

## EFFECTS OF LANDSCAPE STRUCTURE ON NESTING SONGBIRD DISTRIBUTION IN A HARVESTED BOREAL FOREST<sup>1</sup>

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**Abstract.** We studied the effects of forest cover and configuration on nesting songbird distribution in a harvested boreal forest. To emphasize landscape-level effects relative to stand effects, point count stations were established in mature stands only, but were surrounded by contrasting 100-ha landscapes. Seven of the 14 species studied responded significantly to landscape structure, but responses to specific landscape measures were found only in three species. Bay-breasted Warbler (*Dendroica castanea*) was absent from landscapes with <55% forest cover. Solitary Vireo (*Vireo solitarius*) also was associated with high forest cover per se. Conversely, American Robin (*Turdus migratorius*) was associated with poorly-forested landscapes. No species responded to mature forest configuration. Thus, clearcutting in boreal forests will reduce the use of remnant forest patches by certain species through a decrease of surrounding mature forest cover rather than changes in its spatial configuration.

**Key words:** boreal forest, forest edge, forest management, fragmentation, landscape, songbirds.

Despite the abundant literature on forest fragmentation in deciduous forests, it is difficult to infer that boreal forest songbirds suffer from clearcutting in a similar way to those in deciduous, agricultural, and peri-urban areas. There are five main reasons for this: (1) current clearcutting in boreal forests creates landscape mosaics that are less different from original landscapes than agriculture or peri-urbanization. Thus, birds may be able to adapt to harvested forest landscapes if the latter approximate natural perturbations (Hunter 1992); (2) unlike agricultural and peri-urban landscapes, gaps between mature stands in harvested forests are temporary and may therefore have a limited effect on avian dispersal in the long term (Edenius and Elmberg 1996); (3) harvested forests often have larger tracts of mature forest than other fragmented forest landscapes (André

1992); (4) stand edges in harvested forests are abrupt and are not reported to create distinct species assemblages as in agricultural landscapes (Wiens 1995); and (5) edge effects on nest predation risk are small or nonexistent in the boreal forests studied so far in northeastern North America (Rudnický and Hunter 1993, Darveau et al. 1997). Nevertheless, temporary landscape alterations caused by clearcutting may be sufficient to modify species assemblages in remaining mature stands of boreal forests.

In the last decade, emphasis on patch size effects following the work of Robbins et al. (1989) led many to advocate the conservation of sizeable boreal forest patches for woodland songbirds. However, patches of suitable size may still be inadequate nesting habitats for some species, depending on the amount and spatial arrangement of forest in surrounding landscapes. Unfortunately, landscape-level effects on patch use by birds remain little documented, especially in boreal forests (reviewed by Villard et al. 1999).

Here, we assess the combined and separate influences of forest cover and configuration at the landscape scale on stand occupancy by boreal forest songbirds with small (<5 ha) home ranges. We emphasize landscape-level effects by limiting our sampling to stands with comparable vegetation characteristics (i.e., species composition, height, density).

### METHODS

#### STUDY AREA

The study was conducted in the Laurentian hills, 60 km north of Québec city, Canada (47°13'–47°26'N, 71°00'–71°14'W, Fig. 1). The vegetation was typical of second-growth boreal balsam fir (*Abies balsamea*) forest found in eastern Québec, with black spruce (*Picea mariana*), white spruce (*P. glauca*), and white birch (*Betula papyrifera*) as the main companion species (Darveau et al. 1997). Local natural perturbations were mainly spruce budworm (*Choristoneura fumiferana*) outbreaks and windthrow, which produced a landscape mosaic of seral stages. Most stands in the region originated from clearcuts made between 1941 and 1944. Variation in forest cover and edge length originated from different landscape management strategies that provided a gradient of forest fragmentation: (1) large tracts of continuous coniferous forest, (2) small

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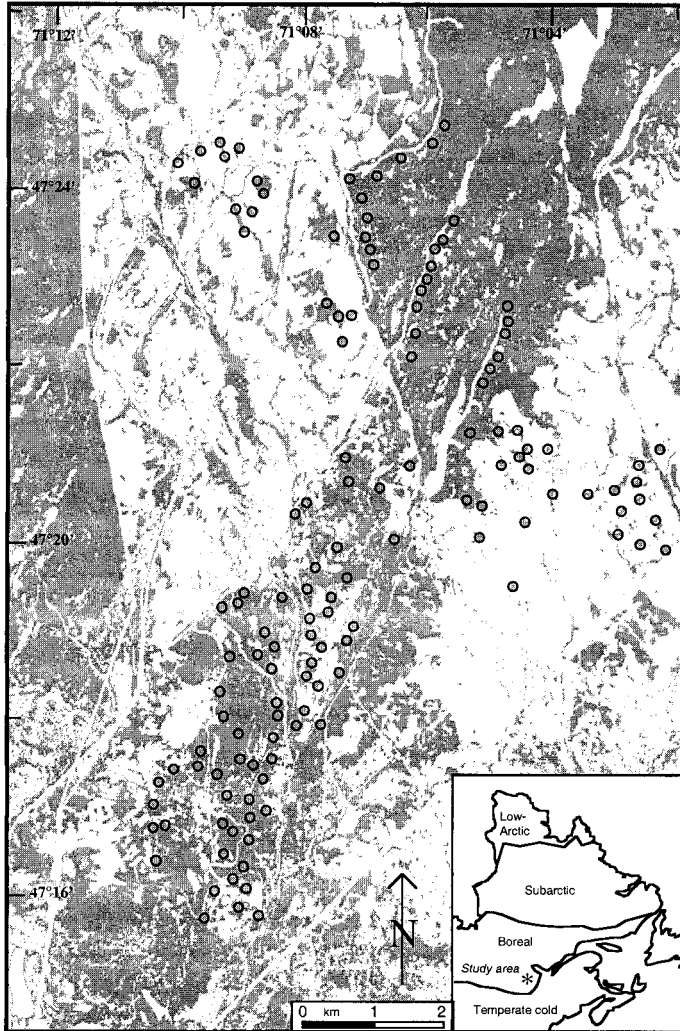


FIGURE 1. Layout of 136 point count stations over the classified satellite image. Gray areas represent mature coniferous forests and white areas include all other types of stands (mixed regeneration, clearcuts, windthrow, spruce budworm outbreaks), roads, and aquatic habitats located in the Laurentian hills, north of Québec city, Canada.

(<30 ha) clearcuts embedded in a forest matrix, and (3) large clearcuts that delineate small mature coniferous patches.

#### BIRD CENSUSES

We conducted 136 limited-radius point counts with a duration of 15 min (Ralph et al. 1993) in which we recorded all bird species seen or heard within 50 m. Point counts were made twice, between 5 and 28 June 1995, by different observers and at different times between 04:30 and 09:30, on days with no rain or wind > 30 km hr<sup>-1</sup>.

The perimeters of all point count stations were separated by > 200 m and located > 50 m from edges in balsam fir and black spruce stands with less than 25%

white birch. All sampled stands were larger than 3 ha. Point count stations were located in similar stands, but within contrasting landscapes. Sampling stands were 10 to 14 m high, with less than 14% of cover visibly affected by spruce budworm. Stand characteristics were obtained from forestry maps based on aerial photos taken in 1990. No point counts were made near clearcuts < 3 years old, to avoid possible time lags in bird response to change in landscape structure at a given site due to site fidelity of adult birds.

#### LANDSCAPE STRUCTURE

Based on a SPOT2 multispectral satellite image (Canadian Space Agency 1995), landscape structure was calculated from 100-ha square maps centered on each

point count station. We assume that 100-ha maps were sufficiently large to describe landscapes as perceived by songbirds in the study area, which generally have territories < 5 ha (Gauthier and Aubry 1995). To quantify coniferous forest cover in each 100-ha landscape, we used an image classification program (PICEA; Bélanger and Gagnon 1993). The satellite image was taken on 28 August 1995, with a 12.5 m resolution in frequency bands 3 (visible), 4, and 5 (infrared). Four homogeneous patch types were classified: (1) mature coniferous (49% of total area), (2) mixed regeneration (35%), (3) clearcuts, severe windthrow, and spruce budworm outbreaks (15%), and (4) aquatic (1%; Delage and Fournier, unpubl. data).

We analyzed landscapes with FRAGSTATS 2.4 (McGarigal and Marks 1995). Patches were composed of identical adjacent pixels (diagonal contacts included). For the analyses, we retained the three landscape measures that best characterized the spatial arrangement of coniferous stands: total forest cover (ha), total core area (total forest cover [ha] > 100 m from edge), and total length of forest edge (km).

#### DATA ANALYSIS

Because of low bird-densities in our study area, only presence-absence data were used. Species were classified as present when encountered on either of the two visits. To prevent spurious effects caused by low population density and to minimize the risk of type II statistical errors (see below), we excluded 14 of the 38 species recorded because they were found in less than 10% of point count stations. Eleven of the excluded species were typically associated with habitats other than mature coniferous forest. We maximized statistical independence of songbird records among nearby point count stations by excluding species that ranged across the study area at sampling time, like corvids and fringillids.

Logistic regressions were used to assess relationships between songbird occurrence and landscape structure, with landscape measures taken together or separately. To account for relationships among independent variables (see below), the separate effects of forest cover, edge and core area were tested after partialling out the two other variables and their square in statistical models. We also tested the combined effect of all three measures and their squares on species occurrence, to assess general responses to landscape by each species.

The use of minimum distances between point count stations did not necessarily preclude statistical dependence of occurrence data, because nonrandom arrangement of songbird territories may occur, even after accounting for landscape measures. Furthermore, spatial autocorrelation may vary greatly among species. Thus, for each species we assessed spatial autocorrelation of presence-absence data, that is, the tendency of conspecific territories to be found in clusters or in regular arrays, after accounting for spatial variation in the landscape (by using residuals of logistic regressions based on landscape metrics mentioned above instead of actual occurrences, to avoid the confounding effect of spatial autocorrelation of landscape data). We used Moran's I coefficients to measure the significance of

spatial autocorrelation (Legendre and Fortin 1989). Only two species were positively spatially autocorrelated within 1,250 m ( $P < 0.05$ ). Those species were excluded from the analyses: White-throated Sparrow (*Zonotrichia albicollis*) and Magnolia Warbler (*Dendroica magnolia*). We assume that spatial autocorrelation with the 14 remaining species was sufficiently weak or not significant to consider point counts statistically independent.

The reliability of nonsignificant results was tested with power analyses based on Monte Carlo simulations. The power analyses for separate effects of cover, edge and core area were conducted in two steps. First, to account for nonlinear relationships between landscape measures as was done in the actual analyses, we calculated residuals for each landscape measure from a multiple linear regression with the two other measures and their squares as independent variables. We considered those residuals as measures of separate contribution of each landscape measure at each of the point count stations. Then, for each landscape measure, we simulated 1,000 logistic regressions with its residual as independent variable and pseudo-random binomial variates with known expected means as simulated presence-absence data. To assess the overall power of models with combined variables, we performed simulated logistic regressions with forest cover as the only independent variable, thus ignoring the two other variables. We preferred the latter approach over an exact simulation of our six-variable models for simplicity, because edge and core area were strongly associated to forest cover. We used the proportion of simulated results that were significant as measures of statistical power. Based on the results of power analyses (see below), significance level was established at  $\alpha = 0.10$ .

#### RESULTS

Forest cover within 100-ha landscapes varied from a few hectares of remaining forest to more than 90 ha. Total forest cover, forest edge and core area were strongly related to each other in a nonlinear fashion (Fig. 2). Nevertheless, for given amounts of forest cover, both core area and forest edge varied widely, thus allowing a statistical separation of forest amount and configuration effects. Five species accounted for 63% of the 687 songbird records included in the analysis, and one, the Yellow-rumped Warbler, was recorded in 81% of point count stations (scientific names in Table 1).

#### OCCURRENCE PATTERNS

The occurrence of 7 of the 14 species analyzed was significantly correlated with landscape structure (Table 1). However, we were able to identify associations to landscape composition per se (total cover) to only three of the species responsive to landscape structure, whereas no species responded to landscape configuration (edge and core area) after partialling out other effects ( $P > 0.24$ ). The Bay-breasted Warbler was by far the most responsive to landscape composition, being absent from all stations with <55% forest cover (Fig. 2). Although responses to specific variables were not as strong, Solitary Vireo was disproportionately more frequent in well-forested landscapes ( $\bar{x} = 58\%$ ), as opposed to American Robin ( $P = 0.1$ ), which was

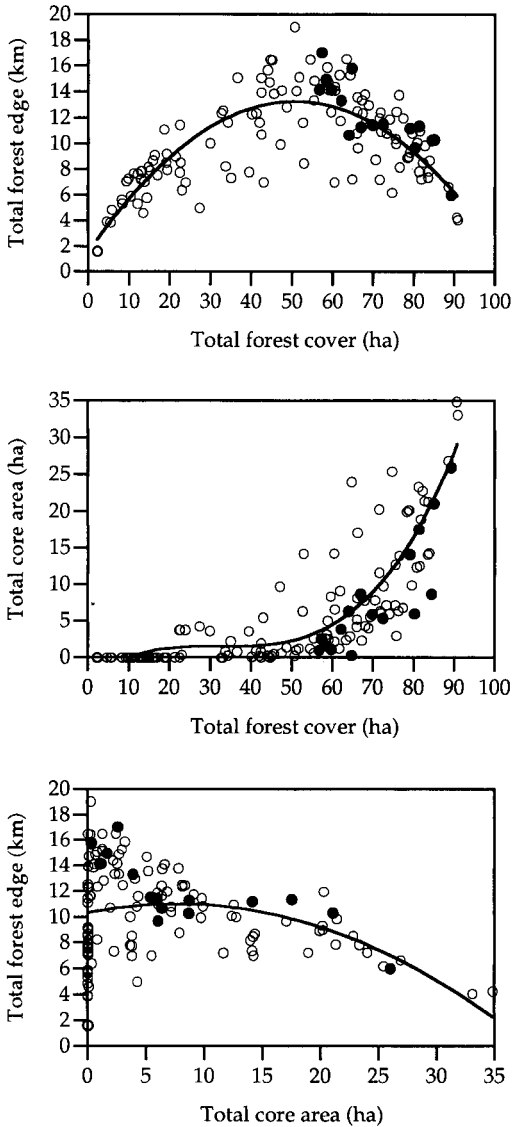


FIGURE 2. Associations between total forest cover, total forest edge, and total core area calculated at each point count station from 100-ha maps, with data from Bay-breasted Warbler. Filled circles represent presences, open circles represent absences.

associated to less-forested landscapes ( $\bar{x} = 46\%$ ). Golden-crowned Kinglet, Black-throated Green Warbler, Blackpoll Warbler, and Ruby-crowned Kinglet were not associated ( $P > 0.1$ ) to residual effects of specific landscape measures but still responded to their combined effect.

#### STATISTICAL POWER

Statistical power was very similar for the three landscape measures. The probabilities of detecting a linear

increase of occurrence of 50% (mean 25%) in response to the observed range of residuals were 79%, 82%, and 80% for total cover, edge and core area, respectively ( $\alpha = 0.10$ ). With  $\alpha = 0.05$ , statistical power for testing separate effects of cover, edge and core area was much lower (<60%). Tests for forest cover effects, without accounting for other variables, were markedly more powerful than the above tests because of greater variation in raw data than in residuals. They allowed us to detect a linear increase of occurrence of 20% (mean 10%) from the lowest to the highest forest cover in 76% of Monte Carlo simulations, with  $\alpha = 0.10$ . Given that all species studied had an observed frequency > 10%, we had a 20% probability of being wrong for any species when declaring it insensitive to our combined landscape measures (Table 1).

#### DISCUSSION

Even though vegetation characteristics were held constant within censused stands, 7 of the 14 songbird species included in the analysis responded significantly to landscape structure. Four of those species responded to the combined measures of landscape without being associated in a simple way to forest cover, edge or core area. This could be attributed for example to a response to forest cover being itself dependent on the amount of total edge. However, the three other species were associated clearly to forest cover per se. As in some agricultural and peri-urban landscapes, boreal forest reduction caused by logging led to changes of occurrence of nesting songbirds not only in logged stands, but also in surrounding, untouched stands (Hinsley et al. 1995, Villard et al. 1999). Thus, forest remnants sufficiently large to include an average songbird territory (ca. > 5 ha) can be inadequate for species such as the Bay-breasted Warbler and the Solitary Vireo, when embedded in a clearcut dominated landscape. In other words, the relationship between remaining population size and remaining forest cover is unlikely to be linear for several bird species.

The absence of edge and core effect even for the Bay-breasted Warbler and the Solitary Vireo shows that the need for forested landscapes does not imply a need for large core area of forest. In support of Fahrig's (1997) simulation study, our results thus emphasized the role of forest cover relative to forest configuration in determining landscape use by birds. The remarkably similar statistical power of analyses of effects of forest cover, edge and core area rules out an explanation based on a statistical bias against detecting effects of configuration. This may not be necessarily true in other studies, which rarely, if ever, conducted power analyses. Comparisons of effects of intricately linked landscape variables should be made in light of statistical power in further studies.

Although statistically significant in half of the species, the percentage of variation explained by our models was too low to allow quantitative predictions of species occurrences in different management scenarios. This cannot be explained by lack of variability, because songbird occurrences were compared over a broad range of landscape structure, which translated into adequate statistical power. It suggests instead that local vegetation structure, population dynamics, or

TABLE 1. Species responses to landscape structure, based on 136 landscapes of 100 ha located in a harvested boreal forest, Québec, Canada. Species frequency (F), corrected  $R^2$  (Nagelkerke 1991), and probability for logistical regressions with (1) forest cover, core, edge, and their squares as independent variables and (2) forest cover, after partialling out core area, edge, and their squared values. + signs represent associations with forest cover. Species are ranked by decreasing  $R^2$ . Goodness-of-fit of all models was adequate ( $P > 0.1$ ; Hosmer and Lemeshow 1989).

Species	F	Forest cover, edge, and core area combined			Forest cover
		$R^2$	P		P
Bay-breasted Warbler <i>Dendroica castanea</i>	16	0.31	***	+	***
American Robin <i>Turdus migratorius</i>	19	0.23	**		
Golden-crowned Kinglet <i>Regulus satrapa</i>	87	0.19	**		
Blackpoll Warbler <i>Dendroica striata</i>	38	0.18	**		
Black-throated Green Warbler <i>Dendroica virens</i>	49	0.17	**		
Solitary Vireo <i>Vireo solitarius</i>	23	0.15	*	+	*
Ruby-crowned Kinglet <i>Regulus calendula</i>	66	0.13	*		
Boreal Chickadee <i>Parus hudsonicus</i>	32		ns		
Dark-eyed Junco <i>Junco hyemalis</i>	28		ns		
Nashville Warbler <i>Vermivora ruficapilla</i>	14		ns		
Swainson's Thrush <i>Catharus ustulatus</i>	90		ns		
Winter Wren <i>Troglodytes troglodytes</i>	78		ns		
Yellow-bellied Flycatcher <i>Empidonax flaviventris</i>	37		ns		
Yellow-rumped Warbler <i>Dendroica coronata</i>	110		ns		

\*  $P \leq 0.05$ , \*\*  $P \leq 0.01$ , \*\*\*  $P \leq 0.001$ .

time since isolation could be more important than landscape structure in explaining songbird occurrence (Villard et al. 1995, Jokimäki and Huhta 1996). Also, landscape mosaics created by clearcutting in the boreal forest tend to resemble mosaics originating from natural disturbances, unlike other patterns of land use. Furthermore, clearcuts separating mature stands rapidly revert to woodland, and songbirds may be less reluctant to cross habitats like forest regrowth than hayfields or built-up areas, thus leading to a less pronounced response of boreal songbirds to changes in harvested forests than in other landscapes (Andrén 1994). Despite low predictive power, we argue that landscape effects of logging are not trivial for songbirds, because the decline of certain species in remaining stands may exacerbate further decline, for example by lowering mating success (Gibbs and Wenny 1993).

What makes some species avoid poorly-forested landscapes? The answers still elude us, but it is unlikely that the observed patterns were caused by high levels of brood parasitism or nest predation as has been reported in agricultural landscapes (reviewed by Paton 1994). Brood parasites are rare in our study area and nest predation risk does not increase within 250 m of forest edges in our study area (Darveau et al. 1997; J. Ibarzabal, unpubl. data). However, it is possible that landscape structure influenced some species because of their reluctance to fly into the openings created by clearcutting (Desrochers and Hannon 1997). This effect may constrain either establishment of nesting pairs and/or fledging dispersal in more fragmented landscape than in continuous ones. Whether bird responses arise from decreased quality of forest patches for nesting, thwarted dispersal, or other causes is currently under study.

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