Available online at www.sciencedirect.com
SCIENCE DIRECT®

Forest Ecology and Management 209 (2005) 101–115

Forest Ecology and Management

www.elsevier.com/locate/foreco

Effects of strip and single-tree selection cutting on birds and their habitat in a southwestern Quebec northern hardwood forest

Frédérik Doyon [a,*], Daniel Gagnon [b], Jean-Francois Giroux [b]

[a] *Institut Québécois d'Aménagement de la Forêt Feuillue, 58, rue principale, Ripon, Que., Canada J0V 1V0*
[b] *Groupe de Recherche en Écologie Forestière Interuniversitaire, Université du Québec à Montréal, C.P. 8888, Succ. Centre-Ville, Montréal, Que., Canada H3C 3P8*

Abstract

In the northern hardwood forest of northeastern North America, ecological and social perceptions call for forest management systems using reduced-impact silviculture such as single-tree selection cutting and small clearcuts. When applied over large areas, single-tree selection cut and small clearcut systems are likely to generate different local habitat structures and spatio-temporal habitat distribution in the landscape. This study assessed the effects of strip cutting and single-tree selection cutting on forest breeding birds when extensively applied in a northern hardwood forest in southwestern Quebec, a decade after timber harvest. Birds were surveyed twice during two consecutive breeding seasons by 270 point counts, equally distributed in a single-tree selection cut forest, a strip cut forest, and an untreated forest. At each point count, habitat features and horizontal heterogeneity of these features were measured. Managed forest habitats had a much more developed understory, fewer snags and more downed woody debris. Horizontal heterogeneity was higher in the strip cut forest and lower in the single-tree selection cut forest. Of the 20 bird species analyzed, 13 showed a difference in abundance between at least two of the three treatments. *Dendroica pensylvanica* was mostly seen in the treated forests while *Dendroica virens* and *Seiurus aurocapillus* were more abundant in the untreated forest. *Pheucticus ludovicianus* was twice as abundant in the strip cut forest, while *Catharus ustulatus* was more frequently observed in the single-tree selection cut forest. Habitat vertical structure variables that differed among the three treatments were the most correlated with bird abundance. The results of this study support the use of a mix of silvicultural systems within the same forest in order to sustain habitat diversity for maintaining the regional avian cortege.

Keywords: Coarse woody debris; Passerines; Low-impact silviculture; Vertical and horizontal habitat structure; Forest management; Biodiversity

* Corresponding author. Tel.: +1 819 983 2206; fax: +1 819 983 6588.
E-mail address: fdoyon@iqaff.qc.ca (F. Doyon).

0378-1127/$ – see front matter
doi:10.1016/j.foreco.2005.01.005

1. Introduction

Managing forests for timber affects bird communities at the stand level by altering the vegetation composition of the habitat (Temple et al., 1979; Holmes and Robinson, 1981), the vertical (MacArthur, 1958; Anderson and Shugart, 1974; James and Wamer, 1982; Probst et al., 1992) and the horizontal habitat structure (Wiens, 1974; Freemark and Merriam, 1986), and the availability of coarse woody debris (Raphael and White, 1984). Many studies have looked at the effects of timber harvesting on songbirds in northern hardwood forests, particularly after clearcutting (Conner and Adkisson, 1975; Crawford et al., 1981; Maurer et al., 1981), and have related it to some habitat variables. However, alternative silvicultural methods such as small clearcut systems (≤10 ha) (Yahner, 1984; Freedman et al., 1981; Lent and Capen, 1995) and single-tree selection cutting (Webb et al., 1977; Whitcomb et al., 1977; Maurer et al., 1981; and Hagan and Grove, 1996) have been far less studied.

In Quebec, clearcutting in northern hardwood forest has given rise to public concern in recent years, mainly because of its negative impacts on biological and aesthetical values (Anonymous, 1991). Recently, low-impact forest management systems such as small clearcut systems and single-tree selection cutting have been proposed as alternatives to large clearcuts in northern hardwood stands (Anonymous, 1997). Because these systems differ in size, intensity, frequency, and in the pattern of disturbance, local habitat structures and spatio-temporal habitat distribution in the landscape should be quite different. This is also true when comparisons are made with unmanaged forests under a typical northern hardwood natural disturbance regime (Runkle, 1985, 1990; Frelich and Lorimer, 1991; Seymour et al., 2002).

In this study, our objective was to assess the effects on forest birds of strip cutting and single-tree selection cutting, extensively applied in a northern hardwood forest, a decade after timber harvest. More specifically, we wanted to: (1) identify key habitat variables, in terms of vegetation composition, vertical and horizontal structure, and coarse woody debris modified by the two harvesting systems; (2) determine which bird species were affected by the harvesting systems; (3) determine correlations between habitat structure and bird species abundance.

2. Methods

2.1. Study area

Field work was conducted in the Gatineau Experimental Forest (GEF), a 36 km^2 forest located in southwestern Quebec, 65 km north of Ottawa (45°45′N, 76°05′W). The vegetation and the ecological conditions of the GEF have been well-described and mapped (Majcen et al., 1985, 1986) and are typical of the L-4c section of the Great Lakes-St. Lawrence River forest region (Rowe, 1972). The GEF sits in an extensively forested region (approximately 95%) (Robitaille and Saucier, 1998) dominated by northern hardwood stands composed of sugar maple (*Acer saccharum* Marsh.), beech (*Fagus grandifolia* Erh.), yellow birch (*Betula alleghaniensis* Britton), American basswood (*Tilia americana* L.) and white ash (*Fraxinus americana* L.), with some eastern hemlock (*Tsuga canadensis* L.), on acid-rock glacial tills. Mixedwood stands, composed of red maple (*Acer rubrum* L.), balsam fir (*Abies balsamea* L.) and white spruce (*Picea glauca* Moench.), are found on fluvio-glacial deposits in lowlands, while red oak (*Quercus rubra* L.) and white pine (*Pinus strobus* L.) stands are found on the thin, well-drained upland till deposits. Early secondary succession stands are usually composed of red maple, trembling aspen (*Populus tremuloides* Michx.), largetooth aspen (*Populus grandidentata* Michx.) and white birch (*Betula papyrifera* Marsh.).

The GEF is divided into two large units, the Doyley Lake Forest (approximately, 1100 ha) and the Isabelle Lake Forest (approximately, 2500 ha), which are located 8 km apart. Between 1982 and 1985, the entire Doyley Lake Forest was strip cut and about half of the Isabelle Lake Forest was single-tree selection cut. All stands of the GEF were mature and composed of sawtimber-sized trees prior to treatments. In the strip cut forest, all stems with ≥10 cm diameter at breast height (dbh, 1.3 m) were to be removed in one of three strips every 40 years. Different widths of strips, including 30, 60 and 90 m, were used. At the time of the study, only one strip had been cut and the strip was in its sapling-to-pole stage. Single-tree selection cutting varied in intensity between 25% and 35% of the basal area, removing trees from all commercial (dbh ≥ 10 cm) diameter classes while trying to obtain

Table 1
Proportion of sampling plots by habitat types and availability of habitat types prior to treatment in strip cut, single-tree selection cut and untreated forests in Gatineau Experimental Forest, southwestern Quebec

Habitat types	Strip cut plots, % (availability, %)	Selection cut plots, % (availability, %)	Untreated plots, % (availability, %)	Total plots, % (availability, %)
Tolerant hardwoods	54 (32)	74 (66)	64 (38)	64 (47)
Intolerant hardwoods	30 (45)	13 (12)	17 (22)	20 (25)
Mixedwood-conifer	16 (23)	13 (22)	19 (40)	16 (28)

a balanced residual stem diameter distribution (Nyland, 1987; Majcen et al., 1990). The other half of the Lake Isabelle Forest, which served as the ‘‘untreated forest’’, has never been harvested and is representative of the regional forest vegetation. No sign of sugar maple decline was observed in the GEF (Lachance, 1985).

2.2. Sampling

2.2.1. Habitat

The forest was stratified into shade-tolerant hardwood, intolerant hardwood and mixedwood-conifer habitat types (Table 1), using forest cover maps (Anonymous, 1986; Majcen et al., 1986). Sampling plots were then randomly located across the three treatment forests but with the spatial constraint that the plots had to be $\geq$250 m apart and 100 m from any body of water or wetland. We strove to keep the distribution of the plots balanced across the habitat types in the three forests (Table 1).

We sampled 270 plots (91 in strip cut, 95 in single-tree selection cut, and 84 in untreated forest) during summer 1993. Thus, when we started the study, treatments had been applied since 9 to 12 years (including the year being treated). Each plot measured 60 m $\times$ 60 m and consisted of five 80 m^2 circular micro-plots, located at the four corners and at the center. Because of the random nature of the sampling design, some micro-plots in the strip cut forest were in cut areas, some were in uncut areas, and some straddled the two. In each micro-plot, we recorded the species and the dbh of all living ($\geq$10 cm dbh) and dead trees ($\geq$5 cm dbh) (hereafter called snags), with a caliper. Snags were classified in five decay classes, using characteristics described in Doyon et al. (1999). We visually estimated vegetation cover in classes (0–1%, 2–5%, 6–25%, 26–40%, 41–60%, 61–80%, 81–100%) for different height layers (upper tree: $\geq$12 m, lower tree: $\geq$6 and $<$12 m, upper shrub: $\geq$1 and $<$6 m, lower shrub: $<$1 m, herb, and moss) divided in vegetation types (upper and lower tree: tolerant hardwood, intolerant hardwood, conifer, red oak; upper shrub: tolerant hardwood, intolerant hardwood, conifer; lower shrub: hardwood, conifer, other; herb: large-leaved, fern, graminoid). We also estimated soil moisture (1 [very dry] to 6 [hydric]) and measured duff thickness and % slope at the plot center. In each micro-plot center, a 5-m transect was laid on the ground following a random orientation and was used to sample downed woody debris (DWD) and bare ground. For all woody debris (diameter $\geq$ 5 cm) crossing the transect, we noted the diameter at the crossing point and the length of the entire woody debris and evaluated the decay stage following the same five classes used by Tyrrell and Crow (1994). Each time the transect crossed a rock (crossing section $\geq$ 5 cm) or bare ground, we noted the length of that crossing section. Areal measures of density for DWD and bare ground patches were obtained using DeVries’ (1974) unbiased estimator. DWD volume was obtained using Van Wagner’s (1982) equation. For an areal measure of bare ground per unit area, we assumed that each measured bare ground length represented the diameter of a circular patch. We then added areas of all patches and divided by the area of a circle with a diameter equal to the transect length.

In addition to these variables, which described different covers (*sensu* Rotenberry and Wiens, 1980) within the plot, we also evaluated structural heterogeneity in both the vertical and the horizontal planes. We computed an index of ‘‘vegetation vertical inertia’’ to express the mid-point location of the vertical distribution of leaf biomass. This was obtained by summing the mid-height point of each vegetation height class multiplied by its corresponding cover value, and then dividing by the sum of the cover of all vegetation height classes. We applied the Shannon–

Wiener diversity index (Shannon, 1948) using the cover of the different vegetation layers (upper tree, lower tree, upper shrub, lower shrub, herbaceous, and moss) to express the vertical diversity at the micro-plot scale as well as at the plot scale. At the micro-plot scale, we averaged the vertical diversity index of the five micro-plots. At the plot scale, we first summed the cover of each layer over the five micro-plots and then computed the index with these summed values.

Secondly, inspired by previous work (Wiens, 1974; Roth, 1976; Freemark and Merriam, 1986), we created an index of horizontal heterogeneity (HH) (Eq. (1)):

$$\mathrm{HH}_{xp} = \frac{\sum_{i=1}^{5}\sum_{j=i+1}^{5}|x_{ip}-x_{jp}|}{\left(\sum_{k=1}^{270}\sum_{i=1}^{5}\sum_{j=i+1}^{5}|x_{ik}-x_{jk}|\right)/270} \qquad (1)$$

where x is the variable evaluated for horizontal heterogeneity and p is the plot in which the HH is evaluated.

This index gives a relative value of the HH for variable x in a plot p when compared with all 270 plots. A total index of HH for each plot was obtained by summing the HH values of the different vegetation layers (upper tree, lower tree, upper shrub, lower shrub and herb total cover).

2.2.2. Birds

Birds were censused during two consecutive years (1993 and 1994), twice during the breeding season (period 1, June 1–30; period 2, July 2–23) using the fixed-radius point count method (Blondel et al., 1970), at each of the 270 sampling plots. We alternated the surveys among the three treatments during the entire sampling season to reduce potential seasonal bias. Observers differed between years but each was trained for two weeks before the census period using exercises suggested by Kepler and Scott (1981). After many tests of distance estimation (Scott et al., 1981) in different habitats, we settled for a 60 m radius. All counts were conducted between 05:15 and 11:00. Surveyors were asked to stop sampling when wind or rain conditions could reduce their ability to hear birds. After 2 min of immobility, the point count was started and, for a period of 10 min, all birds seen or heard were recorded. Any additional individual of a species was noted only if there was evidence of it being distinct from those previously recorded.

2.3. Data analysis

Differences in habitat structure among the three forests were compared for each habitat variable using ANOVA. Because DWD volume distributions were highly skewed, we log-transformed ($\log(x+1)$) the DWD variables before using the ANOVA. When a significant effect was found ($P \leq 0.05$), LSD a posteriori tests were conducted to detect significant differences among means ($P \leq 0.05$). Pearson correlations were computed between habitat cover variables and their HH to verify if HH brought new information.

Discriminant analysis was used to detect which variables contributed the most in differentiating the three forests. Even if discriminant analysis is quite robust to deviation from multinormality (Williams, 1983), variables that were not normal were transformed in order to better approximate this condition. Equality of group covariance was tested using Box's M-test and prior probabilities were attributed according to the number of plots in each forest. Variables were introduced in the discriminant model through a stepwise procedure, selecting the variables to create a function which minimizes the sum of the unexplained variation between groups, with a $P(F)$ to enter fixed at 0.01 and $P(F)$ to remove fixed at 0.05 (SPSS Inc., 1988). Multicollinearity ($|r| > 0.50$) was tested with previously selected variables before introducing the new variable in the discriminant model.

For each year, the maximum number of individuals of a species detected in a sample plot during any of the two survey periods was used as an index of relative abundance. Statistical analyses were conducted only for species detected in more than 40 sample plots (15%). For these species, we compared detections between years and then among the three forests for each year separately with the Kruskal–Wallis test. When a significant effect was found ($P \leq 0.05$), differences among treatments were tested using a multiple rank comparison test ($P \leq 0.05$, Shirley, 1987). We classified the birds in foraging and nesting stratigraphic guilds (DeGraaf et al., 1985; Freemark and Merriam, 1986; Ehrlich et al., 1988). Guild numbers of individuals were compared between the 2 years, then among the three forests for each year separately with ANOVA mean comparisons (SPSS Inc., 1988). When a significant effect was found

Table 2
Vegetation layer cover (%) in strip cut, single-tree selection cut and untreated forests in Gatineau Experimental Forest, southwestern Quebec

Variables	P[a]	Strip cut	Selection cut	Untreated
Upper tree layer (UT)	$\leq$0.001	50.5 ± 1.8a[b]	65.8 ± 1.8b	72.4 ± 1.9c
Low tree layer (LT)	$\leq$0.001	44.0 ± 1.8a	43.7 ± 1.7a	53.0 ± 1.8b
Upper shrub layer (US)	$\leq$0.001	52.3 ± 1.8a	49.7 ± 1.8a	30.4 ± 1.9b
Low shrub layer (LS)	$\leq$0.001	29.0 ± 1.67a	49.5 ± 1.64b	39.7 ± 1.74c
Herb layer (HT)	$\leq$0.001	35.9 ± 2.05a	19.0 ± 2.00b	22.3 ± 2.13b
Moss layer (M)	N.S.	4.82 ± 0.52	3.87 ± 0.52	5.93 ± 0.83

[a] One-way ANOVA.
[b] Mean ± 1S.E. Means followed by different letters indicate differences among treatments.

($P \leq 0.05$), differences among treatments were tested using the LSD test ($P \leq 0.05$). To detect which variables could potentially cause the differences in abundance observed among the three forest sections, species abundance (summed over the 2 years) was rank-correlated with the selected discriminant habitat variables.

3. Results

3.1. Habitat

A decade after the harvest, high vegetation layer cover (upper and lower tree combined) were 31% and 16% less important in the strip cut and single-tree selection cut forests, respectively, than in the untreated forest (Table 2). The harvest effect was still reflected in a reduced basal area (Table 3). Creating canopy openings in the treated forests facilitated the development of understory layers; upper shrub cover was considerably higher in the two treated forests (Table 2). However, the two treatments differed from each other in the percent cover of the two lowest vegetation layers. Herb layers have benefited from the type of openings executed in the strip cut while the lower shrub layer was more developed in the single-tree selection cut forest. As a result of these differences in vegetation profiles, the vegetation vertical inertia showed its lowest mean value in the strip cut forest and its highest mean value in the untreated forest (Table 3).

This increase in cover of the lower vegetation layers compensated for the loss in upper layers as

Table 3
Habitat structure variables and environmental variables in strip cut, single-tree selection cut and untreated forests in Gatineau Experimental Forest, southwestern Quebec

Variables (abbreviation)	P[a]	Strip cut	Selection cut	Untreated
Total vegetation cover (%)[b]	$\leq$0.01	216 ± 3.4a[c]	231 ± 3.3b	223 ± 3.5ab
Micro-plot vertical diversity	$\leq$0.001	1.31 ± 0.016a	1.37 ± 0.009b	1.36 ± 0.011b
Plot vertical diversity	N.S.	1.55 ± 0.012	1.53 ± 0.010	1.53 ± 0.011
Vegetation vertical inertia (m)	$\leq$0.001	6.51 ± 0.17a	7.24 ± 0.12b	8.08 ± 0.12c
Total HH index	$\leq$0.001	5.52 ± 0.15a	4.75 ± 0.13b	4.72 ± 0.13b
dbh (cm)	$\leq$0.001	19.3 ± 0.35a	21.6 ± 0.35b	20.1 ± 0.37a
dbh standard deviation (cm)	$\leq$0.049	1.8 ± 0.8ab	2.0 ± 0.9a	1.7 ± 0.7b
Basal area ($m^2 ha^{-1}$)	$\leq$0.001	21.1 ± 0.9a	21.8 ± 0.6a	25.7 ± 0.8b
Tree species richness	$\leq$0.001	6.3 ± 0.2a	5.1 ± 0.2b	6.6 ± 0.2a
Duff thickness (cm)	N.S.	2.6 ± 0.06[a]	2.8 ± 0.07	2.7 ± 0.10
Moisture (1–7)	N.S.	2.9 ± 0.04	2.9 ± 0.03	2.9 ± 0.05
Slope (%)	N.S.	16.7 ± 0.8	17.7 ± 0.8	18.4 ± 0.8

[a] One-way ANOVA.
[b] Mean of the sum of each vegetation cover variable over the five micro-plots. As vegetation layers overlap vertically, it can be greater than 100%.
[c] Mean ± 1S.E. Means followed by different letters indicate differences among treatments.

Table 4
Coarse woody debris variables in strip cut, single-tree selection cut and untreated forests in Gatineau Experimental Forest, southwestern Quebec

Variables	P[a]	Strip cut	Selection cut	Untreated
DWD density ($\times$1000 ha^{-1})[b]	$\leq$0.001	1.41 $\pm$ 0.19a[c]	1.72 $\pm$ 0.11a	0.91 $\pm$ 0.20b
Volume-weighted DWD decay class average[d]	$\leq$0.001	3.3 $\pm$ 0.05a	2.8 $\pm$ 0.05b	3.2 $\pm$ 0.06a
Stand DWD volume (m^3 ha^{-1})[b]	$\leq$0.05	46.8 $\pm$ 12.5ab	60.7 $\pm$ 7.1a	36.2 $\pm$ 13.0b
Snag density (ha^{-1})	$\leq$0.001	119 $\pm$ 9a	97 $\pm$ 9a	156 $\pm$ 9b
Decayed[e] snag density (ha^{-1})	$\leq$0.001	68 $\pm$ 5a	56 $\pm$ 6a	98 $\pm$ 8b
Snag basal area (m^2 ha^{-1})	$\leq$0.001	2.0 $\pm$ 0.26a	2.0 $\pm$ 0.25a	3.3 $\pm$ 0.27b

[a] One-way ANOVA.
[b] Mean $\pm$ 1S.E. Means followed by different letters indicate differences between treatment.
[c] ANOVA on the log-transformed ($\log(x + 1)$) variable.
[d] On a 5-classes increasing scale (1 = almost intact, 5 = almost completely decayed).
[e] Snags of decay class of 3 and more.

shown by the weak difference in overall vegetation cover (Table 3). The vertical diversity, when assessed at the micro-plot, was higher in the single-tree selection cut and the untreated forest than in the strip cut forest. Average dbh was slightly higher in the single-tree selection cut forest than in the two others, with a wider array of size classes as expressed by dbh standard deviation. Tree species richness was lowest, by one species, in the single-tree selection cut forest. Environmental factors, as expressed by duff thickness, soil moisture and slope, were similar across the three treatments (Table 3). Snags and decayed snags were more abundant in the untreated forest (Table 4). Inversely, the DWD density and volume were higher in the treated forests, particularly in the single-tree selection cut forest, where DWD were less decayed.

For many habitat variables, the average value over the five micro-plots was not correlated ($r \leq 0.25$) with its horizontal heterogeneity, suggesting that the spatial distribution of the variable was not related to its abundance. Strip cutting has undoubtedly raised the internal habitat patchiness, as expressed by the total HH index (Table 2) and other horizontal heterogeneity variables (Table 5).

Eight habitat variables were selected by discriminant analysis to differentiate treatments (Table 6). The inclusion of these variables significantly improved the fit of the model (Wilk's lambda $\geq$ 0.276, d.f. = 16, 7;

Table 5
Horizontal heterogeneity of habitat variables (vegetation layer cover, structure and some essential habitat elements), in strip cut, single-tree selection cut and untreated forests in Gatineau Experimental Forest, southwestern Quebec

Variables	P[a]	Strip cut	Selection cut	Untreated	r[c]
Upper tree layer (%)	$\leq$0.001	1.24 $\pm$ 0.05a[b]	0.90 $\pm$ 0.05b	0.84 $\pm$ 0.05b	-0.21^{***}
Low tree layer (%)	N.S.	1.06 $\pm$ 0.04	0.95 $\pm$ 0.04	0.99 $\pm$ 0.04	-0.04
Upper shrub layer (%)	N.S.	1.07 $\pm$ 0.04	1.00 $\pm$ 0.04	0.93 $\pm$ 0.04	0.13^{*}
Low shrub layer (%)	N.S.	0.94 $\pm$ 0.04	1.06 $\pm$ 0.04	1.00 $\pm$ 0.04	0.15^{*}
Herb layer (%)	$\leq$0.001	1.21 $\pm$ 0.07a	0.83 $\pm$ 0.07b	0.96 $\pm$ 0.07b	0.19^{**}
Total vegetation cover (%)	$\leq$0.05	1.08 $\pm$ 0.05a	0.98 $\pm$ 0.04ab	0.93 $\pm$ 0.04b	-0.03
Vertical diversity (micro-plot)	$\leq$0.001	1.33 $\pm$ 0.03a	0.90 $\pm$ 0.02b	0.76 $\pm$ 0.01b	0.00
Vegetation vertical inertia (m)	N.S.	1.00 $\pm$ 0.03	1.04 $\pm$ 0.04	0.96 $\pm$ 0.03	-0.70^{***}
DWD density (ha^{-1})	$\leq$0.01	0.99 $\pm$ 0.05ab	1.12 $\pm$ 0.05a	0.88 $\pm$ 0.06b	0.09
Stand DWD volume (m^3 ha^{-1})	N.S.	1.00 $\pm$ 0.19	0.91 $\pm$ 0.19	1.10 $\pm$ 0.20	0.30^{***}

[a] One-way ANOVA.
[b] Mean $\pm$ 1S.E. Means followed by different letters indicate differences between treatments.
[c] Pearson correlations between the HH of a variable and the variable are provided.
* $P \leq 0.05$.
** $P \leq 0.01$.
*** $P \leq 0.001$.

Table 6
Canonical discriminant functions of habitat variables that best discriminate between strip cut, single-tree selection cut and untreated forests in Gatineau Experimental Forest, southwestern Quebec

Habitat variables[a] (abbreviations)	Function 1	Function 2
HH of Upper shrub intolerant hardwood (HH US_IH)	0.434	-0.236×10^{-2}
Upper shrub tolerant hardwood (%) (US_TH)	0.432×10^{-2}	0.773×10^{-2}
Upper shrub intolerant hardwood (%) (US_IH)	0.145×10^{-1}	0.189×10^{-2}
Lower shrub (%) (LS)	-0.622×10^{-2}	0.535×10^{-4}
Basswood density (ha^{-1}) (Tia)	0.272	-0.311×10^{-2}
DWD density (ha^{-1}) (# DWD)	-0.460×10^{-1}	0.131
HH of Upper shrub tolerant hardwood (HH US_TH)	0.988×10^{-1}	0.808
Upper tree intolerant hardwood (UT_IH)	0.314×10^{-2}	-0.193×10^{-2}
Constant	−0.690	−2.583

[a] Variables are listed in order of selection.

$P < 0.001$, Bartlett's *V*-test). Equality of within-group covariation was not obtained (Box's $M = 536.9$, d.f. = 72, $P < 0.000$) because of a higher within-group variation in the strip cut forest covariance matrix. However, the large ratio of samples to variables probably reduced the likelihood of obtaining unstable classification results (Brennan et al., 1986, p. 181). A total of 78.5% of the plots were correctly re-classified by the discriminant functions.

Structurally, forests under single-tree selection cutting were much more similar to what was observed in the untreated forest than in the strip cut forest. Indeed, the first canonical function, which expressed 76.6% of the explained variance, discriminated between the strip cut and the two other treatments. The second canonical function, which expressed 23.4% of the explained variance, served to discriminate between single-tree selection cut and untreated forests. The first canonical function was positively correlated with HH in intolerant hardwood upper shrub cover, intolerant hardwood upper shrub cover and density of basswood, and negatively correlated with low shrub cover. The second canonical function was positively correlated with tolerant hardwood upper shrub cover, HH in tolerant hardwood upper shrub cover and density of DWD, and negatively correlated with intolerant hardwood upper tree cover.

3.2. Birds

Over 2 years, 5360 observations of 74 species were made during the 180 h of sampling (see Doyon (2000) for a complete list). Total bird observations were higher ($P = 0.039$) in the single-tree selection cut forest (10.40 obs./plot ± 0.28S.E.) than in the strip cut (9.47 obs./plot ± 0.29S.E.) and untreated forests (9.57 obs./plot ± 0.29S.E.). About 95% of these observations were from 20 species that fulfilled the frequency criterion of 15% of occurrence for analysis. About half of the studied species (11 species in 1993 and 8 in 1994) responded to the treatment effect in at least 1 year ($P \leq 0.05$, Table 8). Of these 11 species, five were more abundant in the strip cut than in the untreated forest, and four were more abundant in the single-tree selection cut than in the untreated forest. Black-throated green warblers, ovenbirds and white-breasted nuthatches were more abundant, at least 1 year, in the untreated forest. Least flycatcher and great crested flycatcher also had a tendency to avoid both treated forests, but the differences in abundance were not significant ($P > 0.05$).

Species classified in the shrub/lower canopy foraging and nesting stratum guilds were particularly more abundant in the treated forests (Table 7). Of this stratigraphic guild, rose-breasted grosbeak was more abundant in strip cut forest while American redstart and chestnut-sided warbler were associated with the two types of treated forests in both years (Table 8). Of this stratigraphic guild, the black-throated blue warbler was strongly associated with the single-tree selection cut forest but not with the strip cut forest. Species like the black-throated green warbler and the blackburnian warbler, which accomplish much of their activities in the upper canopy, were more abundant in the untreated and the single-tree selection cut forests. Of that stratigraphic guild, the red-eyed vireo did not differ in abundance among the three forests. There was

Table 7
Mean number of bird detections per point count grouped by foraging stratum and nesting stratum guilds in strip cut, single-tree selection cut, and untreated forests, in Gatineau Experimental Forest, southwestern Quebec, during summer 1993 and 1994

Species	Year[a]	Strip cut	Selection cut	Untreated	P[b]
Foraging stratum guilds					
Air	93	0.43 ± 0.07a[c]	0.57 ± 0.11a	0.93 ± 0.14b	0.013
	94	0.45 ± 0.09	0.48 ± 0.09	0.68 ± 0.12	0.331
Bark	93	1.35 ± 0.12a	0.92 ± 0.09b	1.30 ± 0.13a	0.033
	94	0.85 ± 0.08	1.03 ± 0.11	0.85 ± 0.09	0.579
Ground	93	3.02 ± 0.18	3.12 ± 0.19	3.13 ± 0.20	0.853
	94	2.38 ± 0.14	2.45 ± 0.13	2.52 ± 0.14	0.697
Shrub/lower canopy	93	3.12 ± 0.23a	3.79 ± 0.25b	1.94 ± 0.16c	<0.001
	94	2.38 ± 0.15a	2.67 ± 0.16a	1.24 ± 0.11b	<0.001
Upper canopy	93	2.46 ± 0.21a	2.84 ± 0.17ab	3.09 ± 0.23b	0.046
	94	2.33 ± 0.13a	2.68 ± 0.13a	3.08 ± 0.17b	0.005
Nesting stratum guilds					
Ground	93	3.67 ± 0.23	3.42 ± 0.20	3.59 ± 0.22	0.764
	94	2.62 ± 0.14	2.97 ± 0.16	2.76 ± 0.18	0.291
Hole	93	1.37 ± 0.13	1.31 ± 0.13	1.55 ± 0.14	0.305
	94	0.80 ± 0.09	0.86 ± 0.10	0.85 ± 0.10	0.985
Shrub/lower canopy	93	2.55 ± 0.19a	3.14 ± 0.22b	1.41 ± 0.14c	<0.001
	94	2.24 ± 0.14a	2.63 ± 0.15b	1.23 ± 0.11c	<0.001
Upper canopy	93	2.76 ± 0.22a	3.37 ± 0.22ab	3.83 ± 0.28b	0.013
	94	2.70 ± 0.16a	2.93 ± 0.15a	3.59 ± 0.18b	0.005

[a] One-way ANOVA. The year with the highest number of detections per point count is underlined when significantly different ($P \leq 0.05$).
[b] One-way ANOVA.
[c] Mean ± 1S.E. Means followed by different letters within each row are significantly different.

no consistency in the response of the bird species of the ground guild to the treatment effect. Of the bark-foraging/hole nesting guild, only the white-breasted nuthatch responded to the treatment effect and was more abundant in the untreated forest (Table 8).

Among the eight discriminant variables, % low shrub cover, % intolerant hardwood low tree cover, % intolerant hardwood upper shrub cover and % tolerant hardwood upper shrub cover were most often significantly correlated with bird abundance (Table 9). Species more abundant in the strip cut forest (American redstart, chestnut-sided warbler, rose-breasted grosbeak and veery) were positively associated with hardwood (intolerant hardwood or tolerant hardwood) cover of the upper shrub layer and density of DWD. On the other hand, species associated with the untreated forest (black-throated blue warbler, black-throated green warbler, blackburnian warbler and Swainson's thrush) decreased with those same variables. Species abundant in the single-tree selection cut forest (American redstart, black-throated blue warbler, chestnut-sided warbler and Swainson's thrush) were positively associated with the percent low shrub cover. Red-eyed vireo showed strong associations with four discriminant variables. Although its abundance was not significantly different among the three treatments, its pattern of association with these discriminant variables was similar to the one of the species showing higher abundance in the single-tree selection cut forest.

4. Discussion

When compared to the untreated forest, three major changes in habitat structure were observed in treated forests: an increase in lower vegetation layers covers, a modification of the habitat horizontal heterogeneity, and a change in the availability of coarse woody debris.

Table 8
Mean number of bird detections per point count in strip cut, single-tree selection cut, and untreated forests, in Gatineau Experimental Forest, southwestern Quebec during summer 1993 and 1994

Species	Year[a]	No. of plots			P[b]
		91	95	84	
		Strip cut	Selection cut	Untreated	
American redstart (*Setophaga ruticilla*)	93	0.62 ± 0.09a[c]	0.93 ± 0.12a	0.15 ± 0.05b	0.000
	94	0.37 ± 0.06a	0.42 ± 0.07a	0.08 ± 0.03b	0.000
Black-and-white warbler (*Mniotilta varia*)	93	0.45 ± 0.07a	0.14 ± 0.04b	0.26 ± 0.05c	0.000
	94	0.29 ± 0.05	0.43 ± 0.06	0.31 ± 0.06	0.151
Black-capped chickadee (*Parus atricapillus*)	93	0.36 ± 0.07	0.44 ± 0.08	0.35 ± 0.07	0.903
	94	0.11 ± 0.03	0.12 ± 0.04	0.10 ± 0.04	0.818
Black-throated blue warbler (*Dendroica cearulescens*)	93	0.44 ± 0.06a	0.88 ± 0.08b	0.61 ± 0.08a	0.000
	94	0.32 ± 0.05a	0.72 ± 0.07b	0.55 ± 0.05b	0.000
Black-throated green warbler (*Dendroica virens*)	93	0.66 ± 0.10a	0.86 ± 0.10a	1.19 ± 0.12b	0.001
	94	0.65 ± 0.08a	0.82 ± 0.08b	1.07 ± 0.07b	0.001
Blackburnian warbler (*Dendroica fusca*)	93	0.15 ± 0.04a	0.48 ± 0.08b	0.52 ± 0.10b	0.001
	94	0.31 ± 0.05	0.43 ± 0.06	0.48 ± 0.08	0.268
Blue jay (*Cyanocitta cristate*)	93	0.09 ± 0.04	0.05 ± 0.03	0.07 ± 0.03	0.761
	94	0.08 ± 0.03	0.10 ± 0.03	0.13 ± 0.04	0.625
Chestnut-sided warbler (*Dendroica pensylvanica*)	93	0.56 ± 0.06a	0.93 ± 0.07b	0.04 ± 0.02c	0.00
	94	0.70 ± 0.07a	0.81 ± 0.08a	0.02 ± 0.02b	0.000
Great crested flycatcher (*Myiarchus crinitus*)	93	0.07 ± 0.03	0.08 ± 0.03	0.15 ± 0.05	0.541
	94	0.05 ± 0.02	0.12 ± 0.04	0.13 ± 0.04	0.315
Hermit thrush (*Catharus guttatus*)	93	0.22 ± 0.05	0.15 ± 0.04	0.23 ± 0.05	0.328
	94	0.20 ± 0.04	0.19 ± 0.04	0.23 ± 0.05	0.948
Least flycatcher (*Empidonax minimus*)	93	0.24 ± 0.07	0.41 ± 0.10	0.62 ± 0.12	0.055
	94	0.25 ± 0.06	0.26 ± 0.07	0.42 ± 0.09	0.342
Ovenbird (*Seiurus aurocapillus*)	93	1.69 ± 0.13a	1.68 ± 0.12a	2.12 ± 0.14b	0.033
	94	1.23 ± 0.08	1.19 ± 0.08	1.30 ± 0.08	0.594
Red-breasted nuthatch (*Sitta Canadensis*)	93	0.20 ± 0.05	0.08 ± 0.03	0.19 ± 0.05	0.089
	94	0.02 ± 0.02	0.02 ± 0.01	0.01 ± 0.01	0.863
Red-eyed vireo (*Vireo olivaceous*)	93	1.25 ± 0.12	1.19 ± 0.10	1.07 ± 0.11	0.419
	94	0.87 ± 0.07	1.02 ± 0.06	0.89 ± 0.07	0.129
Rose-breasted grosbeak (*Pheucticus ludovicianus*)	93	0.36 ± 0.07a	0.15 ± 0.04b	0.18 ± 0.04b	0.023
	94	0.45 ± 0.06a	0.19 ± 0.04b	0.21 ± 0.05b	0.000
Swainson's thrush (*Catharus ustulatus*)	93	0.08 ± 0.04a	0.33 ± 0.06b	0.21 ± 0.05b	0.001
	94	0.07 ± 0.04a	0.30 ± 0.06b	0.14 ± 0.05a	0.000
Veery (*Catharus fuscescens*)	93	0.66 ± 0.08a	0.58 ± 0.08ab	0.37 ± 0.07b	0.041
	94	0.52 ± 0.06a	0.43 ± 0.06ab	0.32 ± 0.06b	0.039
White-breasted nuthatch (*Sitta carolinensis*)	93	0.03 ± 0.02a	0.19 ± 0.05b	0.20 ± 0.05b	0.003
	94	0.02 ± 0.02ab	0.00 ± 0.00a	0.07 ± 0.03b	0.017
Winter wren (*Troglodytes troglodytes*)	93	0.11 ± 0.03	0.07 ± 0.03	0.11 ± 0.04	0.693
	94	0.08 ± 0.03	0.13 ± 0.04	0.17 ± 0.04	0.189
Yellow-bellied sapsucker (*Sphyrapicus varius*)	93	0.51 ± 0.07	0.33 ± 0.05	0.44 ± 0.07	0.281
	94	0.47 ± 0.07	0.49 ± 0.06	0.35 ± 0.05	0.280

[a] One-way ANOVA. The year with the highest number of detections per point count is underlined when significantly different ($P \leq 0.05$).
[b] One-way ANOVA.
[c] Mean ± 1S.E. Means followed by different letters within each row are significantly different.

Table 9
Spearman correlation coefficients between bird abundance (sum of years 1993 and 1994) and habitat variables discriminating strip cut, single-tree selection cut and untreated forests of Gatineau Experimental Forest, southwestern Quebec

Species	LS[a]	LT_IH	US_IH	US_TH	HH HS_IH	HH HS_TH	# DWD	Tia
American redstart	0.14[*]	−0.19[*]	–	0.47[**]	–	–	–	–
Black-and-white warbler	−0.16[*]	0.28[**]	0.24[**]	−0.18[*]	–	–	–	–
Black-capped chickadee	–	0.24[**]	–	−0.16[*]	–	–	–	–
Black-throated blue warbler	0.33[**]	−0.20[**]	−0.21[**]	–	–	–	–	–
Black-throated green warbler	–	–	−0.15[*]	–	–	–	−0.17[*]	–
Blackburnian warbler	–	–	–	−0.27[**]	–	–	–	–
Blue jay	–	–	–	–	–	–	–	–
Chestnut-sided warbler	0.22[**]	–	–	0.33[**]	–	–	0.17[*]	–
Great crested flycatcher	–	0.16[*]	–	–	–	–	–	–
Hermit thrush	−0.18[*]	0.21[**]	–	–	–	–	–	–
Least flycatcher	0.16[*]	−0.24[**]	−0.17[*]	–	–	–	–	–
Ovenbird	–	–	−0.14[*]	–	–	–	–	–
Red-breasted nuthatch	−0.16[*]	0.24[**]	–	−0.26[**]	–	–	–	–
Red-eyed vireo	0.20[**]	−0.31[**]	−0.21[**]	0.36[**]	–	–	–	0.15[*]
Rose-breasted grosbeak	–	–	0.15[*]	–	–	–	–	–
Swainson's thrush	0.18[*]	–	−0.26[**]	–	−0.20[**]	–	–	–
Veery	–	–	0.18[*]	–	0.14[*]	–	–	–
White-breasted nuthatch	–	–	–	–	–	–	–	–
Winter wren	–	0.14[*]	–	−0.21[**]	–	–	–	–
Yellow-bellied sapsucker	–	–	–	–	–	–	–	–

[a] See Table 6 for abbreviations.
[*] $P \leq 0.05$.
[**] $P \leq 0.01$.

4.1. Vegetation cover

In the treated forests, the reduction of the tree layers through tree harvesting allowed more light to reach the forest floor. This led to the proliferation of understory layers, particularly the upper and lower shrub layers that were important variables to discriminate the habitats of the three forests. This change benefited the shrub/lower canopy foraging and nesting stratigraphic guilds. For example, American redstart and chestnut-sided warbler were 5 and 25 times more abundant, respectively, in the treated forests than in the untreated forest. Both species were first associated to hardwood upper shrub cover, reflecting their preference for high foliage volume (DeGraaf and Chadwick, 1987; Thompson and Capen, 1988; Hagan et al., 1997 and others). These two species have also been observed elsewhere in higher abundance in forests under selection cutting and clearcutting regimes (Webb et al., 1977; Freedman et al., 1981; Welsh and Healy, 1993; Hagan and Grove, 1996). Chestnut-sided warbler was even more stenotypic than American redstart and was practically absent from the untreated forest where early secondary succession habitats were very rare.

A decade after the first entry, strip cutting and single-tree selection cutting largely differed in the size and the spatial distribution of disturbances produced, and therefore, created different light and micro-climate environments, as in gaps of different sizes. The low shrub and herb layer covers mostly reflected the differences in vegetation response to these disturbances. Single-tree selection cutting produced small gaps throughout the entire forest, at the same time. Light under the canopy was sufficient to promote the development of a thick low shrub layer, mostly represented by tolerant hardwood seedling and sapling banks (Canham, 1985). The black-throated blue warbler, which nests and forages in that vegetation layer (Steele, 1992), was favored by the increase of low shrub cover observed in the single-tree selection cut. It has been classified as an intermediate-canopy/dense-understory dweller in northern hardwood forests of Vermont (DeGraaf and Chadwick, 1987) and its abundance has also been related to shrub density (Sherry and Holmes, 1985).

According to the vegetation dynamics usually observed following clearcutting in hardwoods stands (Crowell and Freedman, 1994), the regenerating stands in the strip cut were at the peak of the shrub cover when surveyed. This cohort formed a compact upper shrub layer of mainly shade-intolerant species, practically opaque for the layers under it. This habitat was highly used by the rose-breasted grosbeak, which was twice as abundant in the strip cut forests as it was in the single-tree selection cut and untreated forests. Among all the discriminating variables, intolerant hardwood upper shrub cover was correlated with rose-breasted grosbeak abundance. These elements taken together confirm the status of rose-breasted grosbeak as a sapling/pole specialist (Probst et al., 1992; Hagan et al., 1997; Schieck and Nietfeld, 1995). With such an affinity, this species is more abundant in forest landscapes under even-aged management (Derleth et al., 1989; Welsh and Healy, 1993).

The increased abundance of lower stratigraphic guild species in the treated forests occurred at the expense of the upper stratigraphic guild species, particularly in the strip cut forest. Thompson et al. (1993) stated that single-tree selection cutting could potentially affect canopy-obligatory species. We observed that the black-throated green warbler and the least flycatcher had their highest abundance in the untreated forest.

Species belonging to the ground stratigraphic guild did not show a clear response to forest treatments. Ovenbird had a higher abundance in the untreated forest in one of the 2 years of survey, veery in the strip cut forest, Swainson's thrush in the single-tree selection cut forest, and hermit thrush abundance did not differ among the three forests. Whitcomb et al. (1977) stated that the beneath-canopy habitat under and beside the openings is often so entangled after cutting that the habitat is no longer suitable to the ovenbird, since it prefers thinner understory (Crawford et al., 1981; Smith and Shugart, 1987; Burke and Nol, 1998). The negative relationship between ovenbird abundance and intolerant hardwood upper shrub cover indicates that it could also be the case in this study. Conversely, the presence of the veery was positively correlated with that variable, which reaches its highest value in strip cut forest. The Swainson's thrush was much more abundant in the single-tree selection cut habitat, as also shown by Hagan and Grove (1996). This low shrub nester (Ehrlich et al., 1988) uses a foraging mode that consists of scrutinizing the litter from a low branch near the ground to spot and then to hawk prey (Holmes and Robinson, 1988). Its abundance was correlated with low shrub cover, a vegetation layer well-developed in the single-tree selection cut forest but weakly so in the strip cut forest, and it is reasonable to believe that this species has cued in on this feature to fulfill its foraging requirements when selecting its habitat.

4.2. Coarse woody debris

Already after a first entry, both harvesting systems had an important effect on coarse woody debris. The single-tree selection cut forest had fewer snags per unit area than the untreated forest, but the difference was not as marked as what McComb and Noble (1980) had found. The fact that the forest they studied was under selection cutting for 65 years, meaning that three to four entries had been executed, probably explains the difference. In the strip cut forest, as snag residuals were practically absent in the cut strip, snag density was about a third lower than in the untreated forest.

DWD volumes observed in this study were much larger than what Hagan and Grove (1996) (11–21 $m^3\ ha^{-1}$, Maine), and Fleming and Freedman (1997) (13–20 $m^3\ ha^{-1}$, New Brunswick) found in hardwood forests. However, our results are comparable to what Muller and Liu (1991) found in an old-growth deciduous forest in southeastern Kentucky (47.8 $m^3\ ha^{-1}$), and to what Tyrrell and Crow (1994) found in hardwood forests of northern Wisconsin-Michigan (mean = 54.3 $m^3\ ha^{-1}$).

When comparing DWD volume between treatments, we found the inverse of what was found with snags. A lot of the dead woody material that was standing, as well as live trees, was broken down through the felling of culled trees, decreasing the importance of snags but increasing that of DWD. Although almost no snags were observed in the cut strip, DWD were present, as observed by Gore and Patterson (1986) in recently cut stands. Among the logging slash we observed, tops of harvested trees were still important and considerably increased the DWD density, but also reduced their average size. This effect was particularly important in the single-tree selection cut because harvested tolerant hardwood species usually have a more developed crown with more limbs and branches. Both Gore and Patterson (1986) and Hagan and Grove (1996) also noticed this shift in proportion of volume by DWD size class in single-tree selection cut hardwood stands in New England.

Despite the large difference in snag density, the bark-foraging/hole-nesting guilds were not clearly reduced in the two treated forests. In terms of nesting sites, considering that the snag densities (dbh $\geq$ 10 cm) in the treated forests were actually still higher than in many other mature untreated hardwood forests (McComb and Noble, 1980; Chadwick et al., 1986; Rosenberg et al., 1988), we believe suitable snags were still at densities greater than the one that starts to limit cavity-nesting populations (*sensu* Raphael and White's (1984, p. 57) model).

4.3. Horizontal heterogeneity

By creating disturbances varying in opening size, shape and spatial distribution pattern, habitat internal patchiness in strip cut and single-tree selection cut forests differed greatly. Strip cutting, even after just one entry, promoted horizontal heterogeneity at the expense of local vertical diversity, while the inverse was observed in the single-tree selection cut. Parallel distribution of openings in the strip cut resulted in a wave-like distribution of the vegetation layers that contributed to an increase in horizontal heterogeneity at the scale it was assessed. An even much greater horizontal heterogeneity is likely to occur after the second entry when clearcut habitat will be adjacent to a 40 years old pole-size stand, on one side, and to an old-growth sawtimber-sized stand on the other side.

On the other hand, the systematic synchronously created small-grain openings distributed throughout the entire single-tree selection cut forest have spatially homogenized the sub-canopy structure as expressed by the horizontal heterogeneity in the single-tree selection cut forest that was as low, for most of the habitat variables, as it was in the untreated forest. Therefore, at the scale we assessed horizontal heterogeneity, single-tree selection cutting did not create a patchier habitat, contrary to what Maurer et al. (1981) suggested. The horizontal heterogeneity was rather low in the untreated forest since the more common habitat was a closed unbroken canopy with a poorly developed understory. Moreover, the road network that created many ecotones in the treated forests was absent in the untreated forest.

5. Conclusion

Systematically applying one silvicultural system over a large area creates recurrent habitat conditions, which benefit some species of the regional avian cortege at the expense of some others. In this study, major differences in habitat structure were observed between the three treatments in terms of cover of lower vegetation layers, of habitat horizontal heterogeneity, and of availability of coarse woody debris. As vertical vegetation profile was the most important for predicting avian assemblages, silvicultural systems can be seen as a toolbox of recurrent habitats classified in terms of vertical structure. Small clearcut silvicultural systems, with the different stand development stages they create, may provide more options to maintain the array of habitats needed by bird species (DeGraaf, 1991). However, there is a risk of using a rotation period so short that habitat optimal suitability for late-successional species is never reached. Even if we did not yet detect such an effect after the first entry, with a suggested 120 years rotation for tolerant hardwood stands (Anonymous, 1997), a stand development truncation effect might be progressively detectable in the strip cut forest, particularly after the third entry when no stand older than 80 years will be available.

Single-tree selection cut forests can maintain habitat conditions that are closer to the requirements of late-successional species. However, also with this silvicultural system, it may not be sufficient for species specialized for late-succession forest conditions (like *D. virens*, *Empidonax minimus*, *S. aurocapillus*, and *Sitta carolinensis*), which are usually abundant in landscapes under the gap-phase natural disturbance regime of the northern hardwood forest (Seymour et al., 2002).

Source-sink dynamics acting at a larger scale might have also attenuated the effect of treatments observed in this study for species dependent on mature/old-growth forest habitat (Pulliam and Danielson, 1992). The GEF is embedded in a forested region ($>$10000 km^2) where surrounding mature forest habitat is sufficiently extensive to maintain source populations that could replenish potential sink populations in less suitable habitats. Such metapopulation dynamics could possibly have prevented us from detecting a difference in abundance despite different productivities (Van Horne, 1983; Vickery et al., 1992). Considering treated forests as habitats, which are suitable for the species for which we did not detect a difference with untreated forests can be pernicious, as Bourque and Villard (2001) have demonstrated for the black-throated blue warbler and the ovenbird.

At the other end of the stand development gradient, early secondary succession species are jeopardized in forests that are extensively managed under single-tree selection cut because seedling/sapling-size stands are almost non-existent (DeGraaf and Yamasaki, 2003). In fact, the strongest differences in abundance we observed were rather for species that were common in the strip cut forest but were almost absent in the untreated forest (chesnut-sided warbler, American redstart and rose-breasted grosbeak).

These results support the use of a mix of silvicultural systems, in combination with habitat conservation measures, to sustain regional habitat diversity close to what would be observed under the natural disturbance regime. Currently, in 95% of the northern hardwood forest of Quebec, single-tree selection cut is applied. We suggest that systematically and extensively applying only one silvicultural system, without addressing the concerns discussed above, could result in an impoverishment of the regional avian diversity.

Acknowledgements

Funding and logistic support were provided by the Institut Québécois d'Aménagement de la Forêt Feuillue, the Natural Sciences and Enginering Research Council of Canada, FCAR of the Quebec Government, the Canadian Wildlife Service, the Groupe de Recherche en Écologie Forestière of the Université du Québec à Montréal and the ministère de l'Environnement et de la Faune du Québec. Bird surveys were conducted by S. Barrette, M. Aubé, J.-F. Ouellette, G. St.-Hilaire and F. Gérardin. We thank E. Painchaud, J. Deslandes, M. St.-Laurent, L. Tremblay and C. Roy for their invaluable help in the field. We are also indebted to all the readers that have commented on the manuscript and helped to improve it, particularly R. Berzel and P. Nolet.

References

Anderson, S.H., Shugart Jr., H.H., 1974. Habitat selection of breeding birds in east Tennesse deciduous forest. Ecology 55, 828–837.

Anonymous, 1986. Forest cover maps, 1:20 000. Gouvernement du Québec. Terres et Forêts, Ministère de l'Énergie et des Ressources. Sheets 31F16-200-0202, 31F16-200-0102, and 31F09-200-0202.

Anonymous, 1991. Des forêts en santé. Rapport sur la Commission sur la protection des forêts. Bureau des audiences publiques sur l'environnement. Gouvernement du Québec. Les Publications du Québec. Rapport numéro 2. Québec, Qué. 277 pp.

Anonymous, 1997. Manuel d'aménagement forestier. third ed. Gouvernement du Québec, Ministère des Ressources naturelles. Direction des programmes forestiers. 122 pp.

Blondel, J., Ferry, C., Frochot, B., 1970. La méthode des indices ponctuels d'abundance (IPA) ou des relevés d'avifaune par "stations d'écoute". Alauda 38, 55–71.

Bourque, J., Villard, M.-A., 2001. Effects of single-tree selection cutting and landscape-scale harvesting on the reproductive success of two neotropical migrant bird species. Cons. Biol. 15, 184–195.

Brennan, L.A., Block, W.M., Guttiérrez, R.J., 1986. The use of multivariate statistics for developing habitat suitability index models. In: Verner, J., Morrison, M.L., Ralph, C.J. (Eds.), Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates. University of Wisconsin Press, Wisconsin, pp. 177–182.

Burke, D.M., Nol, E., 1998. Influence of food abundance nest-site habitat, and forest fragmentation on breeding ovenbirds. The Auk. 115, 96–104.

Canham, C.D., 1985. Suppression and release during canopy recruitment in *Acer saccharum*. Bull. Torrey Bot. 112, 134–145.

Chadwick, N.L., Progulske, D.R., Finn, J.T., 1986. Effects of fuelwood cutting on birds in southern New England. J. Wildl. Manage. 50, 398–405.

Conner, R.N., Adkisson, C.S., 1975. Effects of clearcutting on the diversity of breeding birds. J. For. 73, 781–785.

Crawford, H.S., Hooper, R.G., Titterington, R.W., 1981. Songbird population response to silvicultural practices in central Appalachia. J. Wildl. Manage. 45, 680–692.

Crowell, M., Freedman, B., 1994. Vegetation development in a hardwood-forest chronosequence in Nova Scotia. Can. J. For. Res. 24, 260–271.

DeGraaf, R.M., 1991. Breeding bird assemblages in managed northern hardwood forest in New England. In: Rodiek, J.E., Bolen, E.G. (Eds.), Wildlife and Habitats in Managed Landscapes. Island Press, Washington, DC, pp. 155–171.

DeGraaf, R.M., Chadwick, N.L., 1987. Forest type, timber sizeclass, and New England breeding birds. J. Wildl. Manage. 51, 212–217.

DeGraaf, R.M., Tilghman, N.G., Anderson, S.H., 1985. Foraging guilds of North American birds. Environ. Manage. 9, 493–536.

DeGraaf, R.M., Yamasaki, M., 2003. Options for managing early-successional forest and shrubland bird habitats in the northeastern United States. For. Ecol. Manage. 185, 179–191.

Derleth, E.L., McAuley, D.G., Dwyer, T., 1989. Avian community response to small-scale habitat disturbance in Maine. Can. J. Zool. 67, 385–390.

De Vries, P.G., 1974. Multi-stage line intersect sampling. For. Sci. 20, 129–133.

Doyon, F., 2000. Effets de différents types de récolte forestière sur les oiseaux en forêt feuillue à l'échelle de l'habitat et du paysage. Ph.D. Dissertation. Université du Québec à Montréal, Montréal, Qué., Canada, 178 pp.

Doyon, F., Savard, J.-P.L., Gagnon, D., Giroux, J.-F., 1999. Snag characteristics and their use as woodpecker drilling sites in harvested and non-harvested northern hardwood forests. In: Diamond, A.W., Nettleship, D.N. (Eds.), Biology and Conservation of Forest Birds. Society of Canadian Ornithologists, Fredericton, New Brunswick, Canada, (Special Publication No. 1), pp. 103–114.

Ehrlich, P.R., Dobkin, D.S., Wheye, D., 1988. The birders handbook. A field guide to the natural history of North American birds. Simon and Shuster Inc., New York, NY, p. 785.

Fleming, T.L., Freedman, B., 1997. Conversion of natural, mixed-species forests to conifer plantations in New-Brunswick, Canada: implications for dead organic matter and carbon storage. Research report, Department of Biology, Dalhousie University, Halifax, N.S., p. 67.

Freedman, B., Beauchamp, C., McLaren, J.A., Tingley, S.I., 1981. Forestry management practices and populations of breeding birds in a hardwood forest in Nova Scotia. Can. Field Nat. 95, 307–311.

Freemark, K.E., Merriam, H.G., 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. Biol. Cons. 36, 115–141.

Frelich, L.E., Lorimer, C.G., 1991. Natural disturbance regimes in hardwood-hemlock forests of the upper Great Lakes region. Ecol. Monogr. 61, 145–164.

Gore, J.A., Patterson III, W.A., 1986. Mass of downed wood in northern hardwood forests in New Hampshire: potential effects of forest management. Can. J. For. Res. 16, 335–339.

James, F.C., Wamer, N.O., 1982. Relationships between temperate forest bird communities and vegetation structure. Ecology 63, 159–171.

Hagan, J.M., Grove, S.L., 1996. 1995 Report: Single-tree Selection Cutting, Old-Growth, Birds, and Forest Structure in Maine. Division of Conservation Forestry, Manomet Observatory. Report MODCF-96002 of the Manomet Observatory of Conservation Sciences, 26 pp.

Hagan, J.M., McKinley, P.S., Meehan, A.L., Grove, S.L., 1997. Diversity and abundance of landbirds in a northeastern industrial forest. J. Wildl. Manage. 61, 718–735.

Holmes, R.T., Robinson, S.K., 1981. Tree species preferences of foraging insectivorous birds in a northern hardwoods forest. Oecologia 48, 31–35.

Holmes, R.T., Robinson, S.K., 1988. Spatial patterns, foraging tactics, and diet of ground-foraging birds in northern hardwoods forest. Wilson. Bull. 100, 377–394.

Kepler, C.B., Scott, J.M., 1981. Reducing bird count variability by training observers. Stud. Avian Biol. 6, 366–371.

Lachance, D., 1985. Geographic distribution and intensity of sugar maple decline in maple stands in Quebec. Phytoprotection 66, 83–90.

Lent, R.A., Capen, D.E., 1995. Effects of small-scale habitat disturbance on the ecology of breeding birds in a Vermont (USA) hardwood forest. Ecography 18, 97–108.

MacArthur, R.W., 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39, 599–619.

Majcen, Z., Boulay, P., Castonguay R., 1986. Carte Écologique de la forêt expérimentale de Gatineau. Terres et Forêts, Ministère de l'Énergie et des Ressources, Québec. 2 Sheets 1/10000.

Majcen, Z., Richard, Y., Ménard, M., 1985. Composition, structure et rendement des érablières dans cinq secteurs de la région de l'Outaouais. Gouvernement du Québec. Ministère de l'Énergie et des Ressources, Direction de la Recherche et du Développement. Mémoire No. 88. xiv + 130 pp.

Majcen, Z., Richard, Y., Ménard M., Grenier, Y, 1990. Choix des tiges à marquer pour le jardinage des érablières inéquiennes. Guide technique. Direction de la Recherche et du Développement. Ministère de l'Énergie et des Ressources (Forêts). Mémoire no. 96, 96 pp.

Maurer, B.A., McArthur, L.B., Whitmore, R.C., 1981. Effects of logging on guild structure of a forest bird community in West Virginia. Am. Birds 35, 11–13.

McComb, W.C., Noble, R.E., 1980. Effects of single-tree selection cutting upon snag and natural cavity characteristics in Connecticut. Transactions of the Northeast Section of the Wildlife Society, Fish and Wildlife Conference, vol. 37. pp. 50–57.

Muller, R.N., Liu, Y., 1991. Coarse wood debris in an old-growth deciduous forest on the Cumberland plateau, south eastern Kentucky. Can. J. For. Res. 21, 1567–1572.

Nyland, R.D., 1987. Selection system and its application to uneven-aged northern hardwoods. In: Nyland, R.D. (Ed.), Managing Northern Hardwoods: Proceedings of a Silvicultural Symposium, 23–25 June 1986, Society of American Foresters Publication No. 87-03, Syracuse, NY, pp. 49–80.

Probst, J.R., Rakstad, D.S., Rugg, D.J., 1992. Breeding bird communities in regenerating and mature broadleaf forests in the USA Lake States. For. Ecol. Manage. 49, 43–60.

Pulliam, H.R., Danielson, B.J., 1992. Sources, sinks and habitat selection: a landscape perspective on population dynamics. Am. Nat. 137, 550–566.

Raphael, R.G., White, M., 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildl. Monogr. 86, 1–66.

Robitaille, A., Saucier, J.-P., 1998. Paysages régionaux du Québec méridional. Les Publications du Québec. Gouvernement du Québec. Ministère des Resources naturelles. Direction de la gestion des stocks forestiers et Direction des relations publiques, 213 pp.

Rosenberg, D.K., Fraser, J.D., Stauffer, D.F., 1988. Use and characteristics of snags in young and old forest stands in southwest Virginia. For. Sci. 34, 224–228.

Rotenberry, J.T., Wiens, J.A., 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. Ecology 61, 1228–1250.

Roth, R.R., 1976. Spatial heterogeneity and bird species diversity. Ecology 57, 773–782.

Rowe, J.S., 1972. Forest Regions of Canada. Department of Northern Affairs and National Resources, Forestry Branch, Ottawa, 71 pp.

Runkle, J.R., 1985. Disturbance regimes in temperate forests. In: Pickett, S.T.A., White, P.S. (Eds.), The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Orlando, FL, pp. 17–33.

Runkle, J.R., 1990. Gap dynamics in an Ohio *Acer-Fagus* forest and speculations on the geography of disturbance. Can. J. For. Res. 20, 632–641.

Schieck, J., Nietfeld, M., 1995. Bird species richness and abundance in relation to stand age and structure in aspen mixed-wood forests in Alberta. In: Stelfox, J.B. (Ed.), Relationships between Stand Age, Stand Structure, and Biodiversity in Aspen Mixed-Wood Forests in Alberta. Jointly published by the Alberta Environmental Centre, Vegreville, Alberta, and the Canadian Forest Service, Edmonton, AB, Canada, pp. 115–158.

Scott, J.M., Ramsey, F.L., Kepler, C.B., 1981. Distance estimation as a variable in estimating bird numbers from vocalizations. Stud. Avian Biol. 6, 334–340.

Seymour, R.S., White, A.S., deMaynadier, P.G., 2002. Natural disturbance regimes in northeastern North America – evaluating silvicultural systems using natural scales and frequencies. For. Ecol. Manage. 155, 357–367.

Shannon, C.E., 1948. A mathematical theory of communications. Bell Syst. Tech. J. 27, 379–423, 623–656.

Sherry, T.W., Holmes, R.T., 1985. Dispersion patterns and habitat responses of birds in northern hardwood forest. In: Cody, M.L. (Ed.), Habitat Selection in Birds. Academic Press, Orlando, FL, pp. 283–309.

Shirley, E.A.C., 1987. Application of ranking methods to multiple comparison procedure and factorial experiments. Appl. Stat. 36, 205–213.

Smith, T.M., Shugart, H.H., 1987. Territory size variation in the ovenbird: the role of habitat structure. Ecology 68, 704–795.

SPSS Inc., 1988. SPSS-X User's Guide, third ed. SPSS Inc., Chicago, IL, 1072 pp.

Steele, B.B., 1992. Habitat selection by breeding black-throated blue warblers at two scales. Ornis Scand. 23, 33–42.

Temple, S.A., Mossman, M.J., Ambuel, B., 1979. The ecology and management of avian communities in mixed hardwood-coniferous forests. In: DeGraaf, R.M., Evans, K.E. (Eds.), Proceedings of the Management of North Central and Northeastern Forest for Nongame Birds. General Technical Report NC-51, 23–24 January 1979. Minneapolis, Minnesota, USDA For. Serv., North Central Forest Experimental Station, St. Paul, MN, pp. 132–151.

Thompson III, F.R., Capen, D.E., 1988. Avian assemblages in seral stages of a Vermont forest. J. Wildl. Manage. 52, 771–777.

Thompson III, F.R., Probst, J.R., Raphael, M.G., 1993. Silviculture options of neotropical migratory birds. In: Finch, D.M., Stangel, P. (Eds.), Proceedings of the Status and Management of Neotropical Migratory Birds. General Technical Report RM-229, 1992 September 21–25; Estes Park, CO, USDA Forest Services, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, pp. 353–362.

Tyrrell, L.E., Crow, T.R., 1994. Dynamics of dead wood in old-growth hardwood-hemlock forests of northern Wisconsin and northern Michigan. Can. J. For. Res. 24, 1672–1683.

Van Horne, B., 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47, 893–901.

VanWagner, C.E., 1982. Practical Aspects of the Line Intersect Method. Can. For. Serv., Petawawa National Forestry Institute, Chalk River, Information Report PI-X, 12 pp.

Vickery, P.D., Hunter, M.L., Wells, J.V., 1992. Is density an indicator of breeding success? The Auk. 109, 706–710.

Webb, W.L., Behrend, D.F., Saisorn, B., 1977. Effect of logging on songbird populations in a northern hardwood forest. Wildl. Monogr. 55, 1–55.

Welsh, C.J.E., Healy, W.M., 1993. Effect of even-aged timber management on bird species diversity and composition in northern hardwoods of New Hampshire. Wildl. Soc. Bull. 21, 143–154.

Whitcomb, B.L., Whitcomb, R.F., Bystrak, D., 1977. Long-term turnover and effects of selective logging on the avifauna of forest fragments. Am. Birds 31, 17–23.

Wiens, J.A., 1974. Habitat heterogeneity and avian community structure in North American grasslands. Am. Midl. Nat. 91, 195–213.

Williams, B.K., 1983. Some observations on the use of discriminant analysis in ecology. Ecology 64, 1283–1291.

Yahner, R.H., 1984. Effects of habitat patchiness created by a Ruffed Grouse management plan on avian communities. Am. Midl. Nat. 111, 409–413.