SPATIAL RELATIONSHIPS BETWEEN VEGETATION AND FOREST BIRD BOUNDARIES IN A MIXED-WOOD MANAGED FOREST

by

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Title of

Spatial Relationships between Vegetation and Forest Bird Boundaries
in a Mixed-Wood Managed Forest

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ABSTRACT

A major current threat to the persistence of forest birds in Canada is forest fragmentation caused by industrial timber harvesting. The traditional silvicultural method of clearcutting creates forest fragments delineated by sharp boundaries. Conversely, selective logging techniques strive to mimic natural disturbance patterns and to produce smoother boundaries. Forest boundaries influence the ecological behaviour of forest birds in a species-specific manner. To assess the effect of forest fragmentation on bird occurrence and to derive management guidelines, I investigate the spatial association between boundaries of six bird species and forest features in a moderately harvested landscape (MHL) and an intensively harvested landscape (IHL) in New Brunswick. The focal bird species were used as indicator species for the effects of forest fragmentation. These analyses were carried out at both stand and landscape scales. I hypothesized that 1) the association of birds with forest variables would be i) species-specific and ii) stronger in the IHL than in the MHL; 2) that birds would have more common boundaries in the in the IHL than in the MHL; 3) that both scales would yield complementary results, whereby the stand scale would refine coarse-scale ecological relationships of birds.

By means of boundary detection algorithms and overlap statistics, I found that boundary spatial associations between vegetation and birds were more clearly defined at the stand scale in the IHL. I suggest that the spatial confinement of forest birds in clearcut forests fragments accounts for this relationships. Overall, understory forest components primarily influenced bird occurrence, yet bird response to forest features was species-specific. My findings were consistent at both analysis scales.

Management efforts to preserve forest birds should strive to recreate the complexity and variability of natural ecosystems. A multi-scale approach is required in ecological research and monitoring of bird species in fragmented landscapes. For further research, I recommend that studies should include uncut controls, a broader range of treatments than the two that I analyzed, and some replication at all spatial scales. New spatial analytical tools such as boundary detection algorithms and overlap statistics are an asset to ecological studies. The methodology I used offers an objective means for evaluating land fragmentation and the effects of edges/ecotones on populations.

A mis papás por su inmenso amor y constante apoyo en cualquier camino que decida yo tomar

A mis hermanos y sobrinines por existir

A mi Noni por su gran cariño

Y a mis amigos en México también.

…and while she was tossing sea stars back into the ocean, he came and said: - " nonsense! You will never finish rescuing all these sea stars, the shore is full of them and the sea keeps bringing more and more". She responded: -"I may not be able to rescue them all" - and tossing one sea star into the sea she said…-"but for this one I made the difference!"

MR

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INTRODUCTION

The presence and abundances of forest birds depend on vegetation composition, forest cover, and the spatial configuration of landscapes. Many studies have investigated the role of such forest features aiming to identify and quantify factors that affect the presence of various bird species (e.g., McGarigal and McComb, 1995; Thompson *et al.*, 1995; Mazzerolle and Villard, 1999). For instance, Robichaud and Villard (1999) found that black-throated green warblers (*Dendroica virens*) select territories based on conifer distribution in boreal mixed-wood forests of Northern Alberta. Variation in bird responses depends on the species life history and area requirements (Villard *et al.,* 1995). Hoover *et al.* (1995) reported that nesting success of Wood Thrush (*Hylocichla mustelina*) in sites with low forest cover (<42%) was below sustainable levels. Fahrig (1997) estimated that bird survival is reduced below a vegetation cover threshold of 20 percent.

Despite considerable evidence of the response of birds to structural attributes and spatial configuration of forest fragments, controversy continues as to the identification of the most important factors for birds' persistence. Andrén (1994) noted that spatial arrangement of the forest mosaic is a relevant feature affecting bird species in landscapes with small forest fragments and limited vegetation cover. More recent studies on the importance of forest configuration (McGarigal and McComb, 1995) and forest cover (Trzcinski *et al.*, 1999) have demonstrated that the former factor has a greater effect on bird breeding success. However, Villard *et al.* (1999) argued that within a range of 3 to 65 percent forest cover, spatial configuration of residual stands in a fragmented landscape is a good predictor for the presence of forest birds. Overall, the structural and biophysical characteristics of the land influence bird species persistence and habitat (Drolet *et al.*, 1999).

Both natural (e.g., fire, insect outbreaks) and human (e.g., logging) disturbances affect the structure, composition, and spatial configuration of forest ecosystems. For example, industrial timber harvesting has altered the natural state of forested landscapes at an increasing rate (Franklin and Forman, 1987). The extensive implementation of clearcutting has caused high degrees of forest fragmentation (Turner *et al.*, 1998, Bergeron, 2000). Although clearcutting creates new habitat for some forest-edge birds, it causes loss of habitat for forest-interior species (Opdam *et al.*, 1995, Pulliam *et al.*, 1995). Specifically, the extensive removal of trees, snags, logs, and woody debris destroys critical habitat for forest birds that rely on such elements to survive. Consequently, forest birds may fail to breed or have to do so in poor habitat during or after relocating themselves to the closest available forest remnant (Drolet *et al.*, 1999; Hannon, 1999; Smith, 2000 pers. comm). Clearcutting also implies the creation of sharp edges delineating forest stands. Such edges differ from natural vegetation gradients (i.e., ecotones) that typically surround treefalls or gaps generated by insect outbreaks in unmanaged landscapes during natural succession.

Other silvicultural practices affect local forest structure directly or indirectly and alter vegetation composition (Thompson III *et al.*, 1995). Compared to clearcutting, alternative silvicultural systems aim to mimic the natural dynamics, functional complexity, and structural heterogeneity of forests, thus preserving its native bird community (Bergeron and Harvey, 1997; Franklin *et al.*, 1997; Bergeron *et al.*, 1999). Robinson and Robinson (1999) showed that selective logging effectively preserves bird populations of mature and old-growth deciduous forests.

Although much scientific research has examined how forestry operations affect bird species, most investigations have focused only on clearcutting. Few studies have focused on new approaches to forestry such as selective logging (Annand and Thompson, 1997; Maraj, 1999; Robinson and Robinson, 1999). Moreover, ecological studies and management guidelines are often undertaken either at the stand or landscape scale but rarely at both scales. The interaction of variables across scales is critical in shaping the spatial dynamics of species because factors at either scale may enhance or constrain effects at another scale. Birds can perceive land use changes at both stand and landscape scales (e.g., Mazzerolle and Villard, 1999). The spatial sensitivity of birds is related to their home range size and influenced by the habitat patch size where they occur. Hence, the response of birds to land fragmentation can be better understood if both stand and landscape scales are incorporated in to ecological studies.

My research compares the effects of clearcutting and selective logging on forest birds at the stand and landscape scale. In particular, I ask how birds respond to the sharper boundaries and bigger openings of clearcut forests compared to more gradual boundaries and smaller gaps of selectively logged forests.

OBJECTIVES AND HYPOTHESES

In this study, I investigate the spatial association of five songbirds and one woodpecker to particular forest features such as vertical and horizontal structure and species composition. My analysis is based on data collected by Dr. Marc-André Villard (researcher at the Université de Moncton) in 1996-1997 at moderately harvested and intensively harvested landscapes (i.e., 70 % and 45% of vegetation cover retention, respectively) in northwestern New Brunswick, Canada (see Villard, 1999). My prime goal is to provide insight into how clearcutting vs. selective cutting affects the presence of forest birds at the stand and landscape scales. My specific objectives are 1) to assess the impact of forest fragmentation caused by clearcutting and selective logging on the occurrence of six forest bird species; 2) to analyze spatial relationships between bird-to-bird and bird-to-vegetation boundaries; and 3) to formulate management key points for the preservation of forest birds and their habitat by treating the six bird species studied as indicator species.

Forest birds inhabiting highly fragmented landscapes are spatially confined to forest fragments bounded by clearcuts. Therefore, I hypothesized that 1) the association of birds with forest variables would be clearer and stronger in the intensively harvested landscape than in the moderately harvested one; 2) each species studied would show a specific response to the forest horizontal and vertical structure and forest composition; 3) birds would have more common boundaries in the in the intensively harvested landscape than in the moderately harvested one; 4) the response of the focal bird species to the spatial features of the study sites would provide insight into the impact of forest fragmentation on larger bird communities.

My research is one of only a few studies that has examined the spatial relationships between boundaries of bird occurrence and various forest components in a heterogeneous landscape. Previously, most ecological investigations have used a single species approach and most management decisions have been made at the stand scale. Also, attempts to offset logging impacts on forested ecosystems are still done at the stand scale (Hannon, 1999), in spite of the demand of a multi-scale approach. My study is innovative in that it presents a double-scale assessment on various bird species. I presumed that both stand and landscape scales would complement one another and that the smaller scale would refine coarse relationships between birds and their environment. Analyses that quantify the spatial relationships between ecological boundaries are useful to identify the most important factors affecting the ecology of forest birds (Fortin *et al.*, 1996).

BACKGROUND

Ecological boundaries

Boundaries are defined as areas of environmental transition that separate two homogenous stands, communities, regions, or ecosystems. Boundaries may be caused by clearcuts, forest fires, treefall gaps, insect epidemics, or by gradual or drastic changes in microclimate (Fortin *et al.*, 1996). While sharp boundaries (edges) are common in landscapes modified by human activity, smoother boundaries (ecotones) occur in undisturbed forests as a result of the continuous variation in forest components (Lent and Capen, 1995).

Boundaries are of scientific interest because their locations can reflect underlying physical and/or biological processes (Maruca and Jacquez, 1997). Abiotic and biotic factors at boundaries do not appear to act independently from each other. Instead, these factors combine to affect the occurrence and distribution of bird species. For example, microclimate near forest edges changes considerably relative to the forest interior (Chen, 1994). Climatic factors often limit bird distribution due to physiological constraints on metabolic rates, the timing of breeding, and reproductive success (McCollin, 1998). Also, forest edges influence the availability of prey for insectivorous birds making these predators, in turn, available to their predators (McCollin, 1998; Desrochers and Fortin, 2000). Desrochers and Fortin (2000) have shown that edges influence the behaviour of forest birds. They suggested that black-capped chickadees (*Poecile atricapillus*) use forest boundaries as movement conduits rather than as foraging sites. Hawrot and Niemi (1996) assumed that boundaries can also enhance population size by providing a higher diversity of microhabitat conditions and resources to forest birds. This hypothesis, however, is dependent on the type of edge: whether it is abrupt or gradual, or whether it occurs between habitat fragments or in the forest interior. Logically, a boundary roughly defined from the scale of human observation can be irrelevant to a forest bird. To test this idea, objective techniques for defining boundaries are needed to assess the effects of land fragmentation on birds. Here, I identified bird and vegetation boundaries by using a boundary detection algorithm and overlap statistics that reduce subjectivity.

Response of birds to land changes

Given the high rate of forest fragmentation worldwide and extirpation of bird species from fragmented landscapes, studies aimed at evaluating the effect of habitat change on birds have increased. Scientists have found that the persistence of both resident and migratory bird populations relates partly to the extent of land change (Reed 1989; Andrén, 1994; Hanski *et al.*, 1994, Askins, 1995). The presence and abundance of birds may differ between managed (agricultural or silvicultural) and unmanaged landscapes. In the Oregon Cascades (USA), Hansen *et al.* (1995) reported significant differences in bird species abundance between natural and managed stands (i.e., clearcut, canopy retention, closed canopy plantation, mature forests, and old growth). They found that bird presence was associated with stand types. In addition, modelling has shown that bird population persistence in fragmented landscapes also relates to the creation and distribution of small, scattered habitat patches, to the proportion of forest edges, and to microhabitat features (Hanski, 1989; Lescourret and Genard, 1994; Pulliam, *et al.*, 1995; Bascompte and Sole, 1996).

Changes in bird population dynamics and demographic parameters may follow fragmentation. In a study on habitat fragmentation and pairing success of ovenbirds (*Seiurus aurocapillus*), Villard *et al.* (1993) reported lower male densities in forest fragments than in continuous forests. Also, abundance of ovenbirds decreased after harvesting because of lower female densities (Gibbs and Faarborg, 1990; Villard *et al.,* 1993). Subsequently, Villard *et al.* (1999) demonstrated that silvicultural treatments also affected the occurrence of other forest songbird species and reduced the reproductive success of black-throated blue warblers (*Dendroica caerulescens*) and ovenbirds.

Although most forest birds are highly mobile and can travel long distances, open areas between isolated forest fragments usually act as movement barriers. Such open land can have detrimental effects on the persistence of bird populations during the breeding season and other events of their life cycle. St. Clair *et al.* (1998) evaluated the movement of forest birds and compared the willingness of wintering residents to travel along continuous forest, narrow corridors, and across forest cover gaps. They found that birds were less likely to cross open areas as the gap distance increased. Therefore, forested links between landscape forest patches, commonly referred to as corridors, may facilitate bird movements while acting as safeguards against predators (Desrochers and Hannon, 1997; Beier and Noss, 1998).

In addition, it is generally believed that landscapes with poor habitat quality and isolated forest fragments support only small populations due to increases in the mortality of dispersing birds (Wilcove, 1985; Martin, 1988; Fahrig and Merriam, 1994; Robinson and Robinson, 1999). Particularly, yearlings and territorial birds appear to be most affected (Bélisle *et al.*, 2000) because they lack the searching ability to find new and suitable places. Isolated fragments may further reduce mating and breeding success (Shields 1984; Villard 1998) through increased nest predation, nest parasitism, food scarcity, and habitat loss (Wilcove, 1985; Martin, 1988; Robinson, 1990).

The composition of avian communities also changes according to the successional stage of the forest (McComb *et al.,* 1993), which can be altered by forestry practices. Many bird species are thus associated with restricted stages of stand development (Catt, 1991, Thompson, *et al.*, 1995). In a subalpine forest of western Canada, Catt (1991) reported that dusky flycatchers (*Empidonax oberholseri*) tend to occur in young forest stands, in which Engelmann spruce (*Picea engelmannii*) begins to dominate the canopy (55 to 150 yrs. post-fire). Likewise, DeGraaf *et al.* (1998) noted that American redstarts (*Setophaga ruticilla*) showed strong preference for sapling stands throughout forests in New Hampshire and Maine (USA). In contrast black-throated blue warblers and blackburnian warblers (*Dendroica fusca*) are closely associated with mature forest components. Fraucet and Warmer (1982) concluded that species richness is higher in second growth forests where an intermediate level of tree density, canopy height, and vegetation diversity occurs. My study, because it was carried out in landscapes with both patches of older trees and regenerating components, allowed me to relate the territory locations of forest birds to various forest features. Understanding the spatial association of forest components and birds is critical since drastic changes occur in both when forest practices alter the landscape.

Forest management and the use of forest birds as indicators

Due to the urgent need to achieve sustainable forest management that preserves bird populations, much effort has been aimed at understanding the impact of traditional and alternative silvicultural practices on forest birds. Selective logging has emerged as an alternative to clearcutting and offers managers various options including: *shelterwood, single tree selection,* and *group tree selection* (Thompson *et al.*, 1995). Similar to clearcutting, shelterwood methods regenerate even-aged stands, yet retain various canopy components to promote tree reproduction, and shelter seedlings, saplings, and other vegetation components. Conversely, group and single tree selection maintain stands with three or more age or size classes of trees, and provide high habitat diversity for birds (Thompson *et al.*, 1995).

Even though alternative logging systems aim to mimic key properties of the natural dynamics of forests, they still generate distinct forest edges. Yet, forest edges do not always constrain birds, especially when stands retain sufficient vegetation cover to provide refuges (Andrèn, 1994; Drolet *et al.*, 1999). The selection of habitat within fragmented landscapes appears to be species-specific. For instance, blue jays (*Cyanocitta cristata*) and brown-headed cowbirds (*Molothrus ater*) concentrate along forest edges (Paton, 1994). Yet, ovenbirds show strong edge avoidance (Kroodsma, 1984) and least flycatchers (*Empidonax minimus*), black-throated green warblers, and yellow-rumped warblers (*D. coronata*) tend to avoid clearcuts (Lent and Capen, 1995), perhaps because of the higher risk of predation (Desrochers and Hannon, 1997). Hence, birds are sensitive enough to track ecotones in vegetation based on their habitat requirements (Sherry and Holmes 1985; Chen *et al.*, 1992).

For management purposes, considering the ability of each species to cope with land use changes is paramount given the species-specific association of forest birds to habitat features. There is evidence that some birds adapt to landscape changes better than others (Trzcinski *et al.*, 1999). Blake (1991) noted that a nested distribution pattern of bird species might develop in different sized patches within isolated woodlots, because of the particular ability of some species to breed successfully there. Furthermore, Villard *et al.* (1999) argued that there are species-specific thresholds of local movement beyond which individuals cannot maintain a positive energetic balance. On the other hand, sustainable management practices have often used forest birds as indicators of ecosystem integrity. Here, I used six forest bird species as indicators to assess the effect of land fragmentation on forest birds. Kneeshaw *et al.* (2000) listed several features that make birds useful for monitoring forest practice impacts on wildlife:

- Forest birds are likely to respond quickly and strongly to changes in forested landscapes both at the stand and landscape-scale,
- They represent a large proportion of terrestrial vertebrate species in temperate forest ecosystems,

- They are relatively easy to survey because of their vocalizations and drumming, respectively, making them an appropriate species to study harvesting effects,

- They can be surveyed at low cost,

- Being mostly insectivorous, songbirds are an important component of the food web in forest landscapes, and may play a role in regulating insect populations (Niemi *et al.*, 1998) and in the enhancement of forest productivity, and

- A considerable body of literature exists describing their ecology.

Stand-scale vs. landscape-scale analyses on avian ecology

To date, little research has been done on how birds respond to environmental variables has using a stand- and landscape-scale approach despite evidence that birds are sensitive to processes at both levels. In their literature review, Mazzerole and Villard (1999) presented evidence on the influence of stand- and landscape-scale characteristics on the density and occurrence of birds and other species. Their review showed that stand and landscape-scale variables complement one another in predicting species behaviour. Therefore, the interaction of variables across scales shapes spatial dynamics of a given species because factors at either scale may enhance effects differentially for a given taxon. Moreover, Mazzerole and Villard found that birds are particularly sensitive to the landscape context of managed forests (Mazzerolle and Villard, 1999). Hence, inferences on local phenomena are better understood if the influence of the surrounding landscape is also considered.

Bird species appear to perceive forest features at various scales according to their life events (i.e., breeding vs. overwinter migration; Cooke, 2000 pers. comm.). Generally, a species perception of spatial features is closely related to the size of its home range. Study scales smaller than the species home range may yield inaccurate inferences about the species behaviour. Thus, one has to consider the scale at which species use the landscape when examining species dynamics.

METHODS

Study area and experimental design

My research is based on data gathered in 1996 and 1997 under the supervision of Dr. Marc-André Villard (see Villard, 1999). The study sites were located in a managed forest landscape in northwestern New Brunswick, north of the village of Plaster Rock (47°11'N, 67°13'W) (Figure 1). A mix of deciduous and coniferous trees characterizes the forest, which occurs within land managed by Fraser Paper Incorporation. This logging company used three main silvicultural practices: clearcutting in mixed and coniferous stands, variable retention in hardwood stands, and plantation of conifers in clearcuts (Fraser Papers Inc. 1995, Villard *et al.*, 1999). The woodland is characterized by a mix of shade-tolerant hardwoods dominated by sugar maple *(Acer saccharum),* American beech *(Fagus grandifolia),* and yellow birch *(Betula alleghaniensis)* on well drained sites, and coniferous stands along streams and rivers and on poor drained sites (Villard 1999).

Systematic square grids of 64 points were established in an intensively harvested forest (IHL) and in a moderately harvested forest (MHL). The MHL retained 70 percent of forest cover, while the IHL retained only 45 percent of forest cover. The square grids consisted of one macro grid (49km^2; landscape scale) within which two meso grids (6.25km^2; stand scale) were nested (Figure 2). Thus, meso grids were similar in stand composition and silvicultural treatment to the macro grids. Yet, both sets of plots differed from each other in year of harvest and in the main silvicultural techniques performed (Table 1). Survey stations were 1 km apart for the macro grid and 250 m apart for the meso grids, approximately. Some points of both the macro and meso grids overlapped resulting in a total of 182 points surveyed in the moderately harvested landscape and 185 points in the intensively harvested landscape.

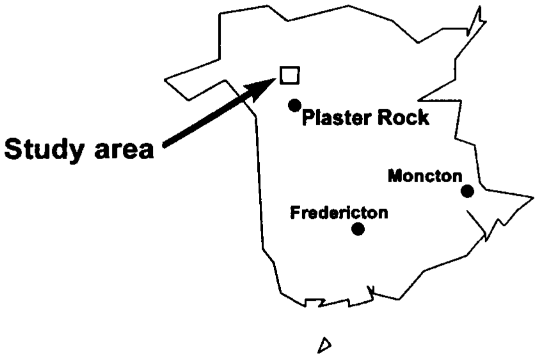

Fig.1. **Study area location in New Brunswick** (Villard, 1999).

Table 1. Landscape management features. Information for the intensively-harvested landscape (IHL) and the moderately-harvested landscape (MHL) is given for the macro grids and nested meso grids nested within such (Villard, 1999).

Landscape	Percent forest cover	Logging technique	Cut block size (ha)	Harvesting years
IHL	45%	clearcutting	>200	1983 - 1995
		selective logging	>400	1991 - 1994
MHL	70%	clearcutting	< 50	1982 - 1989
		selective logging	<100	1993 - 1995

Data collection

Bird Data

My research used point count data on bird species occurrence (i.e., presence/ absence). These data were collected at all stations (367 point counts overall) between 1996 and 1997. The study plots used here were sufficiently large to include a mosaic of microhabitats and a high diversity of bird species. The double-scale approach of my study is appropriate for examining bird responses to habitat features because forest birds are sensitive to both local and landscape scales (Robichaud and Villard, 1999; Villard, 1999).

The community of birds that was surveyed at both the stand and landscape levels was diverse. In the intensively harvested landscape (Figure 2) 81 species of birds were recorded, while 97 bird species were recorded in the moderately harvested landscape. To select the indicator species for my analysis, I first classified the bird community in three groups based on the percent of count points where they occurred. These three groups are: common species (75-100%), intermediate species (25-75%), and rare species (0-25%). Common and rare species were discarded from the analysis. Indeed, given that common species were present in almost all the count points, the analysis would have generated only few boundaries or none. On the other hand, the presence of rare species might have been solely incidental, and thus weakly associated with environmental variables (see Maraj, 1999). Therefore, I focused the analysis on species of intermediate abundance. I selected six bird species because they use a range of habitats (Table 2): least flycatcher *(Empidonax minimus),* black-throated blue warbler *(Dendroica caerulescens),* blackburnian warbler *(Dendroica fusca),* ovenbird *(Seiurus aurocapillus),* American redstart *(Setophaga ruticilla)*, and yellow-bellied sapsucker *(Sphyrapicus varius).* Hence, the response of such birds to forest structure and composition is expected to characterize the overall bird community response to fragmentation (Table 2). To capture the specific sensitivity of birds to forest features while using them as indicator species, I analyzed each species individually.

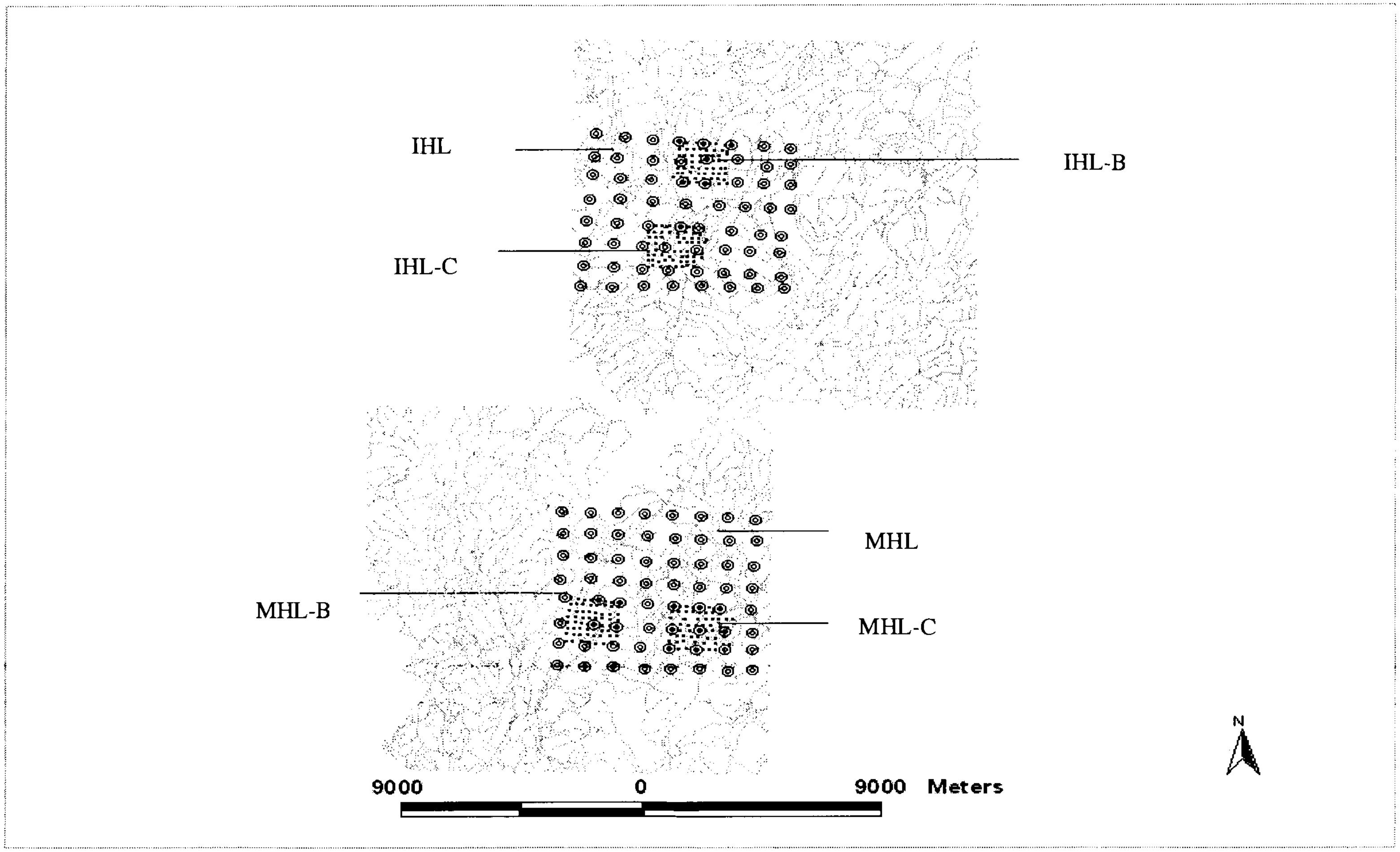

Fig.2. **Study area**. The study sites were established in an intensively harvested (IHL) and a moderately harvested (MHL) landscapes. Circles indicate macro-grids and dots indicate meso-grids for the landscape-scale and stand-scale analyses, respectively.

Table 2. Bird species included in the study. Abundance is shown as absolute number of individuals for each of the study plots (IHL, intensively harvested landscape; MHL, moderately harvested landscape; B and C meso grids within each landscape).

Bird Code*	**Abundance IHL, B, C MHL,B,C**	**Name**	**Forest habitat preference**
AMRE	24, 11, 26 23, 34, 34	American Redstart (*Setophaga ruticilla*)	Open mature stands with deciduous saplings and shrubs; Forages from ground to canopy; Hardwood trees for breeding.
BLWA	23, 21, 30 27, 34, 25	Blackburnian Warbler (*Dendroica fusca*)	Mixed wood mature stands with trees > 18m height; Forages from ground to canopy; conifers for breeding.
BTBW	33, 10, 31, 33, 39, 24	Black-throated blue Warbler (*Dendroica caerulescens*)	Mixedwood stands with dense understory below forest; canopy, understory forager; Mixedwood/ deciduous stands for breeding.
OVEN	41, 42, 44 33, 37, 47	Ovenbird (*Seiurus aurocapillus*)	Mature deciduous, contiguous stands, closed canopy Ground forager Undisturbed forests for breeding.
LEFL	56, 33, 55 32, 57, 48	Least Flycatcher (*Empidonax minimus*)	Semi-open/closed mature, deciduous stands; Deciduous trees for breeding.
YBSA	43, 45, 45 26, 41, 51	Yellow-bellied Sapsucker (*Sphyrapicus varius*)	Mature deciduous/ mixedwood stands, semi-open habitats; Live trees for nesting.

* See Appendix 1 for the meaning of bird codes.

Vegetation Data

Data on forest composition and vegetation layering were collected at each count point. Three 10 m x 20 m plots were sampled: one centered on the station and two 65 meters either to the north, southeast, or southwest (randomly selected direction). Data on forest composition include a count of all the deciduous and coniferous trees, as well as a tally of snags and understory vegetation (i.e., saplings, shrubs, and ground cover). Besides sugar maple and American beech, other deciduous species were also present (Table 3). Seedlings and saplings of deciduous and coniferous species as well as of bryophytes, graminoids, herbs, lichens, among other plants, characterized the understory vegetation.

Table 3. Total abundance of deciduous and coniferous tree species found in a moderately- and intensively-harvested landscapes (MHL & IHL grid sets respectively). ACSA, *Acer saccharum*; FAGR, *Fagus grandifolia*. '**Other**' species for plots IHL-C, MHL-B,-C are the same as IHL-B plot plus the ones indicated by their codes.

			Tree abundance			
	Deciduous trees*				**Coniferous trees**	
	ACSA	**FAGR**	**Other**		**Conifers**	
IHL-B	630	6	188	ACPE, ACRU, ACSSP, BEAL, BEPA, LALA, PRPE, POTR, SASP	486	ABBA, PIGL, PISP, THOC
IHL-C	436	44	218	+ BEPI	639	ABBA, PICE, PIGL, PIMR, THOC, TSCA
MHL-B	956	1013	846	+ ALRU, POBA	998	ABBA, PIGL, PISP, THOC
MHL-C	624	818	350	+ ALRU, POBA	778	ABBA, PIGL, PISP, THOC

* See Appendix 1 for a list of tree species and codes.

Diameter at the breast height (DBH) was recorded, and a decomposition class (Appendix 2) was determined for snags. DBH values were converted into basal area (Appendix 2) for further analysis. Variables describing vegetation layering were vegetation height and percent cover in four different classes: canopy, subcanopy, shrub, and ground (Appendix 3).

Data Analysis

Boundary delineation

Fortin and Drapeau (1995) and Jacquez (1995) developed quantitative spatial methods that can be applied to delineate ecological boundaries. Such methods can also be used to quantify boundary associations between boundaries of one or more variables (Fortin *et al.*, 1996; Fortin, 1999). Fortin and Drapeau (1995) discussed two main techniques to detect and delineate boundaries. The first technique identifies areas where the variable under study rapidly changes over space. The other involves clustering algorithms with spatial constraints that produce spatially homogeneous groups.

To delineate boundaries for bird species and forest components, I used the Hierarchical Agglomerative Clustering technique that incorporates spatial constraints (Maruca and Jacquez, 1997). This technique starts with each object in a group of its own. Then, variables are merged together according to two criteria: 1) two sites of the same group have at least 50 percent similarity in values of variables and; 2) such sites are nearest neighbours. In the latter, the distance between two groups is defined to be the shortest distance between any two members of different groups. Thereby, the spatial relationships among sites are considered in terms of a list of the connections among close neighbours (Fortin and Drapeau, 1995). After each iteration, the closest groups are merged together. In this analysis, 100 iterations were performed and the number of total clusters was set at 15. A preliminary trial yielded 15 as the most appropriate number of clusters that produced more significant results ($p < 0.05$). Also, 15 clusters comprised a balance between too few (number of clusters = 5, 10), thus sparse boundaries, and too many (number of clusters = 25, 30) and contiguous boundaries. In both extreme cases, the analysis would have yielded meaningless results. All the analyses were carried out using GEM software (Maruca and Jacquez, 1997; version 1).

To quantify the association between vegetation and bird species boundaries, and between pairs of bird species, I used two overlap statistics (Jacquez, 1995; Fortin *et al.*, 1996; Appendix 2). To explore whether the location of the vegetation boundaries influences the location of bird species boundaries, I used O_H. This overlap statistic indicates the mean distance from any forest boundary location to the nearest boundary location of each bird species separately. Small minimum distances between boundary locations characterize boundaries that overlap each other. The O_H statistic allows for slight spatial lag between boundaries and implies a certain degree of causality of one variable over another one. Here, I hypothesized that the spatial location of vegetation boundaries influences the distribution of the six bird species studied species-specifically. I used a different statistic, O_S, to assess co-occurrence between bird species. O_S complements O_H by providing information on the how birds relate to each other while responding to spatial variations in vegetation. This statistic computes the number of common boundary locations for all the possible combinations of pairs of birds. This is, the amount of direct overlap (i.e., perfect match) between the boundaries of two bird species.

To examine the significance level for the overlap statistics I used a randomization test (Manly, 1997). This method compares the observed values to their reference distribution. The reference distribution was generated by randomizing the observed bird occurrence across the sample locations (Manly 1997, Fortin 1994). For this analysis, 100 randomizations were performed using Monte Carlo simulations. The assumption behind this procedure is that observed values are equally likely to occur at any location and that they are independent of the values observed at other locations (Manly, 1997).

The hypothesis test using the randomization procedure for O_H focused on the lower *p*-value (p=0.05) of 1-tailed distributions. However, the significance of boundary overlap between bird species was assessed using 2-tailed reference distributions. I used a two-tailed test given that my primary objective was to examine whether the boundaries corresponding to different bird species directly overlapped or not.

RESULTS

Boundary analysis

The main interest of my study lies in examining how bird boundaries relate spatially to particular characteristics of their habitat. The degree of spatial relation is proportional to the distance to the nearest forest boundary location. In other words, spatial proximity between boundaries of vegetation and bird species indicates that vegetation components influence the spatial distribution of birds. Boundary associations were determined between boundary locations in forest structure and composition and bird occurrence as well as between boundaries of pairs of bird species boundaries (see Methods). In analyzing whether forest features influence the occurrence of bird species, an effect of forest features exists on birds when ecological boundary locations are significantly associated in space. The description of the boundary analysis is based on the O_H statistics for the overlap analysis between bird and vegetation boundaries, and O_S for the bird-to-bird boundary examination. All the results are summarized in Tables 4 and 5 respectively. For definition of the codes see Appendices 1 and 3.

Landscape level (IHL and MHL plots)

a) Relationship between forest and bird boundaries

IHL and MHL

Despite the absence of direct spatial overlap (Os) between forest and bird boundaries, a distinct spatial association (O_H) exists between boundaries of vegetation characteristics and bird species occurrence (Figures 3 and 4), and also between bird-to-bird species co-occurrence (Figures 5 and 6). Yet, clear spatial overlap between birds occurred on the IHL: boundaries of black-throated blue warblers (represented by the letters d, e, f, h, i, j, l in Figure 2a) coincided with boundaries in subcanopy height.

At the landscape level for both IHL and MHL only forest structural variables were analyzed (i.e., height and cover of vertical vegetation strata). Based on O_H, the habitat variables in the IHL that were most significantly (positively) related to bird boundary location were canopy, shrub and ground cover height, as well as shrub and ground cover percentage. Looking at each species separately, BTBW presence was positively influenced by all structural variables of the forest. In addition, AMRE, BLWA, and OVEN responded positively to more than 65 percent of such variables (67%, 89% and 78% respectively) whereas LEFL and YBSA had no relationship with these structural variables (Appendix 4).

On the other hand, on the MHL alone, four environmental variables (ground cover, subcanopy, shrub height, and shrub cover percentage) had a positive effect on the location of bird boundaries for the overall community of birds (Appendix 4). In this landscape, AMRE and YBSA responded positively to most of the environmental boundaries at this scale (Table 4).

b) Boundary association among bird species

According to the direct overlap statistics (O_S), the boundaries of AMRE in the IHL significantly overlap with boundaries of all other species except BLWA (Table 5). On the other hand, a direct boundary overlap exists in the MHL between occurrence boundaries of AMRE and BLWA, AMRE and OVEN as well as of LEFL and YBSA (Table 5).

Stand level

a) Relationship between vegetation boundaries and bird boundaries

IHL, B plot

At the stand level, both forest structure and composition boundary locations were considered in the boundary analysis with each of the focal bird species (Appendix 4). The overall outcome of analyzing boundaries at the stand level is that boundaries of the six bird species studied were positively associated with most of the environmental variables measured (Table 4).

Specifically, the boundary analysis showed that each environmental factor analyzed had a significant effect on BTBW [as in the corresponding landscape level, i.e., IHL], while all the variables except 1 to 2 meter tall shrubs positively influenced OVEN boundaries. Moreover, approximately 80 percent and 60 percent of the environmental factors were significantly positively associated with the occurrence of BLWA and AMRE respectively (Table 4). In general, vegetation boundaries that significantly positively influenced the presence of most bird species were height and percent cover of the shrub and ground layer, the 2-4 meter and 4-6 meter tall subcanopy layers, and basal area of American beech and conifers. As on the IHL macro-grid, percent shrub cover was the only variable that significantly affected the occurrence of YBSA since the shrub-YBSA boundaries were close to each other (Appendix 4).

Table 4. Spatial relationship (O_H) between boundary locations of forest structure/composition and bird species. Values refer to the absolute and relative numbers of variables to which each species responded significantly ($p<0.05$). 8 and 19 variables were included in the stand and landscape scale analyses, respectively (IHL, intensively harvested landscape; MHL, moderately-harvested landscape; -B,-C, B and C meso grids within each landscape). See Appendix 4 for a detailed table of the O_H values.

Study site	AMRE*	BLWA	BTBW	LEFL	OVEN	YBSA
IHL	7/8	5/8	8/8	0/8	6/8	1/8
	88%	63%	100%	0%	75%	13%
IHL- B	11/19	15/19	19/19	8/19	18/19	2/19
	58%	79%	100%	42%	95%	11%
IHL-C	12/19	15/19	17/19	16/19	17/19	14/19
	63%	79%	89%	84%	89%	74%
MHL	8/8	3/8	0/8	0/8	3/8	7/8
	100%	38%	0%	0%	38%	88%
MHL-B	11/19	18/19	0/19	2/19	3/19	11/19
	58%	95%	0%	11%	16%	58%
MHL-C	17/19	0/19	19/19	0/19	19/19	0/19
	89%	0%	100%	0%	100%	0%

* Appendix 1 explains the codes.

IHL, C plot

In the IHL-C plot, the environmental factors that have a significant spatial relationship with most bird species were height of the ground cover, percentage of ground cover and shrub cover (both as a single set and subdivided), basal area of both American beech and snags, and the 2-4, 4-6 meter tall subcanopy layer. To a lesser extent, ACSA and other deciduous trees, and conifers had also a positive influence on most bird species.

In the IHL-C plot, a stronger positive effect of the environmental factors on the six bird species occurred. Specifically, the birds responded to approximately 60 percent to 90 percent of the forest characteristics (Table 4). As on the IHL-B plot, BTBW and OVEN were most positively affected by environmental factors. When I analyzed the subcanopy layer as smaller classes (e.g. 2-4, 4-6 meter tall subcanopy) the spatial relationship between the resulting variable boundaries and bird boundaries were more significant than when I examined the subcanopy as a single set. In the former case, the six bird species were spatially significantly related to the 2-4 meter tall and 4-6 meter tall subcanopy strata respectively, whereas in the latter case only LEFL responded. A comparison of boundary analysis outcomes at the stand and landscape levels revealed that significant spatial relationships between bird and vegetation boundaries occurred at the stand level, which were possibly hidden at a larger scale.

MHL, B plot

In the MHL-B plot, the forest characteristics that positively influenced boundaries of most bird species were the assemblage of deciduous trees, and the taller subcanopy (i.e., ≥ 6 meter tall vegetation). In general, the spatial relationship between the boundaries of birds and vegetation locations was weaker and fewer species significantly responded to such elements than in the B plots (Appendix 4).

Boundaries of BLWA were significantly close to most of the vegetation variables. AMRE and YBSA responded similarly to more than 50 percent of the environmental variables. Interestingly, BTBW responded in a peculiar way. Unlike on the IHL-B plot, BTBW showed no relationship with environmental variables in the MHL-B plot (Table 4).

MHL, C plot

In the MHL-C plot, three bird species showed no response to any environmental factor: BLWA, LEFL, and YBSA. The other three species, AMRE, BTBW, and OVEN responded significantly to 90-100 percent of the forest characteristics (Table 4). Therefore, no particular environmental variable had a strong effect on the bird species. Compared to MHL-B plot, boundaries of BTBW on the MHL- C plot were significantly closer to all the forest variables (Appendix 4).

b) Boundary association among bird species

Based on the overlap analysis (Os), there was a boundary association on the IHL-B plot between AMRE and BLWA, BTBW and both LEFL and YBSA, OVEN and YBSA (Table 5). In the IHL-C plot, however, only YBSA had boundaries that spatially overlapped with those of BTBW and LEFL. In contrast to the MHL-B plot, where boundaries of all the pairs of species except BTBW with AMRE and YBSA had significant direct overlap, the only species that show boundary overlap between each other in the MHL-C plot were BTBW with LEFL (Table 5). The number of common bird boundaries was similar in the intensively harvested forest and in the moderately harvested one at both the landscape and stand scale. Yet, birds shared space to a fuller extent in the MHL-B plot (13 common boundaries) than any other plot. The total number of significant common boundaries is summarized in Table 5.

Table 5. Number of common boundary locations (O_S) between pairs of bird species; p-values: * = $p<0.05$, **= $p<0.01$; 2-tail distribution.

	BLWA^{+}	BTBW	LEFL	OVEN	YBSA	Total significant boundaries
	O_S	O_S	O_S	O_S	O_S	O_S
BA						
AMRE	45	44**	46*	45**	46**	5
BLWA		39*	38	38	0	
BTBW			52	47	0	
LEFL				48	0	
OVEN					0	
IHL- B						
AMRE	34*	37	44	40	44	4
BLWA		42	42	43	43	
BTBW			39**	48	42**	
LEFL				42	48	
OVEN					44**	
IHL-C						
AMRE	38	54	46	49	0	2
BLWA		43	37	36	44	
BTBW			46	51	45 *	
LEFL				45	46 *	
OVEN					49	

MHL-A						
AMRE	40**	41	52	39*	41	3
BLWA		48	52	46	35	
BTBW			54	52	44	
LEFL				61	42**	
OVEN					37	
MHL-B						
AMRE	32**	36	34**	30*	31*	13
BLWA		36**	46**	29**	42**	
BTBW			38**	29**	42	
LEFL				31**	46**	
OVEN					29*	
RC						
AMRE	48	40	47	39	50	1
BLWA		44	51	44	51	
BTBW			43*	46	43	
LEFL				42	51	
OVEN					43	

+Appendix 1 explains the codes.

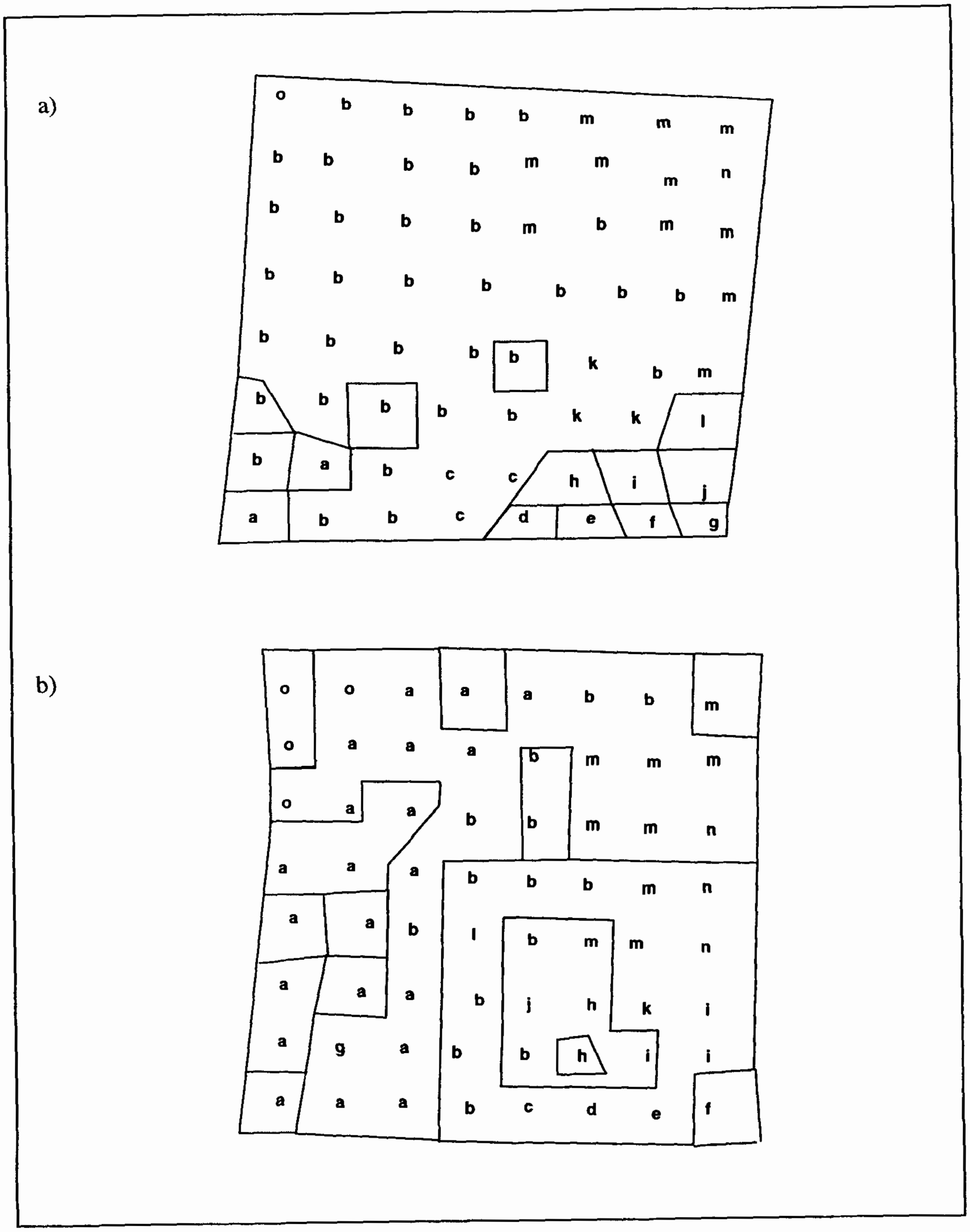

Fig.3. **Ecological boundary overlap at the landscape-scale.** Letters represent bird clusters, polygons refer to forest feature clusters, both resulted from the agglomerative cluster overlap yielding the top 15 groups with the highest occurrence turnover rate. a) cluster overlap (OH=245.34*) between the occurrence of black-throated blue warbler and subcanopy cover height within the intensively harvested landscape (IHL macro-grid); b) cluster overlap (OH=337.07*) between the occurrence of ovenbirds and overall subcanopy height within the moderately harvested landscape (MHL). (* = $p<0.05$, **= $p<0.01$).

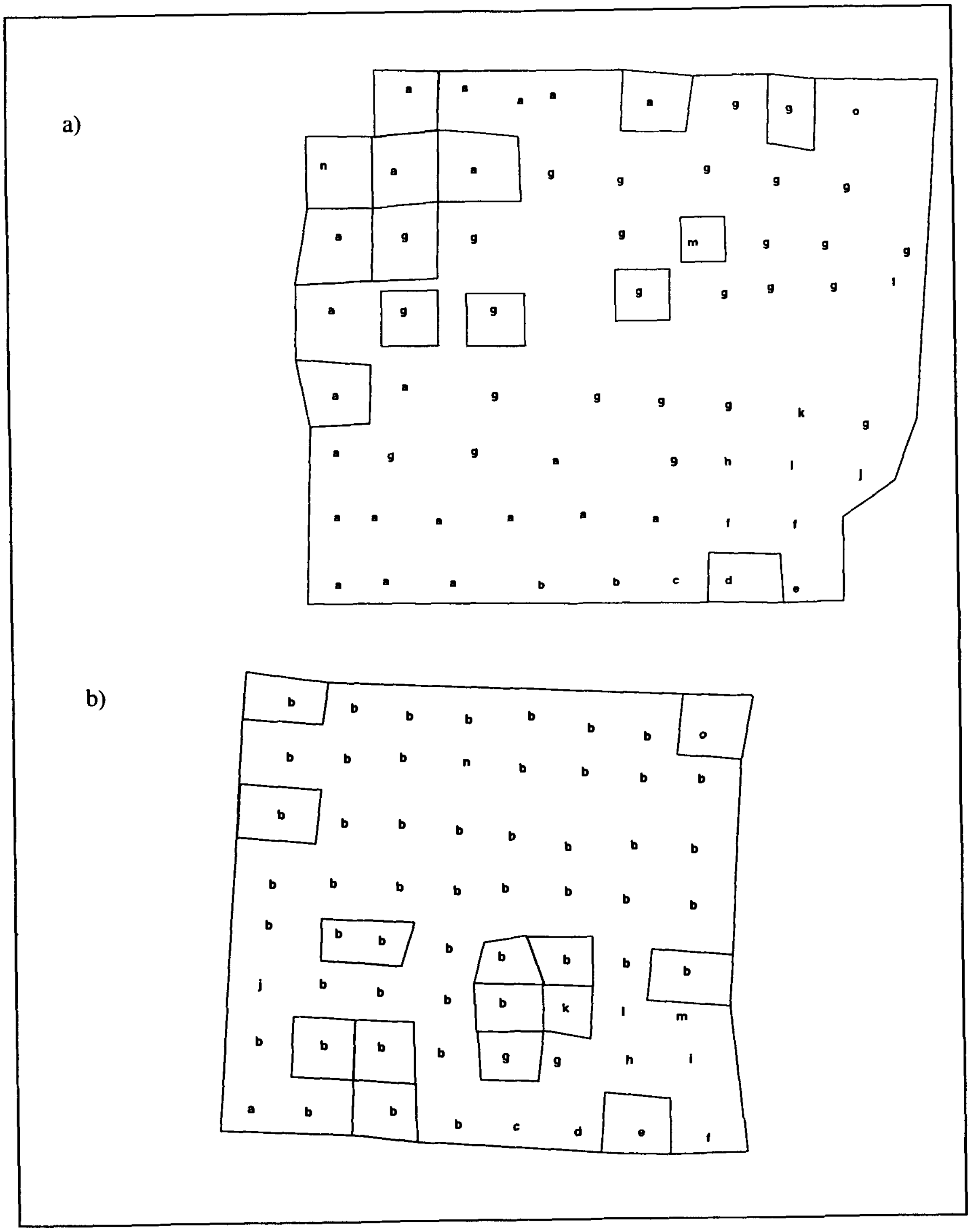

Fig.4.**Ecological boundary overlap at the stand-scale.** Letters represent bird clusters, polygons refer to forest feature clusters, both resulted from the agglomerative cluster overlap yielding the top 15 groups with the highest occurrence turnover rate. a) cluster overlap (O_H=103.81*) between the occurrence of least flycatchers and beech within an intensively harvested stand (IHL-C plot); b) cluster overlap (O_H=233.46**) between the occurrence of ovenbirds and subcanopy cover (class 4-6 m high) within an moderately harvested stand (MHL-B plot). (* = p<0.05, **= p<0.01).

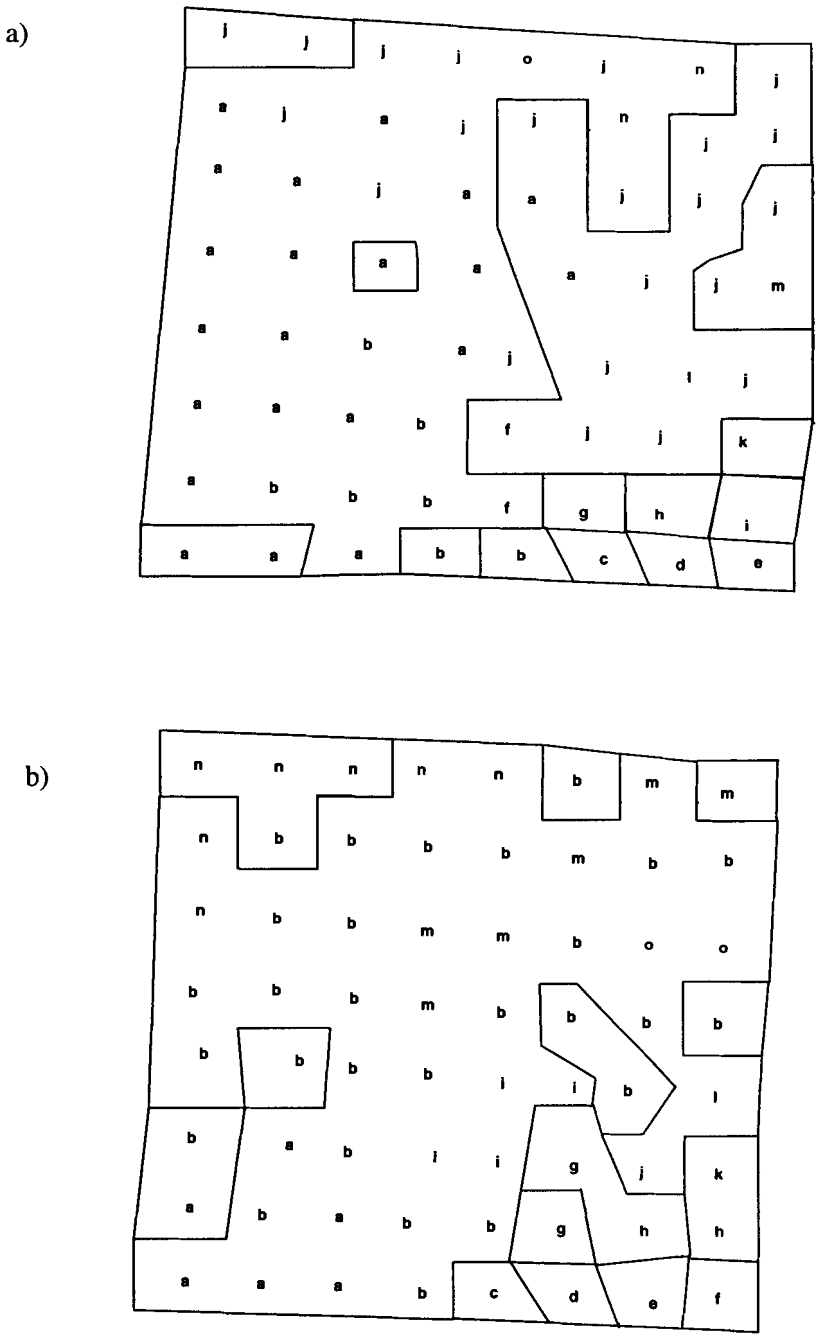

Fig.5. **Bird-bird boundary overlap at the landscape-scale.** Bird clusters resulted from the agglomerative clustering analyses yielding the top 15 bird groups with the highest occurrence turnover rate. a) direct cluster overlap (O_S=46**) between the occurrence of yellow-bellied sapsucker (letters) and American redstarts (polygons) within an intensively harvested landscape (IHL); b) direct cluster overlap (O_S=42**) between the occurrence of least flycatchers (letters) and yellow-belllied sapsuckers (polygons) within an moderately harvested landscape (MHL). (* = p<0.05, **= p<0.01).

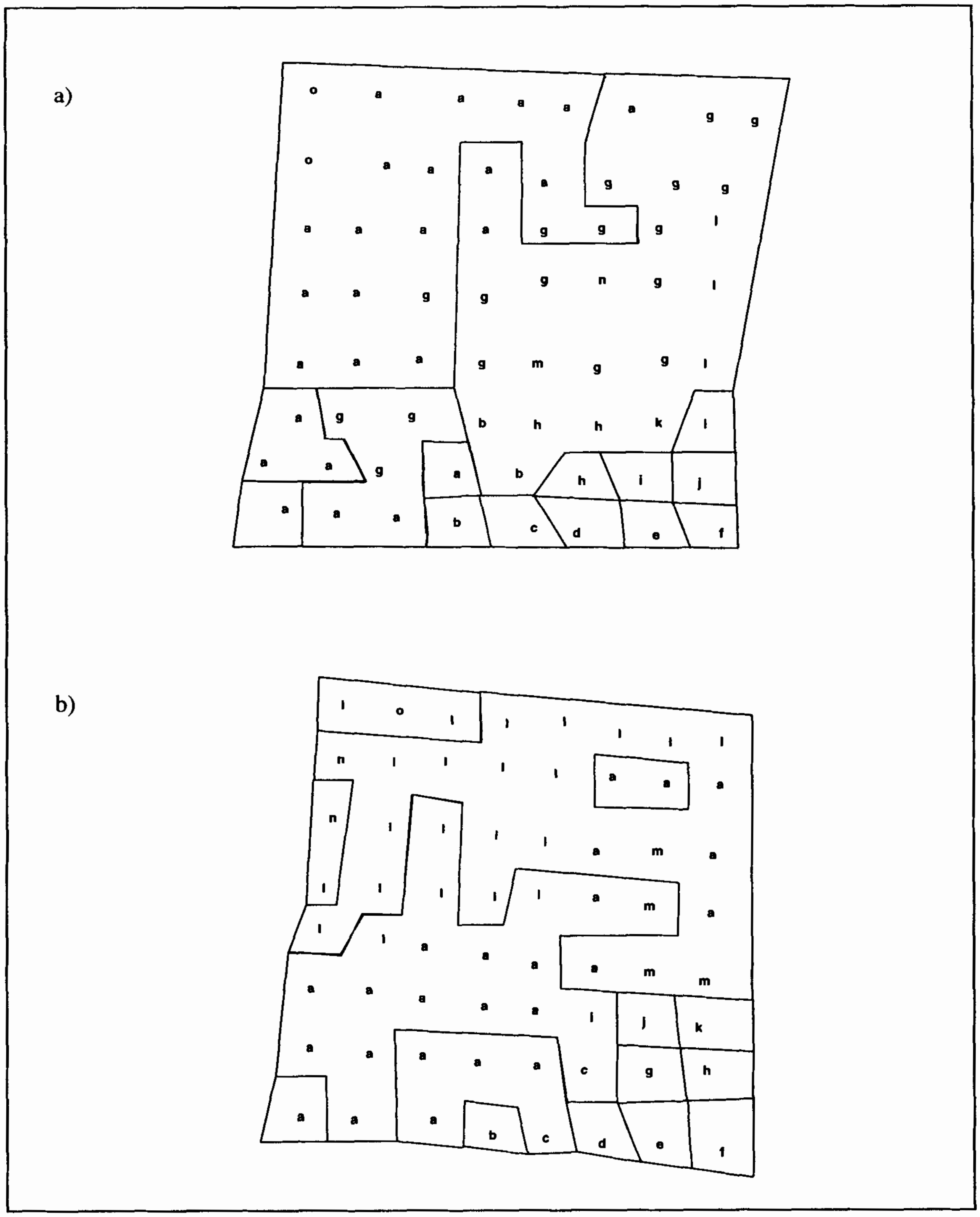

Fig.6. **Bird to bird boundary overlap at the stand-scale.** Clusters of birds resulted from the agglomerative clustering analyses yielding the top 15 bird groups with the highest occurrence turnover rate. a) direct cluster overlap (OS=39**) between the occurrence of least flycatchers (letters) and black-throated blue warbler (polygons) within an intensively harvested stand (IHL-B plot); b) direct cluster overlap (OS=46**) between the occurrence of blackburnian warblers (letters) and least flycatchers (polygons) within an moderately harvested stand (MHL-B plot). (* = $p<0.05$.

DISCUSSION

Birds have distinctive habitat requirements and many species select specific habitats (Whitcomb *et al*, 1981; Litwin and Smith, 1989; Reed, 1989; Freemark and Collins, 1992; Villard, 1998). Moreover, in evaluating associations between bird communities and disturbed habitats as ecological indicators of forest conditions, Canterbury *et al.* (2000) remarked that disaggregating a whole community into guilds could be a useful proxy for evaluating the collective responses of multiple species with a similar ecological behaviour before habitat changes. Hence, the six species that my study included, which I selected from the original avian community, provided reliable information that could be applied to a larger bird species assemblage.

The grouping of birds into common, intermediate and rare species arises from the weak reliability of classifying species along a scale from forest-interior to edge specialists species (Villard, 1998). In a study done to review the empirical evidence for edge avoidance among species currently considered to be forest-interior specialists, Villard (1998) re-evaluated these concepts and their application in ecology and conservation. Villard (1998) concluded that the classification of birds into such guilds has to involve a thorough data collection, which ideally should include nest and territory location information.

Spatial associations of forest and bird boundaries

Landscape scale

Shrub and ground cover boundaries were associated with boundaries of more species than any other structural variable in both the intensively and moderately harvested landscape. This result probably stems from the dense sapling reproduction that takes place in managed forests and, thus, from the availability of diverse foraging and nesting microhabitats for forest birds (Annand and Thompson, 1997). Such a strong association was conspicuous in the intensively harvested landscape for both shrub height and percent ground cover.

In the intensively harvested landscape, black-throated blue warblers showed a positive response to subcanopy cover boundaries. This outcome is consistent with the reported ecology of this species (Holmes and Robinson, 1981; Holmes, 1994; Gauthier and Aubry, 1996). Black-throated blue warblers typically inhabit shrubby sites or forest stands with relatively dense deciduous understory and forage mainly in the lower to mid canopy (Holmes and Robinson, 1981; Holmes, 1994).

American redstarts, on the other hand, have a more flexible association with their habitat. Here, this species responded equally strongly to vertical forest strata in both managed landscapes. Holmes and Robinson (1981) noted that American redstarts and least flycatchers have less tree species preference than other birds such as blackburnian warblers. In these regards, tree species preferences of some birds may be linked to species-specific foraging abilities (Holmes and Robinson, 1981, Robichaud and Villard, 1999). Particularly, American redstarts forage either on the ground or on the upper canopy and occupy a wide variety of open-wooded habitats (Robinson and Holmes, 1984).

Blackburnian warblers and ovenbirds responded similarly to both managed landscapes. Boundaries in ground cover influenced the occurrence of these species. The importance of ground cover boundaries may also be related to these species' foraging behaviour. Blackburnian warblers search for food from near the ground, although they may also feed on the upper canopy of coniferous and/or deciduous forests. Despite findings that blackburnian warblers occupy both high and low canopy (Poole and Gill, 1994), I found that this species exhibited a stronger association with the understory than the upper canopy. Although Holmes and Robinson (1981) reported strong avoidance of sugar maple trees by blackburnian warblers in a northern hardwood forest of New Hampshire, I did not find this pattern at my study sites. The minimum distances (O_H) between the boundaries of blackburnian warbler and sugar maple trees were similar to the distances to beech or conifer trees (Table 4; Appendix 4).

Ovenbirds occur where canopy heights are 16-22 meters, and percent canopy closure ranges from 60-90 percent (VanHorn and Donovan, 1994). In agreement with this, ovenbirds were strongly associated with percent canopy in the intensively harvested landscape. This relationship was stronger in the intensively harvested landscape than in the moderately harvested one (see "Harvest intensity" below). The intermediate frequency of occurrence of most of the six birds in my study, as well as their significant association with the forest understory, can be explained by two additional, interrelated factors. First, these bird species require a solid shrub layer of either deciduous or mixed coniferous/deciduous trees to build their nests (e.g., black throated blue warblers usually nest within 1-1.5 m of the ground; Holmes, 1994). Secondly, bird data collection was carried out during the breeding season, in which these species regularly occupies lower forest strata (Poole and Gill, 1994).

Overall, the strong association of forest cover strata with bird occurrence is consistent with various studies, which have demonstrated that forest cover and forest configuration are good predictors of bird species presence (Villard *et al.*, 1999; McGarigal and McComb, 1995).

Stand scale

St-Louis (2000) studied whether territories of ovenbirds and black-throated blue warblers are bounded by changes in microhabitat. Her results indicated that both biotic and abiotic microhabitat elements (i.e., vegetation features such as conifer and deciduous tree densities, and road proximity, respectively) are associated with the location of bird territories and their limits. Contrary to the null response of least flycatchers to forest components at landscape scale, the stand scale analysis of my study revealed clear boundary associations of least flycatchers and yellow-bellied sapsuckers to forest boundaries (IHL-B and IHL-C plots; Table 4). Yet, least flycatchers did not respond to forest features on the meso and macro-grids of the moderately harvested landscape. Della Sala and Rabe (1987) demonstrated that least flycatchers present a distinctive behaviour before disturbances such as timber harvesting. This species responds to logging in large tracts of forest by shifting breeding aggregations away from disturbances and into the forest interior (Della Sala and Rabe, 1987). Among all the bird species included in this study, least flycatchers avoid harvested areas (Della Sala and Rabe, 1987) and are affected by sugar maple dieback (Gauthier and Aubry, 1996). Sugar maple is the tree species that least flycatchers prefer for nesting (Briskie, 1994). This preference explains why least flycatchers (and yellow-bellied sapsuckers) showed weak associations to forest variables at the stand scale in both landscapes. Indeed, these species are more influenced by forest features in the moderately harvested meso grids than in the intensively harvested ones.

Bird to bird boundary associations

Overlap between boundaries of pairs of bird species was highly variable. Here, boundary analysis was performed in order to assess whether bird species show similar associations with forest attributes. I expected higher number of common boundaries in the intensively harvested landscape than in the moderately harvested one based on the limited habitat area of the former. However, associations between the six bird species birds were similar in both landscapes regardless of the scale of analysis. The presence-absence records used in this study possibly lack the precision needed to yield reliable information on bird spatial locations. In point count surveys, a species is generally recorded if heard or seen within a 100-meter distance. Therefore, presence-absence data yielded only crude information on whether bird territories are distinct or overlapping. Moreover, given that some bird species defend territories against other species (see Villard et al., 1993; Poole and Gill, 1994; Rail et al., 1997), boundary analysis with more precise data (e.g. territory mapping, see Villard et al., 1993; Drolet et al., 1999; Villard 1999; St. Louis, 2000) may better to explain boundary associations between birds. Territory mapping delineates the locations of home ranges allowing a more reliable interpretation of bird community behaviour before land fragmentation and habitat loss. By territory mapping, Kroodsma (1984) found that several songbird species shifted their territories from the forest interior towards the edges of powerline corridors. Territory mapping coupled with surveys of nesting success may also strengthen the ecological association between bird and vegetation boundaries (see "Scope, Limitations, and Recommendations for Future Research" below). However, such survey techniques are more demanding than point count surveys because they require a higher sampling effort.

Scales of analysis (stand scale versus landscape)

In this investigation, I presumed that both stand and landscape scales would complement one another, and that the stand scale would refine coarse relationships between birds and their environment. As I also expected, my results showed that ecological associations were clearer at the stand scale than at the landscape scale. Although this outcome is biased by the inclusion of more parameters in the stand-scale boundary analysis, results at both scales were generally consistent and complementary. Nevertheless, there were unique boundary associations on each plot in both managed forests at the stand scale.

The optimal scale in spatial analysis will depend on the variables studied. For studies of habitat and territory selection by birds, scales of 5-20 hectares (Gauthier and Aubry, 1996) coupled with smaller stand scales produce robust results (Mazzerolle and Villard, 1999; Kroodsma, 1984). Mazzerolle and Villard (1999) reviewed studies where both stand scale and landscape scales were considered. They found that variables at the broader scale predicted species occurrence and abundance in 66 percent of the studies. In Drapeau *et al.'s* (2000) study only 25 percent of the bird species variation in managed and natural forests was explained by scale variables. Specifically, stand-scale variables explained more of this variation than landscape-scale variables. These investigations and my study reinforce the hypothesis that stand and landscape scales complement each other.

As scale is translated from landscape to stand levels, the increase in detail requires more specific experimental variables. Here, subcanopy height boundaries ("subcan") on the C plot of the intensively harvested landscape were significantly associated to least flycatchers occurrence solely, while smaller subcanopy height classes determined the occurrence of the six species. Moreover, the representation of one variable by different measures is also an asset. The importance of incorporating different measures for the same variable (e.g., here, cover percentage and cover height) into ecological analysis is that results may complement each other, and reveal a "hidden" expected outcome, or may differ. In the latter case, further study might be needed to assess the observed differences.

Harvesting intensity

Across landscapes, the relationship between forest birds and vegetation features was stronger in the intensively harvested landscape than in the moderately one. This is consistent with my hypothesis that the intensively harvested landscape would display clearer and stronger ecological associations than the moderately harvested one. Support for this claim is most conclusive in terms of the forest spatial configuration and the resulting forest boundaries or ecotones. This is, the moderately harvested landscape perhaps had more gradual boundaries than the intensively harvested forest. Consequently, birds might have been confined to more limited spaces in the intensively harvested landscape as found by Desrochers and Fortin (2000). Thus, the bird association with forest features could be delineated more precisely by the boundary analysis. Schmiegelow *et al.* (1997) refer to the spatial confinement of species as a "crowding effect". They found that neotropical migrant birds exhibited a stronger crowding effect after harvesting than short distance migrants and residents.

In addition to evidence that birds select their habitat according to species-specific requirements (Canterbury *et al.*, 2000), Lent and Capen (1995) suggested that the spatial relationship between cut and uncut forest fragments in a hardwood forest (Vermont, USA) contributes more to the distribution of birds than inter-specific differences in behaviour. Despite the lack of a control study plot, against which both harvested landscapes of this investigation could have been assessed, there is evidence that managed ecosystems exhibit higher species richness than natural ones (Lent and Capen, 1995; Drapeau *et al.*, 2000). Drapeau *et al.* (2000) found significant differences in the response of birds among three landscapes that have been subject to various large-scale disturbances (human settlement, agriculture, logging, fires, and insect outbreaks). In their study, bird communities of mature forests were more variable in managed forests than in natural forests. Costello *et al.* (2000) found that American redstarts, black-throated blue warblers, and ovenbirds were the most abundant species in group-selection stands and that, along with least flycatchers, these species were also most common in mature natural stands. Thus, it is more feasible to fulfill the diverse habitat requirements of these species in selectively managed forests than in clearcut forests, given that the former present uneven aged vegetation and, thus, a more heterogeneous landscape (Drapeau *et al.*, 2000).

Impacts of timber harvesting on forest ecosystems and forest birds persist over a long time frame (Opdam *et al.*, 1995; Drapeau *et al.*, 2000). The time lag in the distribution of birds after fragmentation depends on the rate of turnover of subpopulations (Opdam *et al.*, 1995). In my study sites, data collection was done about 11-12 years after the last timber harvest. This time lag was sufficient for birds to react to habitat changes and relocate in the forest. It also allowed the forest to regenerate according to the logging rotation periods, and may indeed have provided an optimal habitat mix for a high diversity of birds at the landscape scale. Hence, the ecological associations in both harvested landscapes that were determined through the boundary analysis are logically validated.

Ecological boundary associations

Within fragmented landscapes, boundaries influence the occurrence of bird species (Kroodsma, 1984; Restrepo and Gómez, 1998; St. Louis, 2000). Forest birds are highly sensitive to the width of forest edges (Hawrot and Niemi, 1996; Desrochers and Fortin, 2000; St. Louis, 2000), to the distance from forest interior, and edge age (Restrepo and Gómez, 1998). Despite the hypothesized declines in avian community richness stemming from an increase in brood parasitism and predation rates at the forest boundaries (Villard *et al* 1993; Kneeshaw *et al.*, 2000), both gradual and sharp edges have been linked to higher abundance and diversity of birds (Hawrot and Niemi, 1996). Drapeau *et al.* (2000) noted that boreal forest birds are sensitive to parasitism and predation within 100 meters of fragment edges. In addition, Hawrot and Niemi (1996) argued that breeding birds are sensitive to edge width, amount of suitable habitat, or both. They concluded that bird species diversity was higher at moderately abrupt edges than at sharp or subtle ones.

According to my findings, bird occurrence is influenced not only by boundaries in the vertical structure of the forest, but also by boundaries of various forest components. The space constraint that birds experienced in the intensively harvested plots of my study suggests that forest transition zones and their spatial configuration affect bird presence (see Mazzerolle and Villard, 1999).

SCOPE, LIMITATIONS, AND RECOMMENDATIONS FOR FUTURE RESEARCH

In my research, I explored some analytical tools to determine bird spatial associations with forest boundaries. However, the nature of my data and other limitations of this study limit my conclusions. I now discuss such and consider improvements that could be made in future investigations.

- **Presence-Absence data.** In my study, bird occurrence records were used to investigate associations of birds with habitat features through boundary analysis. Although measures of presence-absence may not necessarily reflect habitat suitability (Hutto, 1998), a first step in evaluating bird habitat involves assessing where species occur to understand their ecology, especially in changing environments. A full understanding of avian community ecology requires additional demographic parameters such as abundance, density, reproductive success and survival, and species diversity. In addition, territory mapping could improve the resolution of distribution patterns (Thompson *et al.*, 1995).

- **Scale of analysis and time frame.** One of the strengths of my study is the use of two scales of analysis. This allowed me to study the response of birds to different forest features. I found that different scales generate different results that provide a baseline for future analyses. Some habitat features may be relevant for birds at one scale but less significant at another (e.g., a tree-fall gap vs. a large clearcut). A multi-scale approach is particularly advantageous in ecological studies of forest birds because many species, like my focal species, have large home ranges and migrate over long routes where they are exposed to many environmental factors.

- **Delineation of edges and ecotones.** The association of birds to edges is challenging because the latter are complex landscape features that may be perceived differently by distinct species. The boundary algorithm and overlap statistics that I used allows analysing spatial data associated with boundaries and model population processes, such as variations in bird population sizes due to landscape changes (see Fortin *et al.*, 2000). These boundary delineation methods reduce the subjectivity that defining edges or ecotones might imply (Hawrot and Niemi, 1996). Furthermore, ecological studies on the association between the behaviour and population dynamics of birds and sharp/gradual edges using different variables (e.g., nest location, dispersion behaviour) would further refine and contribute to my findings (see Bélisle *et al.*, 2000; Desrochers and Fortin, 2000; Walters, 1998). Such studies could also help to explain differential sensitivities of birds to land fragmentation.

◆ **Field experimental design.** In any scientific research, controls provide reference points against which experimental variations may be assessed, and on which management decisions can be based. My findings on spatial boundary associations were different for the 45 percent and 70 percent cover retention. However, the differences were small and more analyses are needed to prescribe a specific harvesting system. Although my objectives were to evaluate how these two specific intensities of harvesting affected the occurrence of birds, a broader range of treatments and uncut controls would have been useful. Future investigations should embrace control and "experimental" variables (see McCollin, 1998) and some replication at all spatial scales studied.

◆ **Ranges of variables included at the stand and landscape level.** Another limitation of this analysis was the uneven information at both scales. The landscape-scale analysis allowed me to examine spatial boundaries of forest structural variables only. At the stand scale, I was able to include boundaries of forest components in my analysis. Ideally, investigations should homogenize the variables that are to be assessed for each study unit. However, I would recommend including variables expressed in different ways (e.g., density/ abundance/ occurrence) in all and each study unit to enhance the scope of analysis.

◆ **Temporal scales.** Long-term studies in avian ecology studies are required because of annual fluctuations in the occurrence and abundance of forest birds (Thompson *et al.*, 1995; Schieck *et al.*, 2000). It is also reasonable to consider that factors extrinsic to the silvicultural treatment shape the ecological associations of birds. Specifically, microclimate may affect the responses of wintering birds to forest boundaries at different life stages (Freemark *et al.*, 1995; Thompson *et al.*, 1995). Studies of the effects of silvicultural practices on the ecology and distribution of birds during non-breeding season are also needed. Assessment of avian ecology over time contributes to the understanding of natural temporal variability.

MANAGEMENT IMPLICATIONS

Generally, the presence of several bird species in both managed landscapes indicates that these species respond flexibly to changes in vegetation composition and forest structure. Particularly, the variable responses of blackburnian and black-throated blue warblers, least flycatchers, and yellow-bellied sapsuckers to forest attributes suggests that these birds are resilient to changes in their habitat. Bird species tend to respond distinctively to habitat changes according to differences in their habitat requirements and the scales at which they interact with the environment (Berg, 1997; Riitters *et al.*, 1996). In addition, persistence of birds in complex landscapes relates to species-specific characteristics, both morphological and behavioural, that allow species adaptation to land changes at different rates (Villard *et al.*, 1993; King *et al.*, 1997, DeGraaf, 1998).

Presumably, species that occur where unnatural disturbances have been frequent can adapt faster to land fragmentation and to subsequent boundary processes than species that have been rarely subject to land changes (King et al., 1997). Schmiegelow *et al.* (1997) argued that such adaptation differences may be related partly to species-specific breeding phenology. Neotropical migrant birds, such as the ones I studied, are normally more constrained in their ability to cope with habitat fragmentation than residents. Normally, migrant birds have limited time during summer to establish their territory, breed, nest, and rear their offspring (Schmiegelow *et al.*, 1997). Intensive and continuous practices of timber harvesting may lead not only to land fragmentation but habitat loss for birds as well. Hence, birds are "forced" to inhabit forest remnants and travel greater distances while bearing unnecessary energy expenditures and increasing susceptibility to predators (Belisle *et al.*, 2000; Villard *et al.*, 1999). In addition, forest patches and their spatial configuration may make it difficult for forest birds like ovenbirds to obtain mates, thus reducing pairing success.

To date, selective logging has been shown to be effective in maintaining the complexity of forests (Bergeron, *et al.*, 1999; Bergeron, 2000). Regardless of the specific approach to alternative forestry, selective logging techniques are designed to mimic the processes that shape forests under natural conditions (Bergeron and Harvey, 1997; Bergeron *et al.*, 1999). Even though new silvicultural systems will never identically resemble natural disturbance dynamics, such practices are far more likely to maintain the complexity of forests than clearcutting (Drapeau *et al.*, 2000). The inherent flexibility of selective forestry makes it more feasible for management objectives to be met.

Studies on conservation ecology have assessed the impact of alternative logging techniques on forest birds (Annand and Thompson, 1997; Darveau *et al.*, 1997; Baker and Lacki, 1997; Costello *et al.*, 2000; Schieck *et al.*, 2000). Annand and Thompson (1997) suggested that a mix of even-aged and uneven-aged silviculture practices creates suitable, heterogeneous habitats for forest birds. Because the ultimate goal in avian conservation is to preserve viable populations of bird species in high quality habitats, I suggest the following management strategies:

♦ **Conduct monitoring of indicator species.** Monitoring is an assessment process of key environmental factors, such as the six indicator bird species of my study, which provides information on changes in bird population dynamics. Monitoring lends itself as a preliminary search for patterns that can be verified in further field studies (DeSante and Rosenberg, 1998). To assess the fitness of neotropical bird populations, I recommend carrying out cross-country-scale monitoring (i.e., local, regional and continental scale; Villard *et al.* 1998), given the long-distance migratory status of the six species I studied and other neotropical birds.

In addition, various bird monitoring programs along migratory routes can be performed to address different aspects of species population dynamics (i.e., "integrated population monitoring", Greenwood *et al.*, 1993). Since migrant birds are affected by environmental changes in different areas throughout their lifetime, scientists and managers would be able to assess ecosystem integrity by monitoring indicator bird species. They would also be able to evaluate their research strategies and management endeavors, and iteratively improve them over time. This approach of considering a management plan as a working hypothesis has been referred to as *adaptive management* and both scientists and managers have successfully implemented it so far (Opdam *et al.*, 1995; Grumbine, 1997).

Similarly to my study, an assemblage of land bird species may serve as indicators to monitor forest ecosystem integrity. The great sensitivity of birds to forest boundaries, as shown in my study and others (e.g., Villard *et al.*, 1993; Villard and Trzincinski, 1999; Desrochers and Fortin, 2000; Kneeshaw *et al.*, 2000; St. Louis, 2000), demonstrates that birds could be used as fine filters to account for the preservation of other organisms. Changes in demographic indices (i.e., declines in population size, reproduction, and overall fitness) of indicator species allow assessing the status of forest habitat quality. The use indicator species may also be effective because: i) large number of species can be monitored simultaneously with a single survey method (see Hutto, 1998); ii) being some of them insectivorous, they play a key role in maintaining the balance of the environment's functions (delaying pest outbreaks) and; iii) their ecological response is possibly representative of other species within the same habitat or community (Niemi *et al.*, 1998; Canterburry *et al.*, 2000; Kneeshaw *et al.*, 2000).

Despite the need to move from a single-species approach to a multi-species one by using a group of indicator species, caution should be taken in the selection and interpretation of the species-specific ecology of birds. Indeed, sole reliance on generalizations regarding the effect of land changes on specific birds could be misleading. My study, among others, showed that each species responds distinctively to habitat and landscape features (i.e., boundaries). For example, in the intensively harvested landscape, ovenbirds are strongly associated with percent canopy while blackburnian warblers respond to the forest understory. Hence, I recommend that forest management should aim to account for species-specific responses within an indicator assemblage. Forest management should also strive to create diverse landscapes to preserve as many species as possible. Despite the pros and cons of most species grouping systems, the use of indicator species may be necessary due to the challenge of meeting the habitat requirements of all species. Once key birds have been selected and management strategies undertaken, my suggestion is that managers should consider monitoring the target species over the long term and over various spatial scales.

Regardless of the indicator system used [1], an ecosystem management approach provides a more integral way for wildlife preservation (Block *et al.*, 1995; Hutto, 1998; Squires *et al.*, 1998). By managing for ecosystem sustainability, positive repercussions for all ecosystem components are derived, including bird populations and communities (Block et al., 1995).

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[1] Some examples of indicator grouping systems are: **ecological guilds** (group of species as functional units), **management assemblage** (group of species that respond in a similar way to the changes in the environment and meet specific management goals), **migratory status** (species that are residents/short-/ long-distance migrants), **hierarchical approach** (monitoring components, structures, and functions of the ecosystem, and **ordination techniques** (identifies groups of species that might be best for monitoring ecosystems) (reviewed by Hutto, 1998).

"To couple good science to management, it is important to develop goals, models, and hypotheses that allow us to systematically learn as we manage. Goals and models guide the development and implementation of management practices. The need to evaluate models and test hypotheses mandates monitoring, which feeds into a continuous cycle of goal and model reformulation" (Haney and Power, 1996)

- **Strive to recreate and maintain the complexity and variability of natural ecosystems in timberlands.** This objective can be reached through alternative silvicultural methods. Bergeron *et al.* (1999) provided a concise framework for selecting the logging technique that best resembles the natural dynamics of the target landscape. Their decision framework is based on the similarities between naturally disturbed forests (e.g. fires, insect outbreaks) and alternative silviculture systems. In mixed-wood forests, as the ones I studied, I recommend to combine various silvicultural treatments and rotate the treatment applied on different stands through time (i.e., "shifting landscape mosaic"; Bergeron and Harvey, 1997; Schieck *et al.*, 2000). This forest management approach will partially recreate the natural composition and structure of stands. It will also resemble the forest age distribution and succession development of a natural landscape (Bergeron *et al.,* 1999). Such management practices are more likely to preserve more diverse bird communities than traditional clearcutting methods. Schieck *et al.* (2000) demonstrated that the retention of vegetation in harvested forests, particularly large tree clumps, may preserve habitat of bird species associated with mature and old growth forests. Thus, a mix of seral stages will possibly benefit some bird populations over others through time (Thompson *et al.*, 1995). However, as long as the entire given landscape mosaic represents particular seral stages, birds will likely find suitable habitats. In a highly fragmented landscape mosaic, I encourage managers to create forested links, or *corridors*, between landscape remnants to facilitate birds in their dispersion (Desrochers and Hannon, 1997; Beier and Noss, 1998).

In addition, management strategies should determine the natural proportions of deciduous, mixed-wood, and coniferous trees in forested landscapes, and incorporate stand succession and edge features into the plans (Hawrot and Niemi, 1996). The entire composition and complexity of a sound forest makes it possible for birds to perform well. In both my study and in Schiek *et al.*'s (2000), even though deciduous saplings and trees dominated the forest, conifers also determined the presence of birds. Thus understanding the complexity and natural variability of the forest is essential for ecosystem management.

- **Ensure a sufficient amount of suitable forested habitat in fragmented landscapes.** As forestry practices continue, management strategies should be aware of the amount of suitable habitat within forest fragments. An intrinsic property of naturally shaped landscapes and selectively cut forests is the presence of ecotones or edges of various types (e.g., widths). Ecotones often display higher biodiversity due to the presence of variety of forest components. As shown here, birds respond distinctively to forest boundaries and can benefit from the resources that are available at boundaries. Desrochers and Fortin (2000) showed that chickadees use vegetation boundaries primarily as movement conduits travelling parallel to them. As a second alternative, birds visit edges to forage since food resources (e.g., arthropods) are more abundant near edges (McCollin, 1998; Desrochers and Fortin, 2000).

If selective logging is widely used, smoother boundaries will become more common. However, the suitability of ecotones as habitats likely has a strong dependence on the amount of forest interior area ("core area"). Indeed, forest fragments with narrow boundaries and large core areas (i.e., high perimeter-area ratio) are more likely to support stable bird populations. Thus, the influence of forest edges and ecotones on birds is positive as long as the forest interior area is large enough to compensate for the negative effect of edges (e.g. predation; Yahner, 1981).

- **Evaluate the appropriate scale of management.** To date, avian researchers have become increasingly aware of the need to include a landscape perspective into their investigations. Particularly, neotropical migratory birds (e.g., AMRE, LEFL, OVEN) cannot be understood only from processes occurring at the habitat level alone (Freemark *et al.*, 1995). Effects of the surrounding landscape are as crucial as microhabitat issues. Thus, I recommend that management decisions be based on both stand and landscape scales. Here, least flycatchers were associated to forest boundaries at the stand scale but not at the landscape scale.

However, the extent of the scale must be relevant to the species under study. Villard *et al.* (1999) suggested that scales in studies on forest birds should be large enough to encompass demographic units of relative independence, at least over short temporal scales. Probably, scales broader than forest bird home ranges are appropriate in a regional context (Freemark *et* *al*., 1995). Moreover, migratory birds are subject to landscape changes along their migratory routes and at their overwintering sites (Cooke, 2000 pers comm.). Since ecological and habitat boundaries are not spatially coincident with geopolitical ones, I consider it essential that researchers and managers establish international decision-making networks. Such networks would improve management strategies by joining efforts and creating conservation partnerships.

CONCLUSIONS

I found clear boundary associations between forest features and six bird species in both the moderately harvested and the intensively harvested landscapes. Spatial boundary relationships between bird and forest components were stronger at the stand scale in the intensively harvested forest. Limited habitat availability (e.g., crowding) in the latter landscape might have been driving such an outcome. Overall, my analysis showed that forest boundaries of the lower forest strata most strongly influenced the occurrence of the six species studied. This result is explained by the extensive coverage of regenerating vegetation common to harvested forests. However, the six bird species I studied appear to perceive boundaries distinctively from one another. My results showed this as species-specific responses to the boundaries of different forest attributes. Hence, my research provides some ecological basis on the differences of bird sensitivity to land fragmentation caused by industrial logging. This study also demonstrated that different scales of analysis identify different components that are implicated in spatial ecological associations. The boundary detection algorithm and overlap statistics used in this study have been shown to be robust and appropriate tools for evaluating land fragmentation and its effects on bird populations. My research has also shown that multi-scale analyses yield more accurate results than those reached by single-scale approaches.

Moreover, my study confirms the importance of habitat heterogeneity for bird populations, based on the significant spatial associations of birds to the location of various forest features. Compared to clearcutting, selective logging creates smoother boundaries and enhances landscape heterogeneity. However, forest managers should consider possible side effects such as crowding. Many ecological studies have shown that the adverse effects of forest fragmentation and forest edges on birds are attributable to the loss of suitable habitat, edge-forest interior ratio, and to the distribution of forest remnants.

Finally, the spatial patterns I found for the six bird species may be generalized to larger communities of birds of conservation concerns. Based on the prompt reaction of birds to forest fragmentation, avian research and management efforts may rely on forest birds to assess the degree and effect of land changes on wildlife.

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APPENDIX 1

Meaning of acronyms for birds and forest trees

Acronyms	**Scientific name**	**Common name**
Bird species		
AMRE	*Setophaga ruticilla*	American redstart
BLWA	*Dendroica fusca*	Blackburnian warbler
BTBW	*Dendroica caerulescens*	black-throated blue warbler
OVEN	*Seirus aurocapillus*	ovenbird
LEFL	*Epidonax minimus*	least flycatcher
YBSA	*Sphyrapicus varius*	yellow-bellied sapsucker
Deciduous trees		
ACPE	*Acer pensilvanicum*	stripped maple
ACRU	*Acer rubrum,*	red maple
ACSA	*Acer saccharum*	sugar maple
ACSSP	*Acer spicatum*	mountain maple
ALRU	*Alnus rugosa*	gray alder
BEAL	*Betula alleghaniensis*	yellow birch
BEPA	*Betula papyrifera*	paper birch
BEPI	*Betula populifolia*	gray birch
FAGR	*Fagus grandifolia*	American beech
LALA	*Larix laricina*	larch
POBA	*Populus balsamifera*	balsam poplar
POTR	*Populus tremuloides*	quaking aspen
PRPE	*Prunus pensylvanica*	pin cherry
SASP	*Salix sp*	willow species

Conifer trees

ABBA	*Abies balsamea*	balsam fir
PICE	*Picea abies*	Norway spruce
PIGL	*Picea glauca*	white spruce
PIMR	*Picea mariana*	black spruce
PISP	*Picea sp*	spruce species
THOC	*Thuja occidentalis*	northern white-cedar
TSCA	*Tsuga canadensis*	eastern hemlock

APPENDIX 2

Basal area conversion

$$BA = 0.000078539816 * DBH^2$$

where:

BA: basal area (m^2)
DBH: diameter at breast height (cm)

Overlap statistics

$$O_s = \mathrm{card}(B_G \cap B_H)$$

$$O_H = \frac{\sum_{j=1}^{N_H} \min(d_{\bullet j})}{N_H}$$

$$O_{GH} = \frac{\sum_{i=1}^{N_G} \min(d_{i\bullet}) + \sum_{j=1}^{N_H} \min(d_{\bullet j})}{N_G + N_H}$$

Decomposition classification

Stage 1
Live

Stage 2
Declining

Stage 3
Dead

APPENDIX 3

Meaning of acronyms for forest features

%can	canopy cover percentage
%GC	ground cover cover percentage
%shrub	shrub cover percentage
%subcan	subcanopy cover percentage
0.5_1	shrub species subclass including trees/shrubs 0.5 to 1 meter in height
1_2	shrub species subclass including trees/shrubs 1 to 2 meter in height
2_4	shrub species subclass including trees/shrubs 2 to 4 meter in height
4_6	subcanopy species subclass including trees/shrubs 4 to 6 meters in height
6_	subcanopy species subclass including trees/shrubs 6 meters and up in height
canopy	canopy height
Ctot	all conifer species
Drest	deciduous species excluding ACSA and FAGR
Dtot	all deciduous species including ACSA, FAGR, and Drest
GC	ground cover species including all non-woody species (excludes water, bare ground, and leaf litter)
hab	canopy, subcanopy, shrub, and GC taken together
shrub	shrub woody species including trees <2 meters
snags	snags (dead standing trees)
subcan	subcanopy species including trees/shrubs 2 to 10 meters in height

APPENDIX 4

Spatial relationships between boundary locations of bird species and forest features. Figures refer to O_H indicating the minimum distance (in meters) from boundaries of any forest element to boundaries of each bird species. *p*-values: * = $p<0.05$, **= $p<0.01$.

	AMRE*	BLWA	BTBW	LEFL	OVEN	YBSA
BA						
canopy	445.39**	781.39*	521.34**	276.62	408.32**	311.03
subcan	351.31*	251.18	245.34*	174.08	206.58	165.10
shrub	448.19**	904.17*	564.42**	323.17	448.89**	311.02
GC	386.36**	828.88*	579.60**	341.64	471.75**	292.37
%can	366.41	634.74	405.61**	250.90	352.43**	252.25
%subcan	353.43*	253.70	248.51*	177.27	210.11	163.27
%shrub	402.91**	844.12*	482.86**	273.74	418.13**	335.93**
%GC	489.14**	1026.10*	694.12**	371.85	543.56**	302.54
BB						
canopy	104.97	129.62*	107.40**	79.71	87.87*	83.03
subcan	90.74	110.75*	119.05**	84.04*	92.13*	58.84
2_4	110.86*	137.20**	154.12**	83.11	110.12**	70.08
4_6	133.99**	127.13**	137.41**	86.98*	116.47**	89.58
6_	87.99	94.80	122.73**	59.62	111.18**	62.85
shrub	147.92**	122.83**	126.46**	87.55*	89.75**	74.81
0.5_1	164.6**	151.09**	159.32**	108.98**	111.94**	79.46
1_2	116.78**	117.37*	124.84*	121.58**	81.92	86.77
GC	136.42**	159.81*	127.16**	93.11	96.68**	87.79*
%can	114.34*	137.85**	11359**	91.72	96.03**	78.77
%subcan	76.27	97.26*	132.51**	46.96	87.59*	41.19
%shrub	147.12*	139.32**	152.03**	87.24*	102.08**	85.52**
%GC	106.15*	141.55**	133.87**	96.88**	94.90**	69.29
ACSA	55.46	104.33*	114.55**	74.63	112.09**	70.17
FAGR	98.65*	52.59	126.93**	70.17*	101.73*	27.97
Dtot	66.26	81.80	117.53**	54.52	110.16**	73.35
Ctot	126.31**	117.19*	127.86**	72.41	107.58**	79.05
Drest	68.94	99.82	152.69**	80.13	136.59**	67.76
Snags	87.22	112.86*	128.93**	54.47	129.57**	81.16
BC						
canopy	81.00	180.19	93.82**	106.50*	103.02**	83.64
subcan	26.63	134.97	22.50	61.92*	32.12	50.09
2_4	100.36**	213.06*	162.10**	94.60**	154.1**	100.52**
4_6	85.73**	255.740*	176.23**	88.08*	142.49**	95.73*
6_	65.92	209.40*	133.84**	101.64**	133.95**	105.26*
shrub	99.36**	262.63*	163.65**	79.39	130.21**	91.28
0.5_1	82.12**	190.55*	171.86**	89.22*	142.97**	101.78**

1_2	94.72**	207.35*	148.98**	105.40**	157.85**	94.88*
GC	71.71*	239.70**	139.87**	90.23**	109.77**	90.57**
%can	83.02*	174.00	97.15*	113.99**	94.60**	75.75
%subcan	37.60	94.74	38.51	91.47*	53.32	45.77
%shrub	101.94**	187.74*	152.25**	106.94**	147.19**	102.59**
%GC	120.71*	314.60*	2216.99**	138.70**	154.05**	142.30**
ACSA	105.29	501.58**	309.22**	118.86*	168.85**	161.67*
FAGR	135.78*	405.45**	298.03**	103.81*	187.29**	141.50*
Dtot	111.88	514.54**	325.10**	118.80	178.63**	147.40*
Ctot	108.01*	427.70*	277.86**	100.72	169.26**	151.02**
Drest	111.88	514.54*	325.10**	118.80*	178.63**	147.40*
Snags	106.40*	351.28*	238.94**	101.05*	172.25**	130.33**
RA						
canopy	525.18**	367.51	305.56	259.30	287.98	515.53*
subcan	503.30**	354.82	323.50	258.79	337.07*	503.02*
shrub	541.43**	381.74*	303.45	228.55	253.44	483.57*
GC	454.86*	377.68*	318.23	228.98	313.52*	499.70*
%can	443.54*	345.90	303.00	255.46	279.61	522.18*
%subcan	534.13**	418.81*	304.93	226.84	285.66	499.03
%shrub	408.91*	318.45	372.36	289.43	325.42*	630.61**
%GC	481.47**	290.45	332.35	274.13	296.81	535.93*
RB						
canopy	218.02	112.66**	176.48	58.18	214.18	131.10
subcan	267.35	127.71**	179.84	71.74	269.61	156.46*
2_4	257.04*	133.98**	135.72	50.53	220.82	120.58
4_6	132.76	119.32**	101.84	78.90	233.46**	156.30**
6_	229.84*	138.87**	138.75	78.94*	217.66	146.08**
shrub	325.01*	124.09	171.96	63.71	246.91	115.11
0.5_1	254.35*	90.84**	168.58	64.38	205.85	112.64
1_2	261.43*	131.92**	183.11	59.63	219.86	150.60*
GC	279.27*	125.32**	182.83	81.75	299.80	125.48
%can	276.66*	127.05**	151.20	73.28	238.44	141.76
%subcan	235.91	118.49**	160.53	72.75	238.86*	141.71*
%shrub	287.76**	124.35**	164.11	73.72	244.66	161.52**
%GC	220.14	144.38**	174.45	82.36*	237.46	167.49**
ACSA	259.11	131.06**	199.74	77.71	266.22	162.15*
FAGR	381.57**	117.98**	154.21	71.60	268.75	112.15
Dtot	269.99**	139.05**	175.68	62.71	235.09*	154.62*
Ctot	183.84	89.73*	140.02	83.00	260.31	122.16
Drest	301.78**	138.7**	183.63	85.58	288.83	169.90**
Snags	215.88	124.92**	174.62	77.06	248.74	151.71*
RC						
canopy	104.58*	84.03	140.5**	78.17	149.63**	129.17
subcan	110.98*	99.43	166.75**	78.49	171.77**	144.31
2_4	106.36*	80.27	115.83*	73.52	117.18**	110.15
4_6	120.96**	70.56	127.29**	78.46	123.84**	112.86
6_	101.36	97.47	197.50**	59.50	205.19**	128.61

shrub	108.91*	87.17	160.12**	77.36	162.90**	122.63
0.5_1	97.62	74.28	129.93*	65.44	139.99**	129.35
1_2	122.19*	98.23	159.83**	75.39	188.79**	137.98
GC	172.35*	125.78	230.60**	73.81	241.97**	159.38
%can	108.02*	82.57	137.61**	65.19	168.40**	124.29
%subcan	126.97*	109.01	173.44**	78.80	186.00**	145.22
%shrub	135.59*	98.58	179.73**	76.91	190.35**	143.39
%GC	141.31*	112.44	182.87**	68.52	200.35**	140.13
ACSA	130.88**	113.22	177.89**	70.83	184.58**	138.51
FAGR	139.06**	119.26	229.51**	63.63	232.57**	164.86
Dtot	116.31*	98.94	164.47**	67.86	164.44**	127.84
Ctot	104.87**	99.88	175.74**	71.85	203.21**	140.76
Drest	113.44*	104.72	160.56**	57.21	185.43**	130.07
Snags	123.52*	110.12	186.01**	77.05	199.82**	138.70

*Appendices 1 and 3 explain the codes.