)*

We found 3–20 species per plot. Tree species composition was the only factor with a significant effect on bird species richness ($F = 10.8353$; df = 1; $P = 0.0020$). The mean species richness in beech plots ($14.12 \pm 4.38$; $n = 24$) was higher than in conifer plots ($10.50 \pm 3.59$; $n = 30$). The variability of the species richness was higher in beech plots than in conifer plots (Fig. 3). In beech plots, the mean species richness of small cutblocks size (uneven-aged system) was not significantly different from the richness in the larger cutblocks, but in both cases, intermediate stages 2 had a lower species richness that masked the higher differences observed with stages 1 and 3 (Fig. 3). When considering only these two stages, uneven-aged plots had higher bird species richness than in even-aged plots, the few cases with extremely low values may explain why these differences were not significant.

**Table 3** List of bird species observed in Belgian Ardenne

| Code | Scientific name | Beech even-aged | Beech uneven-aged | Beech | Conifer even-aged | Conifer uneven-aged | Conifer | Total |
|---|---|---|---|---|---|---|---|---|
| ATRI | *Anthus trivialis* | 3 | 1 | 4 | 2 | 0 | 2 | 6 |
| ACAU | *Carduelis cannabina* | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| CCAR | *Carduelis carduelis* | 0 | 0 | 0 | 1 | 1 | 2 | 2 |
| CSPI | *Carduelis spinus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CBRA | *Certhia brachydactyla* | 1 | 4 | 5 | 0 | 1 | 1 | 6 |
| CFAM | *Certhia familiaris* | 0 | 2 | 2 | 0 | 4 | 4 | 6 |
| CCOC | *Coccothraustes coccothraustes* | 1 | 4 | 5 | 2 | 0 | 2 | 7 |
| CPAL | *Columba palumbus* | 3 | 4 | 7 | 3 | 4 | 7 | 14 |
| CCAN | *Cuculus canorus* | 2 | 1 | 3 | 4 | 0 | 4 | 7 |
| DMAJ | *Dendrocopos major* | 3 | 5 | 8 | 0 | 4 | 4 | 12 |
| DMED | *Dendrocopos medius* | 0 | 3 | 3 | 0 | 0 | 0 | 3 |
| DMIN | *Dendrocopos minor* | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| DMAR | *Dryocopus martius* | 3 | 3 | 6 | 0 | 1 | 1 | 7 |
| ECIT | *Emberiza citrinella* | 1 | 0 | 1 | 1 | 0 | 1 | 2 |
| ERUB | *Erithacus rubecula* | 3 | 5 | 8 | 4 | 6 | 10 | 18 |
| FCOE | *Fringilla coelebs* | 3 | 5 | 8 | 4 | 6 | 10 | 18 |
| GGLA | *Garrulus glandarius* | 2 | 5 | 7 | 2 | 5 | 7 | 14 |
| LCUR | *Loxia curvirostra* | 1 | 0 | 1 | 1 | 1 | 2 | 3 |
| NCAR | *Nucifraga caryocatactes* | 0 | 0 | 0 | 1 | 0 | 1 | 1 |
| PATE | *Parus ater* | 3 | 2 | 5 | 4 | 5 | 9 | 14 |
| PCAE | *Parus caeruleus* | 1 | 5 | 6 | 0 | 2 | 2 | 8 |
| PCRI | *Parus cristatus* | 0 | 2 | 2 | 3 | 2 | 5 | 7 |
| PMAJ | *Parus major* | 3 | 5 | 8 | 3 | 1 | 4 | 12 |
| PMON | *Parus montanus* | 0 | 3 | 3 | 0 | 0 | 0 | 3 |
| PPAL | *Parus palustris* | 3 | 4 | 7 | 1 | 3 | 4 | 11 |
| PCOL | *Phylloscopus collybita* | 3 | 3 | 6 | 3 | 4 | 7 | 13 |
| PSIB | *Phylloscopus sibilatrix* | 3 | 4 | 7 | 0 | 2 | 2 | 9 |
| PTRO | *Phylloscopus trochilus* | 3 | 1 | 4 | 4 | 1 | 5 | 9 |
| PCAN | *Picus canus* | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| PMOD | *Prunella modularis* | 3 | 1 | 4 | 4 | 4 | 8 | 12 |
| PPYR | *Pyrrhula pyrrhula* | 1 | 1 | 2 | 0 | 1 | 1 | 3 |
| RIGN | *Regulus ignicapillus* | 0 | 0 | 0 | 3 | 3 | 6 | 6 |
| RREG | *Regulus regulus* | 1 | 3 | 4 | 4 | 6 | 10 | 14 |
| STOR | *Saxicola torquata* | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| SEUR | *Sitta europaea* | 3 | 5 | 8 | 0 | 2 | 2 | 10 |
| SVUL | *Sturnus vulgaris* | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| SATE | *Sylvia atricapilla* | 3 | 4 | 7 | 4 | 6 | 10 | 17 |
| SBOR | *Sylvia borin* | 1 | 0 | 1 | 1 | 1 | 2 | 3 |
| SCOM | *Sylvia communis* | 0 | 0 | 0 | 1 | 0 | 1 | 1 |
| TTRO | *Troglodytes troglodytes* | 3 | 4 | 7 | 4 | 6 | 10 | 17 |
| TMER | *Turdus merula* | 3 | 5 | 8 | 4 | 6 | 10 | 18 |
| TPHI | *Turdus philomelos* | 3 | 5 | 8 | 4 | 5 | 9 | 17 |
| TPIL | *Turdus pilaris* | 0 | 1 | 1 | 1 | 0 | 1 | 2 |
| TVIS | *Turdus viscivorus* | 3 | 4 | 7 | 4 | 4 | 8 | 15 |

*Note*: Scientific names of the following species have changed in 2007: *Parus ater* is now *Periparus ater*, *Parus caeruleus* is *Cyanistes caeruleus*, *Parus cristatus* is *Lophophanes cristatus*, *Parus montanus* is *Poecile montana*, *Parus palustris* is *Poecile palustris*, *Regulus ignicapillus* is *Regulus ignicapilla* and *Saxicola torquata* is *Saxicola rubicola*

Total is the total number of forests (at silvicultural system level) where a given species was observed; Beech and Conifer are, respectively, the number of beech or conifer forests where a given species was observed (beech + conifer = Total); the same for even-aged and uneven-aged columns, splited according to tree species composition of the forests

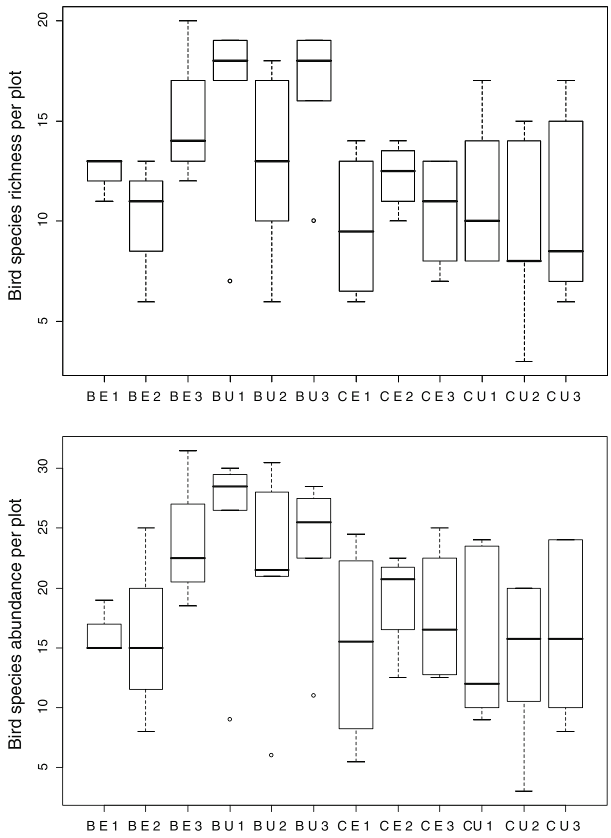


**Fig. 3** Box plots of the bird species richness (top) and abundance (bottom) in sample plots according to tree species composition (B: beech or C: conifer), cutblock size (E: even-aged or U: uneven-aged) and stages (1, 2 or 3)

In conifer plots, no particular differences were identified between species richness according to cutblock size and stage.

Total bird abundance was highly correlated to species richness ($r^2 = 0.86$, $P < 0.001$). As for bird species richness, tree species composition was the only factor explaining a significant part of bird abundance variability ($F = 7.4354$; df = 1; $P = 0.0092$); the highest mean abundance was in beech plots (21.46 ± 7.75; $n = 24$), the lowest in conifer plots (16.03 ± 6.31; $n = 30$) (Fig. 3). In conifer plots, no clear pattern was observed for abundance, nor for species richness. In beech plots, on the other hand, the pattern was different. In even-aged plots, mature stands had clearly a higher abundance (but few samples with extremely low values) than younger stages. Conversely, the highest value was for first stage in uneven-aged plots, but with lower differences with the other stages comparatively with even-aged plots.

*Silvicultural system analysis (stages 1 + 2 + 3 pooled together)*

We found 12–27 species in the silvicultural systems. Cutblock size ($F = 6.8983$; df = 1; $P = 0.0176$) and tree composition ($F = 4.7767$; df = 1; $P = 0.0431$) significantly explained bird species richness variability, with the highest bird species richness in even-aged beech forests (24.67 ± 2.08; $n = 3$) and the lowest in uneven-aged conifer forests (16.33 ± 4.88; $n = 6$) (Fig. 4). The difference of bird species richness between beech and conifer was

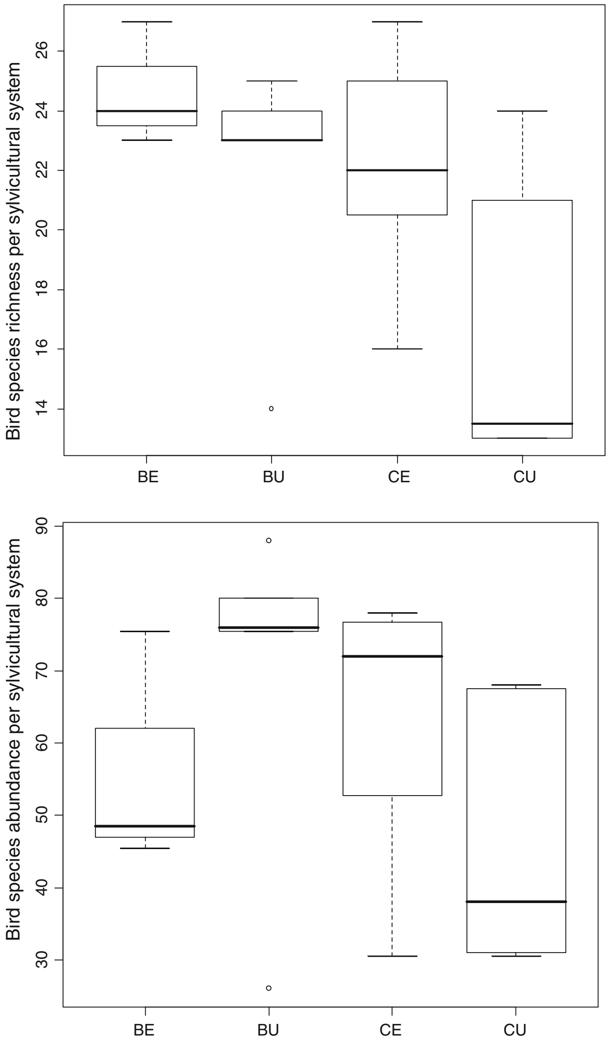


**Fig. 4** Box plots of the bird species richness (top) and abundance (bottom) in silvicultural systems according to tree species composition (B: beech or C: conifer) and cutblock size (E: even-aged or U: uneven-aged)

higher in uneven-aged forests than in even-aged ones. No factor explained a significant part of bird species abundance, however, it can be noticed that in beech forests, the abundance was higher in uneven-aged forests than in even-aged, while the differences were less visible in conifer forests (Fig. 4).

## Species composition

### *Plot analysis*

The first stages of the even-aged silvicultural systems were significantly ($P < 0.001$) separated from the others groups along the first axis of the between group analysis (Fig. 5). The beech plots and the conifer plots of the older stages were separated along the second axis,

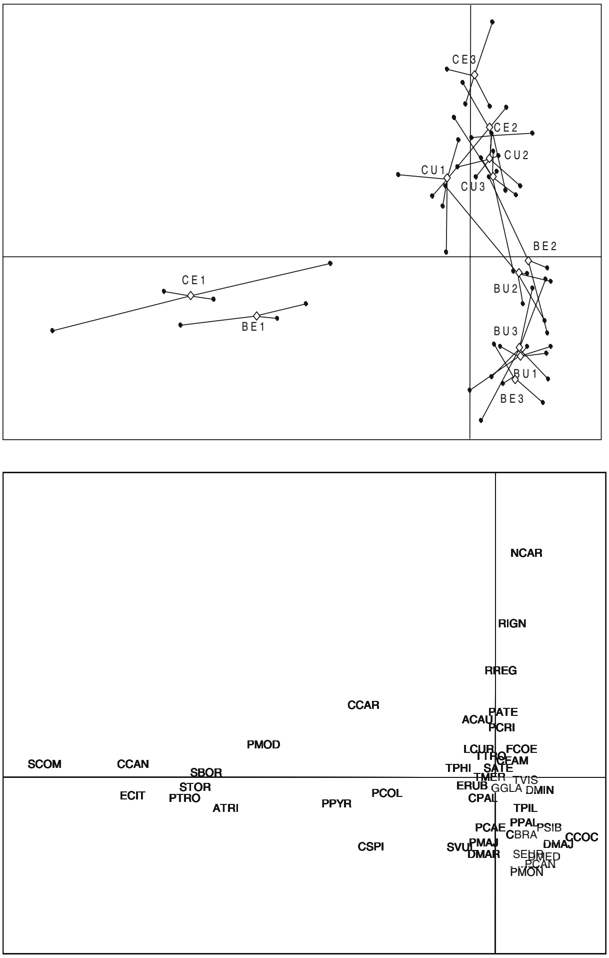


**Fig. 5** Scatterplot of the between group analysis of the bird community data at the sample plot level. Top plot: sample plots (black dots) are linked to the mean position (diamond) of their silvicultural system and stage identified by the following code: EC = Even-aged Conifer; EB = Even-aged Beech; UC = Uneven-aged Conifer; UB = Uneven-aged Beech, the final number indicating the stage (see text and Fig. 2). Bottom plot: Ordination of the bird species on the same axes. The code of the species is based on the first genus letter and the three letters of the scientific name (Table 3). Their positions have been slightly modified for a better readability

but the even-aged and uneven-aged plots in these groups were not separated. *Sylvia communis*, *Emberiza citrinella* and *Carduelis cannabina* were positively associated with even-aged first stage plots, while *Regulus* species and *Nucifraga caryocatactes* were positively associated with coniferous plots. No particular species seemed to be associated with the beech plots, since most of the species close to the position of these plots were close to the origin of the factorial plan and thus were common in most of the samples (Fig. 5).

### *Silvicultural systems analysis*

Conifer plots were separated ($P < 0.001$) from the other ones on the first axis of the between group analysis (Fig. 6). Even-aged beech forests were separated from the other

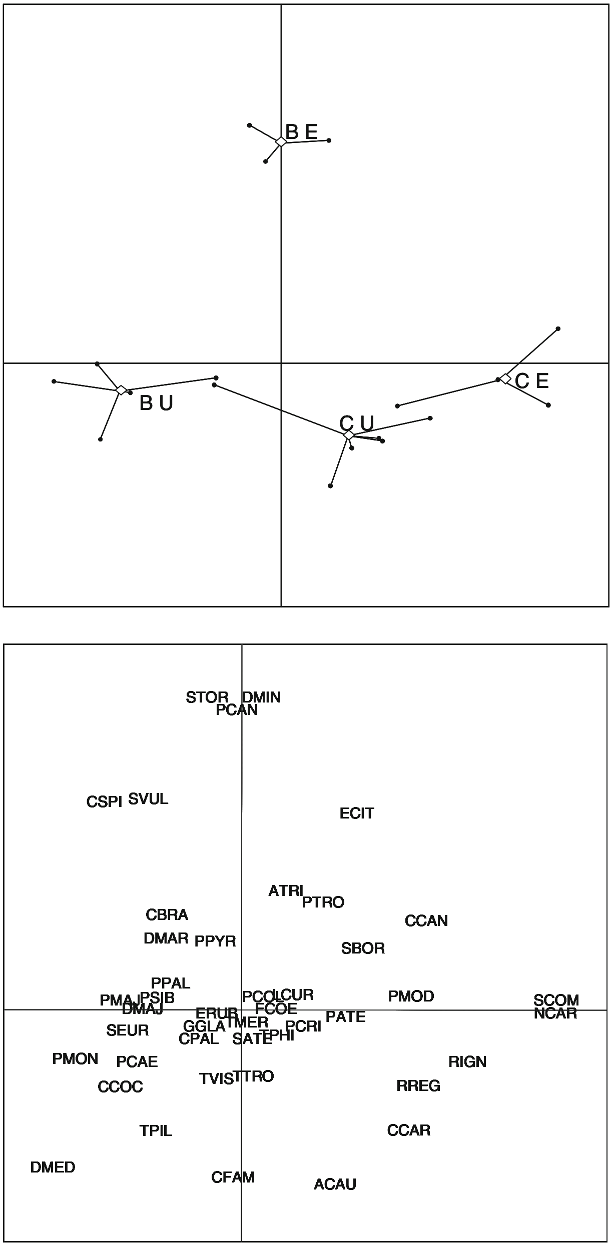


**Fig. 6** Scatterplot of the between group analysis of the bird community data at the silvicultural system level. Top plot: forest (black dots) are linked to the mean position (diamond) of their silvicultural system identified by the following code: EC = Even-aged Conifer; EB = Even-aged Beech; UC = Uneven-aged Conifer; UB = Uneven-aged Beech (see text and Fig. 2). Bottom plot: Ordination of the bird species along the same axes. The code of the species is based on the first genus letter and the three letters of the scientific name (Table 3). Their positions have been slightly modified for a better readability

groups on the second axis, with a lower variability of their composition (distribution along axes). Cutblock size showed a significant effect ($P < 0.001$) in beech forests. *Regulus* species, *Nucifraga caryocactactes*, *Sylvia communis* and *Carduelis carduelis* were associated with the coniferous forests; *Dendrocopos minor*, *Saxicola torquata* and *Picus canus* were associated with the even-aged beech, *Dendrocopos medius* was associated with uneven-aged beech forests.

## Discussion

### Stand composition: conifer vs. beech

Although some studies have identified little impact of tree species composition on bird communities (Müller 1987; Patterson et al. 1995; Donald et al. 1998), most authors have found, as we have, a greater diversity in broadleaf forests compared with coniferous forests of similar stages, at plot level (Moss 1978; James and Wamer 1982; Bibby et al. 1985; Lebreton et al. 1987; Lebreton and Choisy 1991; Baguette et al. 1994; Solonen 1996; Gjerde and Saetersdal 1997) as well at larger levels including the whole silvicultural cycle (Jokimäki and Huhta 1996; Drapeau et al. 2000). Conifer forests seem to attract only few bird species, as suggested by Drapeau et al. (2000). In the Ardenne region, the total bird species richness in mature conifer plantation is estimated to be 43 species with a mean richness per plot of 13 species, while the estimations for beech forests are 44 species for the total richness and 16 species for the mean richness per plot (Paquet et al. 2006). However, historical factors may play an important role in that pattern because Norway spruce stands have been planted for about only 150 years in Belgium and thus bird communities may have not adapted yet to this new habitat.

### Stand structure: even-aged vs. uneven-aged silvicultural systems

Bird community was more related to the dominant tree species (beech vs. conifer) than to cutblock size (Baguette et al. 1994; Jokimäki and Huhta 1996; Kirk and Hobson 2001). The only differences identified were related to the first stages, especially with bird composition: the between group analysis at plot level clearly showed that the bird composition of the first stage of even-aged systems, whatever the tree composition, was different from the other stages (Fig. 5). The species more associated to first stages of even-aged forests were mainly species known to be able to live in open habitats, having adapted to the practice of large clear-cuts (Paquet et al. 2006), while smaller logged areas in uneven-aged forests seem to have fewer associated species. Paquet et al. (2006) demonstrated that the species associated to the open areas in forest are not intermediate between the typical bird communities from agricultural habitat and forests, but were "specific" and contributed to 38.6% to the conservation value in large open areas.

These results do not confirm the main hypothesis of the paper, that uneven-aged management of planted conifer forests improves their bird conservation value. However, this conclusion should be moderated by the spatial dimension of even-aged and uneven-aged silvicultural systems, which has not been taken into account in this study (Picket et al. 1989; Kotliar and Wiens 1990). Even-aged system produces a coarser grain spatial pattern of heterogeneity than uneven-aged systems, with larger patches of even-aged trees. This induces edge-effects that may also have an influence on bird species distribution (Deconchat and Balent 2001).

Stand age: bird diversity according to silvicultural stages

Bird species composition in even-aged stage 1, i.e. large cutblocks, had a sharp contrast with stage 2 and 3. It was characterized by species known to be associated with open habitat conditions (Haila et al. 1980; Fuller and Moreton 1987; Baguette et al. 1994; Jacob 1996). Though Bibby et al. (1985) suggested that very few species require large clear-cuts, a number of species preferred even-aged stage 1 as it has been already noticed by Paquet et al. (2006). We were surprised not to obtain a higher species richness in stage 1 than in stages 2 and 3, as did a number of authors (Müller 1987; Bersier and Meyer 1994, Patterson et al. 1995; Jokimäki and Huhta 1996; Fuller and Green 1998). Indeed, species richness can greatly vary in young stands in plantations (Frochot 1971; Bibby et al. 1985), as well as in natural forest, even under strong disturbances such as coppice clear-cuts (Deconchat and Balent 2001).

Some authors have identified differences in bird communities between medium-aged and mature stands (Fuller and Moreton 1987; Lebreton and Pont 1987) with some bird species associated with old and senescent trees. We did not identify such a pattern, probably because of the intensive silviculture practiced in the Ardenne, based on short rotations, high densities and systematic removal of diseased and dead trees. At stage 3 in our study area, trees were not very large (Table 2), and hollow or dead trees were rare, which makes a difference with the same stage observed in less intensive contexts.

## Conclusion

The results confirm the strong impact of tree species composition on bird species richness, abundance and composition. In the Belgian Ardenne, the massive introduction of spruce plantations has allowed some new species to breed (e.g. *Nucifraga caryocatactes*) but their bird diversity is clearly of lower conservation value than in the beech forests they have supplanted (Ledant et al. 1983). The conversion of even-aged conifer plantations to uneven-aged management (Schütz 2001), which has been proposed as a way to improve biodiversity in conifer forests, does not seem to improve their ability to shelter richer or more diverse bird community than in even-aged plantations. Even-aged management in beech forest was suspected to have negative impacts on biodiversity (Paquet et al. 2006). This opinion is not supported by the results of our study. We observed that the first stage after clear-felling on large zones seemed to offer temporary habitats for species also inhabiting fallow areas and extensive meadows (Delvaux 1998; Paquet et al. 2006), and species richness and composition do not differ much in simple (even-aged) and more complex (uneven-aged) canopies of the same age (stage 2 or 3).

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