
Thresholds in Forest Bird Response to Habitat Alteration as Quantitative Targets for Conservation

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Abstract: *The notion that species might exhibit thresholds in their response to habitat alteration is appealing from a conservation perspective. Such thresholds could be used as targets for conservation in managed landscapes. In New Brunswick, Canada, forest management produces mosaics of varying stand age, species composition, and structure. We sampled this gradient in habitat suitability to examine the shape of species response functions and to look for evidence of statistically significant thresholds. We focused our attention on bird species breeding in late-seral forest and surveyed them at 390 point-count stations sampling broad-leaved deciduous to pure coniferous stands and a variety of silvicultural treatments (patch cutting, single-tree selection, spruce plantation [35–45 years old], and no recent treatment). A principal components analysis (PCA) on local vegetation separated stations along two axes reflecting gradients in stand composition and habitat alteration (increasingly open canopy and decreasing density of large trees/snags), respectively. We combined logistic regression and receiver-operating characteristic (ROC) analysis to detect thresholds in species occurrence along these gradients. Of the 42 species frequent enough to be included in the analyses, 13 (31%) showed a significant ($p < 0.01$) negative response to habitat alteration. Eight of the 13 species sensitive to habitat alteration exhibited thresholds in their occurrence after controlling for the suitability of local habitat. According to curves of the expected number of sensitive species (based on their ROC-derived thresholds), canopy closure and the density of large trees (>30 cm dbh) should be at least 70% and 80 stems/ha, respectively, to expect to find the complete assemblage of bird species. However, these values should be viewed as liberal, given the nature of our response variable. More refined (e.g., fitness) parameters should be used to be conservative. Nonetheless, the approach allowed us to establish preliminary quantitative targets for conservation planning based on time-efficient sampling methods, and to explicitly account for the continuous variability existing within and among silvicultural treatments rather than to assume homogeneity within treatments.*

Key Words: conservation targets, forest management, habitat degradation, logistic regression, ROC analysis, silviculture, thresholds

Umbrales en la Respuesta de Aves de Bosque a la Alteración del Hábitat como Objetivos Cuantitativos para la Conservación

Resumen: *La noción de que las especies pueden presentar umbrales en su respuesta a las alteraciones del hábitat es atractiva desde una perspectiva de conservación. Tales umbrales podrían ser utilizados como objetivos de conservación en paisajes bajo gestión. En Nuevo Brunswick, Canadá, la gestión de bosques produce mosaicos de bosques de edades, composición y estructura de especies diferentes. Muestreamos este la aptitud del hábitat en este gradiente para examinar la forma de las funciones de respuesta de las especies y para buscar evidencia de umbrales estadísticamente significativos. Centramos nuestra atención en la especies de aves que se reproducen en bosque seral tardío y las muestreamos en 390 estaciones conteo por puntos en bosques deciduos de hoja ancha hasta bosques puros de coníferas y una variedad de tratamientos silvícolas (corte por parches, selección de árbol único, plantación de abetos [35–45 años de edad] y sin tratamiento reciente). Un análisis de componentes principales (ACP) de la vegetación local separó estaciones a lo largo de dos ejes*

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que reflejan los gradientes en composición del bosque y alteración del hábitat (dosel progresivamente abierto y reducción en la densidad de árboles/tocones grandes), respectivamente. Combinamos análisis de regresión logística y de característica receptor-operador (CRO) para detectar umbrales en la ocurrencia de especies a lo largo de estos gradientes. De las 42 especies suficientemente frecuentes para ser incluidas en el análisis, 13 (42%) mostraron una respuesta negativa significativa ($p < 0.01$) a la alteración del hábitat. Ocho de las 13 especies sensibles a la alteración del hábitat exhibieron umbrales en su ocurrencia después de controlar para la aptitud del hábitat local. De acuerdo con las curvas del número esperado de especies sensibles (con base en sus umbrales derivados del CRO), la cobertura del dosel y la densidad de árboles grandes (>30 cm dap) por lo menos deberían ser de 70% y 80 tallos/ba, respectivamente, para esperar encontrar al ensamble completo de especies de aves. Sin embargo, estos valores deben ser vistos como liberales, dada la naturaleza de nuestra variable de respuesta. Para ser conservadores se deben utilizar parámetros más refinados (e. g. adaptabilidad). Sin embargo, el método nos permitió establecer objetivos cuantitativos preliminares para la planificación de la conservación basada en métodos de muestreo rentables en tiempo y para dar cuenta explícita de la variabilidad continua que existe dentro y entre los tratamientos silvícolas en lugar de asumir que hay homogeneidad dentro de los tratamientos.

Palabras Clave: análisis CRO, degradación de hábitat, gestión de bosques, objetivos de conservación, regresión logística, silvicultura, umbrales

Introduction

The impacts of forest management are difficult to detect because the contrast among patches is not as clear as in urban or agricultural landscapes. The mosaic created by forestry is composed of stands of different age, structure, and composition, which exhibit subtle contrasts in habitat quality (Robinson & Robinson 2001; Lee et al. 2002; Jobs et al. 2004) or permeability to movement (Bélisle & Desrochers 2002; Gobeil & Villard 2002; Robichaud et al. 2002).

Silvicultural treatments vary in intensity from clearcutting over large areas to single-tree selection. Some of these forestry practices produce marginal habitat for certain forest bird species (Chambers et al. 1999; Rodewald & Yahner 2000; Bourque & Villard 2001). Not surprisingly, low-intensity practices such as single-tree selection or thinning seem to have less of an effect on birds of late-seral forests than more intensive treatments (Crawford et al. 1981; Thompson 1993), but they can still significantly reduce the abundance or productivity of certain species associated with closed-canopy stands (Baker & Lacki 1997; King & DeGraaf 2000; Bourque & Villard 2001).

Post-treatment stands are not necessarily uninhabitable. Their suitability depends on the particular sensitivity of the species and the intensity of the silvicultural treatment (e.g., density of mature trees or snags left standing). Thus, the goal is not to determine whether habitat alteration through harvesting has an impact on forest birds, but rather to identify threshold ranges above which they are significantly affected by this alteration. At the level of species assemblages, the goal might be to find thresholds in habitat alteration beyond which the region's most sensitive species are unlikely to be present or to persist (Mönkkönen & Reunanen 1999). Even a preliminary iden-

tification of such thresholds would be a useful step in a proactive conservation plan (Moser et al. 1995).

Until now, thresholds in ecological phenomena have mainly been sought at the landscape level (Andrén 1994; Fahrig 1997; Villard et al. 1999), specifically the identification of thresholds in habitat amount below which effects of habitat fragmentation are added to the nonspatial effects of habitat loss. Researchers investigating thresholds have used a binary definition of habitat (suitable or unsuitable). Few researchers have examined thresholds in suitable habitat at the local (site) scale (but see Hansen et al. 1995; Bütler et al. 2004). Identifying thresholds in species response to the alteration of local habitat should at least allow classifying sites as suitable, marginal, or unsuitable. Such a classification is crucial given the variability in local habitat suitability observed in real-world landscapes.

Finding thresholds is challenging. The apparent reluctance of many researchers to express their management recommendations in quantitative terms may reflect the paucity of statistical approaches available to objectively identify threshold values. To address this problem, we adapted a statistical approach previously used to assist medical diagnostics (Guénette & Villard 2004). We illustrate its application and propose specific ways to explore threshold responses to uni- or multivariate gradients in habitat suitability. Ultimately, our goal is to identify threshold ranges in habitat alteration that can be tolerated by the most sensitive species. Although we recognize the influence of landscape context, we focused our analyses at the local scale (forest stand) because this is a logical first step when quantifying the amount of suitable habitat in a landscape mosaic. Indeed, landscape effects may not be significant when local habitat conditions are controlled (Hagan & Meehan 2002; Lichstein et al. 2002; Guénette 2003). Our intent here is to provide forest managers and

conservation planners with numerical targets with which to define and map suitable habitat. This information can then be used in tactical and strategic planning that provides enough suitable habitat at all times in forest management units.

Methods

Study Area

The Black Brook District (47°23' N, 67°40' W) is a private, managed forest covering 1891 km² in northwestern New Brunswick, Canada. The area is characterized by rolling hills dominated by shade-tolerant deciduous species (27% of the total area) such as sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.), with valleys and plateaus dominated by mixed-wood (13%) and coniferous forest (20%). The dominant conifer species are white, black, and red spruces (*Picea* spp.) and balsam fir (*Abies balsamea* [L.] Mill.). The remainder of the land base is covered by spruce plantations (36%) and other land uses (e.g., roads and water; 4%).

Approximately 8% of stands characterized as productive forest have been harvested through single-tree selection or patch cutting (a type of group-tree selection). Typically, single-tree selection may remove 20 to 40% of timber volume at each entry, depending on the condition of the treated stand (G. Pelletier, personal communication). Successive entries are normally separated by 20 to 50 years. Patch-cutting prescriptions are even-aged treatments, although the size of openings is much smaller than that of clearcuts (often <0.25 ha). This prescription removes approximately 35% of the stand volume at each entry at intervals of 5 to 15 years. Only a few partially harvested sites (single-tree selection and patch cutting) received two harvest entries. Coniferous stands are mainly managed through clearcutting followed by artificial regeneration (mainly monospecific plantations of black spruce [*Picea mariana* (Mill.) B.S.P.] and herbicide application. Approximately 3% of the volume is left as retention patches. Patch cutting has been applied only in deciduous-dominated stands.

Presence and Reproductive Activity of Forest Birds

We surveyed forest songbirds and woodpeckers at 390 stations with a stratified, systematic sampling scheme. Study sites were selected a priori, with a georeferenced forest inventory, to obtain continuous gradients in stand composition (deciduous, mixed, coniferous) and in the intensity of the various silvicultural treatments: 35- to 45-year-old spruce plantations, patch cuts and single-tree selection (last harvest entry dating from 1 to 12 years), and untreated mature stands of each type. Virtually all mature

stands labeled "untreated" had been subjected to high-grading before the 1950s. Each study site ($n = 43$ sites) consisted of 5–10 stations distributed in a horseshoe between access points along gravel roads. This allowed us to obtain a representative sample of the main stand types and silvicultural treatments present while facilitating logistics. Stations were separated by at least 250 m and were at least 100 m from the nearest anthropogenic edge (e.g., road, clearcut).

We conducted surveys in the summers of 2000, 2001, and 2002 ($n = 210, 83, 97$ stations, respectively). During the 3 years, we sampled 44 stations during successive years specifically to test year effects. We visited each station three times during the breeding season (end of May to mid-July) between 0520 and 1125 (85% of counts completed before 1000). We used the mobbing playback method developed by Gunn et al. (2000). This method consists of a conventional point count of 5 minutes, a second 5-minute period during which we broadcast a recording of Black-capped Chickadee (*Poecile atricapillus*) mobbing calls, and a third 5-minute period of silent point count. Chickadee mobbing calls attract many different species, and they significantly increase the probability of visual detection of individuals (J.-S.G. & M.-A.V., unpublished data). We adjusted playback volume so that it appeared equivalent to the intensity of chickadee calls perceived by the human ear. All individuals detected visually or aurally within a radius of 100 m were recorded. Most of the species surveyed have a small home range (0.1–2.0 ha; Gauthier & Aubry 1995). Thus, we assumed that the buffer of at least 50 m among successive stations made "double counts" of individuals unlikely (Bibby et al. 1992).

Species were considered present at a station when they were detected in at least one of the three visits (total of 45 minutes per station). Censusing was interrupted when weather conditions interfered with species detection (rain or high winds). Species detected at < 5% of our stations were excluded from statistical analyses.

Vegetation Sampling

We collected vegetation data from mid-July to early August each year. We quantified vegetation structure and composition along three 80-m-long transects oriented to the north, southeast, and southwest of each point-count station. Species and diameter at breast height (dbh) were recorded for all trees and snags (dbh ≥ 10 cm) located within a 2-m band on either side of transects. We also counted logs (dbh ≥ 10 cm) crossing each transect. At the station and every 25 m along transects (10 plots/station), we quantified canopy closure, canopy height, and, within a 5-m radius, sapling density (>1 m high; <8 cm dbh) and groundcover (herbs, shrubs, mosses, woody material, and bare ground). Canopy closure and *Usnea* spp. cover were estimated by counting the squares with canopy

foliage through a 5 × 5 transparent grid made of Plexiglas and held overhead. We measured canopy height with a clinometer. From these measurements, we calculated 23 variables reflecting a variety of stand attributes likely to be altered by silvicultural practices and we then selected one variable from strongly correlated sets ($r > 0.9$; Tabachnick & Fidell 1996). The analyses were thus conducted on a subset of 16 variables. In the total sample ($n = 390$), the proportion of deciduous trees averaged 60.2% (SD = 37.1%, range 0–100%), whereas the mean density of trees ≥ 30 cm dbh was 80.6 stems/ha (SD = 53.0%, range 0–260.4).

Statistical Analyses

We used a principal components analysis (PCA) to identify the major multivariate gradients in vegetation structure and composition. Appropriate transformations (e.g., logarithmic, arcsine) were applied to the variables before the analysis (Zar 1999). We determined the number of interpretable principal components and their association with particular variables with the broken-stick criterion (Jackson 1993; Peres-Neto et al. 2003). To examine the variability in the effects of the various silvicultural treatments, we added ellipses for each treatment type on the PCA biplot. Ellipses were set at 68% to include sampling stations within 1SD from the centroid in PCA space. Then we examined the relationships between the probability of presence or reproductive activity of each species and the principal components scores with logistic regression.

We selected species for threshold analyses according to the relative strength of association between their presence or absence and local habitat variables. We conducted this selection with stepwise (forward) logistic regression, which is based on the probability of the Wald statistic ($p < 0.01$ for enter; $p > 0.10$ for removal). We validated these models by comparing those obtained from the stepwise procedure with models built by entering variables manually according to the likelihood ratio test (Hosmer & Lemeshow 2000). Species responding significantly to the habitat alteration gradient (PC2—see Results) were retained for further analyses. Before those analyses, we performed a McNemar test on each species, with data from the 44 stations visited over two separate years, which indicated no year effect on species occurrence patterns.

We found significant spatial autocorrelation in all independent variables. Except for the Blue-headed Vireo, Black-capped Chickadee, and Black-throated Green Warbler (scientific names provided in Table 1), correlograms also indicated significant positive spatial autocorrelation in the presence or absence of all species examined. Typically, spatial autocorrelation in both occurrence and independent variables was significant over distances < 500 m. To reduce the likelihood of committing Type I er-

rors due to spatial autocorrelation and to account for the large number of simultaneous tests, we used a conservative level of significance ($\alpha = 0.01$) in our analyses. Although more sophisticated methods exist for correcting for spatial dependence in variables (Dutilleul 1993), such techniques are restricted to normally distributed variables (Fortin & Payette 2002). Adjusting the α level does not correct spatial autocorrelation per se but does provide some assurance that significant results detected are indeed significant (Dale & Fortin 2002).

The performance of several validation methods used in logistic regression has recently been evaluated (Fielding & Bell 1997; Manel et al. 2001). The majority of these methods are based on a confusion matrix, which classifies cases as (1) true positives, (2) false positives, (3) false negatives, and (4) true negatives by comparing observed values with predictions from the regression model. These techniques assume an arbitrary threshold probability value (usually 0.5). Instead, we used threshold-independent receiver operating characteristic (ROC) curves to assess the performance of our regression models (Zweig & Campbell 1993). The ROC evaluates the performance of a model for all possible threshold values. Therefore, the threshold selected is influenced (or adjusted) by the frequency of occurrence (or prevalence) of the phenomenon under study (Manel et al. 2001; Guénette & Villard 2004). The ROC curve depicts sensitivity and specificity pairs for the entire threshold range, where sensitivity is the proportion of true positives correctly predicted and specificity is the proportion of true negatives correctly predicted (Manel et al. 2001). The area under this curve represents an accurate measure of model performance. A value of 1.0 would represent a perfect model (i.e., perfect discrimination of presence and absence), whereas a value of 0.5 would indicate no significant difference between the two states (DeLeo 1993). We compared area under the ROC curve to Nagelkerke's R^2 and Hosmer-Lemeshow test (Gutzwiller & Barrow 2001).

DeLeo (1993) defined four types of thresholds that can be obtained from ROC curves: (1) optimum sensitivity, (2) optimum specificity, (3) equal sensitivity and specificity, and (4) maximum accuracy. We chose maximum accuracy because we wanted to determine a cut-off value providing the best agreement between observed presence and absence or, in other words, the point where the sum of specificity and sensitivity is maximized. Even though ROC analysis has long been used to identify decision thresholds in medical studies, Manel et al. (2001) reported that ROC curves had been used in $< 1\%$ of published presence or absence studies in ecology, and we know of only one ecological study applying ROC analysis to obtain decision criteria (Bonn & Schröder 2001).

Using the univariate logistic regression equation and the cut-off value obtained through ROC analysis, it is possible to calculate the corresponding threshold value on the x-axis (x_t):

Table 1. Bird species detected in at least 5% of stations in the Black Brook District managed forest ($n = 390$).

Code	Common name	Scientific name	Freq. ^a	Mean ^b	R ^c
YBSA	Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	0.61	1.2 ± 0.5	+
DOWO	Downy Woodpecker	<i>Picoides pubescens</i>	0.18	1.2 ± 0.4	+
HAWO	Hairy Woodpecker	<i>Picoides villosus</i>	0.12	1.2 ± 0.4	
PIWO	Pileated Woodpecker	<i>Dryocopus pileatus</i>	0.08	1.0 ± 0.0	
OSFL	Olive-sided Flycatcher	<i>Contopus borealis</i>	0.07	1.2 ± 0.4	
EAWP	Eastern Wood-Pewee	<i>Contopus virens</i>	0.27	1.2 ± 0.4	+
YBFL	Yellow-bellied Flycatcher	<i>Empidonax flaviventris</i>	0.18	1.3 ± 0.7	–
ALFL	Alder Flycatcher	<i>Empidonax alnorum</i>	0.05	1.4 ± 0.8	+
LEFL	Least Flycatcher	<i>Empidonax minimus</i>	0.37	2.2 ± 1.3	
BHVI	Blue-headed Vireo	<i>Vireo solitarius</i>	0.55	1.4 ± 0.5	–
PHVI	Philadelphia Vireo	<i>Vireo philadelphicus</i>	0.07	1.3 ± 0.5	+
REVI	Red-eyed Vireo	<i>Vireo olivaceus</i>	0.62	1.9 ± 0.8	+
BLJA	Blue Jay	<i>Cyanocitta cristata</i>	0.28	1.3 ± 0.6	
BCCH	Black-capped Chickadee	<i>Poecile atricapillus</i>	0.67	1.8 ± 0.9	
BOCH	Boreal Chickadee	<i>Poecile hudsonia</i>	0.21	1.5 ± 0.7	–
RBNU	Red-breasted Nuthatch	<i>Sitta canadensis</i>	0.17	1.2 ± 0.5	–
BRCR	Brown Creeper	<i>Certhia americana</i>	0.18	1.1 ± 0.3	–
WIWR	Winter Wren	<i>Troglodytes troglodytes</i>	0.51	1.3 ± 0.6	–
GCKI	Golden-crowned Kinglet	<i>Regulus satrapa</i>	0.38	1.4 ± 0.6	–
RCKI	Ruby-crowned Kinglet	<i>Regulus calendula</i>	0.16	1.3 ± 0.5	
SWTH	Swainson's Thrush	<i>Catharus ustulatus</i>	0.60	1.4 ± 0.6	
HETH	Hermit Thrush	<i>Catharus guttatus</i>	0.53	1.2 ± 0.4	
AMRO	American Robin	<i>Turdus migratorius</i>	0.36	1.2 ± 0.4	
NAWA	Nashville Warbler	<i>Vermivora ruficapilla</i>	0.22	1.3 ± 0.6	
NOPA	Northern Parula	<i>Parula americana</i>	0.76	1.5 ± 0.6	–
CSWA	Chestnut-sided Warbler	<i>Dendroica pensylvanica</i>	0.23	1.3 ± 0.6	+
MAWA	Magnolia Warbler	<i>Dendroica magnolia</i>	0.40	1.4 ± 0.6	–
BTBW	Black-throated Blue Warbler	<i>Dendroica caerulescens</i>	0.67	1.7 ± 0.8	+
YRWA	Yellow-rumped Warbler	<i>Dendroica coronata</i>	0.48	1.4 ± 0.7	–
BTNW	Black-throated Green Warbler	<i>Dendroica virens</i>	0.80	1.7 ± 0.7	
BLWA	Blackburnian Warbler	<i>Dendroica fusca</i>	0.43	1.2 ± 0.5	–
BBWA	Bay-breasted Warbler	<i>Dendroica castanea</i>	0.24	1.3 ± 0.6	–
BWWA	Black-and-white Warbler	<i>Mniotilta varia</i>	0.06	1.2 ± 0.6	
AMRE	American Redstart	<i>Setophaga ruticilla</i>	0.26	1.3 ± 0.6	+
OVEN	Ovenbird	<i>Seiurus aurocapilla</i>	0.72	1.8 ± 0.8	–
MOWA	Mourning Warbler	<i>Oporornis philadelphica</i>	0.19	1.2 ± 0.4	+
COYE	Common Yellowthroat	<i>Geothlypis trichas</i>	0.07	1.3 ± 0.5	
SCTA	Scarlet Tanager	<i>Piranga olivacea</i>	0.09	1.2 ± 0.4	
WTSP	White-throated Sparrow	<i>Zonotrichia albicollis</i>	0.34	1.7 ± 0.9	+
DEJU	Dark-eyed Junco	<i>Junco hyemalis</i>	0.29	1.3 ± 0.6	
RBGR	Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	0.26	1.2 ± 0.5	+
PUFI	Purple Finch	<i>Carpodacus purpureus</i>	0.29	1.1 ± 0.4	

^aFrequency of occurrence (i.e., proportion of stations where the species was detected).

^bMean number of individuals detected at each occupied station (±SD).

^cSignificant relationships with habitat alteration: +, species positively related to habitat alteration; –, species negatively related to habitat alteration.

$$x_i = \frac{\ln\left[\frac{1}{c} - 1\right] + \beta_0}{-\beta_1},$$

where β_1 represents the coefficient of regression; β_0 , the intercept; and c , the cut-off value. This equation was obtained by isolating x_i in the logistic regression equation. This value corresponds to the projected point on the x-axis where the logistic curve crosses the cut-off value derived from the ROC analysis.

When identifying occurrence thresholds along the gradient in habitat alteration (PC2, see Results), we controlled for stand composition (PC1). For this purpose,

we selected, for each species, only stands that were suitable (i.e., below or above the threshold obtained on PC1, depending on their compositional preference), and then we ran the ROC analysis again to identify the threshold on PC2.

Results

Over the 3 years of the study, we detected 81 bird species. Among these, 42 species were deemed frequent enough

Table 2. Factor loadings from a principal components analysis on local vegetation variables sampled within the Black Brook District managed forest ($n = 390$).

Variable*	PC1	PC2
Relative proportion of hardwood	0.830	0.354
Coefficient of variation in basal area of trees ≥ 30 cm dbh	0.721	-0.134
Percent ground cover of mosses	-0.643	-0.370
Coefficient of variation in basal area of trees ≥ 10 cm dbh	0.633	0.031
Density of trees ≥ 30 cm dbh (stems/ha)	0.608	-0.607
Percent cover of <i>Usnea</i> spp.	-0.580	-0.365
Percent cover of bare ground	0.507	-0.131
Density of trees ≥ 20 cm dbh (stems/ha)	0.097	-0.900
Basal area of trees ≥ 20 cm dbh (m^2/ha)	0.519	-0.793
Density of snags ≥ 10 cm dbh (stems/ha)	-0.240	-0.652
Percent canopy closure	0.391	-0.461
Number of logs	-0.325	-0.378
Percent cover of herbs	-0.282	-0.158
Sapling density (stems/ha)	-0.044	0.147
Percent cover of coarse woody material	-0.379	0.008
Percent cover of low shrubs	0.456	0.292
Eigenvalue	4.016	3.151
Variance explained	25.098	19.697
Cumulative variance explained	25.098	44.795

*Abbreviation: dbh = diameter at breast height.

to allow statistical analyses (Table 1). The three most frequent species were the Black-throated Green Warbler (80%), the Northern Parula (76%), and the Ovenbird (72%).

The PCA produced two significant axes, which jointly explained 45% of the variance in habitat data (Table 2). The first principal component (PC1) represented a gradient in forest stand composition from coniferous to deciduous stands (Fig. 1). A positive score indicated a high relative density of deciduous trees, a low percent ground-cover of mosses, and a complex structure (high coefficient of variation in basal area). The PC2 chiefly separated stations as a function of the density and basal area of large trees (>20 cm dbh), canopy closure, and snag density (Table 2). We interpret this axis as a gradient in habitat alteration. We use the term *habitat alteration* rather than *harvesting intensity* to reflect that even stands classified as untreated were distributed relatively widely along PC2 (Fig. 1), indicating that they also varied in their structure. The size and overlap of the 68% ellipses corresponding to each silvicultural treatment indicated the high degree of variability existing within and among these treatments (Fig. 1). Selection cuts showed their greatest variability along this axis. Indeed, some of these stands were very lightly harvested, whereas only scattered live trees and snags were left in others. This treatment was applied both to deciduous and mixedwood stands, which explains the width of the corresponding ellipse along PC1.

Of the 42 species included in the analyses, the probability of presence of only 9 (Hairy Woodpecker, Pileated Woodpecker, Black-capped Chickadee, Blue Jay, Swain-

son's Thrush, Hermit Thrush, Black-and-white Warbler, Common Yellowthroat, and Purple Finch) was not significantly related ($p > 0.01$) to at least one of the two axes. According to the area under the ROC curve (AUC), prediction accuracy varied from poor ($AUC < 0.700$) to excellent ($AUC \geq 0.900$). For the 33 species showing a significant relationship with at least one of the two principal components, the AUC was strongly correlated with Nagelkerke's R^2 ($r = 0.920$, $p < 0.001$), whereas its correlation with the Hosmer-Lemeshow statistic ($r = -0.301$, $p = 0.089$) was marginally nonsignificant. Thus, the AUC and Nagelkerke's R^2 provided a very similar assessment of model fit.

Relationships between stand composition (PC1) and bird species presence (Table 3) essentially reflected what is known from the literature (e.g., Gauthier & Aubry 1995) and allowed us to refine our identification of thresholds along the gradient in habitat alteration (i.e., PC2). Relationships were negative for species associated with coniferous forest (e.g., Yellow-bellied Flycatcher, Boreal Chickadee, Golden-crowned Kinglet) and positive for those known to prefer deciduous-dominated stands (e.g., Ovenbird). Species that were not significantly related to this coniferous-deciduous gradient are either generalist in their response to stand composition (e.g., Black-capped Chickadee, Brown Creeper) or show a significant preference for mixed-wood stands (e.g., Blackburnian Warbler; J.-S.G. & M.-A.V., unpublished data).

To determine thresholds in species response to habitat alteration, we retained only the 25 species that had a significant relationship ($p < 0.01$) with PC2. Among these, 13 were negatively affected by habitat alteration and hereafter are referred to as "sensitive species" (Table 3). Of these 13 species, 8 showed significant relationships after accounting for local habitat suitability based on their thresholds along the gradient in stand composition (PC1). Of the 12 species responding positively to habitat alteration (Table 4), 7 showed significant relationships when accounting for stand composition.

The four species exhibiting the highest discrimination between presence or absence based on habitat alteration were the Golden-crowned Kinglet ($AUC = 0.754$), the Winter Wren ($AUC = 0.722$), the Ovenbird ($AUC = 0.717$), and the Blackburnian Warbler ($AUC = 0.713$; Fig. 2). The most sensitive species (i.e., those with the lowest threshold value on PC2) were the Blackburnian Warbler, the Yellow-bellied Flycatcher, and the Brown Creeper. The least sensitive, based on this approach, were the Blue-headed Vireo and the Golden-crowned Kinglet. We delineated "conservation target zones" for four sensitive species on the PCA biplot by shading areas where they were more likely to be present according to the thresholds found on each axis (Fig. 3). This procedure helps to focus the attention on portions of the PCA biplot (i.e., stand and treatment types) corresponding to potential habitat.

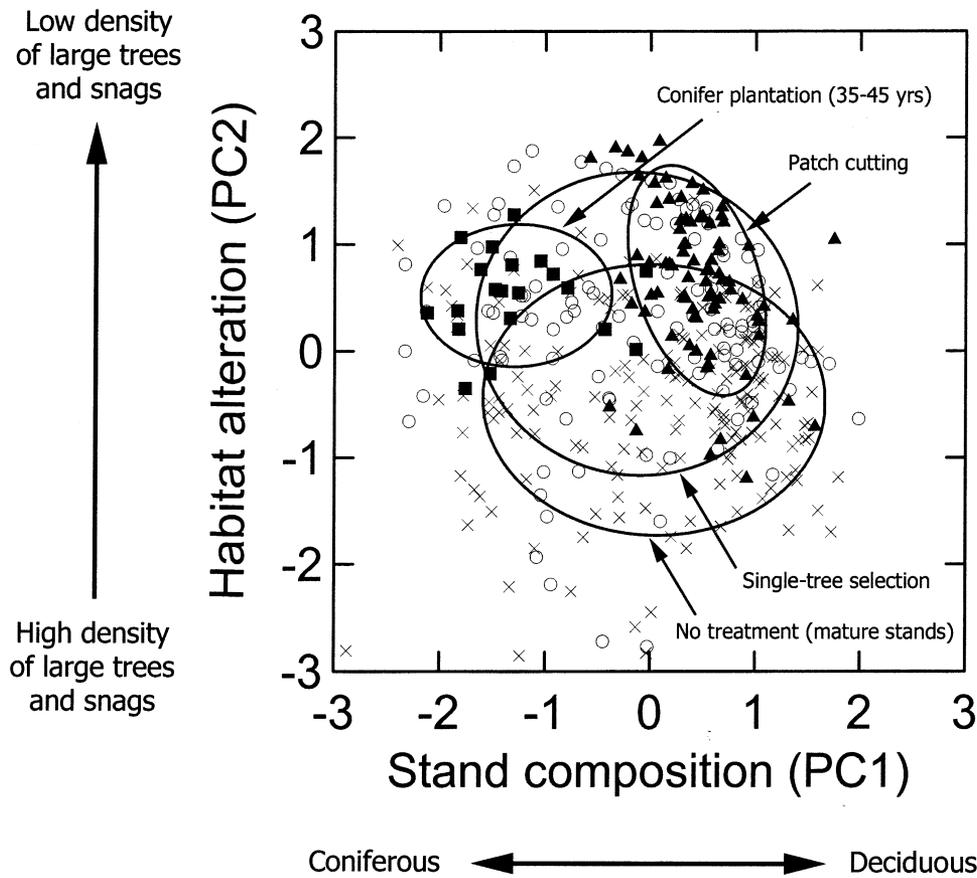


Figure 1. Ordination of the 390 sampling stations obtained from a principal components analysis (PCA) on local vegetation variables (see also Table 2). Confidence ellipses (68%) are shown for each silvicultural treatment sampled (x, no recent treatment; o, single-tree selection;  , patch cutting;  , 35- to 45-year conifer plantation).

Table 3. Thresholds (x_t) in the occurrence of 13 bird species sensitive to habitat alteration, after controlling for the suitability of local habitat (see Methods).

Species ^a	Gradient in stand composition (PC1; n = 390)					Habitat alteration gradient (PC2)					n
	$\beta_r^{b,c}$	β_o^d	AUC ^e	c ^f	x_t^g	$\beta_r^{b,c}$	β_o^d	AUC ^e	c ^f	x_t^g	
YBFL	-1.373***	-2.032	0.830	0.193	-0.44	-0.709***	-0.240	0.680	0.431	0.05	117
BHVI	-0.435***	0.208	0.622	0.549	0.02	-0.513**	0.783	0.674	0.571	0.97	167
BOCH	-1.882***	-2.144	0.902	0.148	-0.21	ns					140
RBNU	-0.474***	-1.627	0.620	0.200	-0.50	ns					112
BRCR	ns					-0.415***	-1.574	0.619	0.167	0.08	390
WIWR	-0.495***	0.027	0.637	0.514	-0.06	-0.797***	0.788	0.722	0.651	0.20	157
GCKI	-1.418***	-0.617	0.834	0.329	0.07	-1.027***	0.956	0.754	0.512	0.88	174
NOPA	1.039***	1.424	0.755	0.624	-0.88	-0.631**	2.015	0.647	0.863	0.28	299
MAWA	-1.095***	-0.483	0.774	0.389	-0.03	ns					162
YRWA	-1.129***	-0.056	0.772	0.523	-0.13	ns					150
BLWA	ns					-0.716***	-0.318	0.713	0.445	-0.14	390
BBWA	-0.958***	-1.390	0.758	0.220	-0.13	ns					150
OVEN	1.334***	1.246	0.815	0.675	-0.39	-0.820***	2.277	0.717	0.868	0.48	269

^a See Table 1 for species codes.

^b Probability: ns, $p > 0.01$, ** $p < 0.01$, *** $p < 0.001$.

^c Parameter estimate.

^d Intercept.

^e Area under the ROC (receiver operating characteristic) curve.

^f Point on the ROC curve where the sum of sensitivity and specificity is maximized (see Methods).

^g Value on the x-axis corresponding to cut-off value.

Table 4. Thresholds (x_t) in the occurrence of 12 bird species showing positive relationships to habitat alteration, after controlling for the suitability of local habitat (see Methods).

Species ^a	Gradient in stand composition (PC1; n = 390)					Habitat alteration gradient (PC2)					n
	$\beta_1^{b,c}$	β_0^d	AUC ^e	c ^f	x_t^g	$\beta_1^{b,c}$	β_0^d	AUC ^e	c ^f	x_t^g	
YBSA	1.074***	0.509	0.769	0.643	0.07	ns					216
DOWO	0.806***	-1.692	0.676	0.143	-0.12	0.516**	-1.084	0.607	0.216	-0.40	239
EAWP	1.052***	-1.209	0.738	0.269	0.20	ns					223
ALFL	ns					0.857**	-3.195	0.696	0.047	0.22	390
PHVI	1.166***	-3.068	0.729	0.052	0.14	ns					213
REVI	1.939***	0.654	0.880	0.690	0.07	ns					216
CSWA	0.605***	-1.299	0.633	0.201	-0.13	0.911***	-0.921	0.696	0.399	0.56	240
BTBW	1.495***	0.928	0.829	0.642	-0.23	0.629***	1.908	0.660	0.861	-0.14	253
AMRE	0.589***	-1.148	0.639	0.219	-0.21	0.833***	-0.776	0.686	0.420	0.54	250
MOWA	ns					0.384**	-1.462	0.604	0.186	-0.04	390
WTSP	-0.702***	-0.735	0.703	0.284	0.27	ns					199
RBGR	0.773***	-1.176	0.673	0.239	0.02	0.759***	-0.570	0.663	0.384	0.13	223

^aSee Table 1 for species codes.

^bProbability: ns, $p > 0.01$, ** $p < 0.01$, *** $p < 0.001$.

^cParameter estimate.

^dIntercept.

^eArea under the ROC (receiver operating characteristic) curve.

^fPoint on the ROC curve where the sum of sensitivity and specificity is maximized (see Methods).

^gValue on the x-axis corresponding to cut-off value.

When plotting the expected number of sensitive species as a function of the degree of habitat alteration (PC2) using the threshold values we obtained (Fig. 4), we observed a sharp decline between -0.14 and $+0.97$, which corresponds to stands with a mean canopy closure of 62% ($\pm 18\%$ SD, $n = 175$) and a density of 70 (± 42 SD, $n = 175$) large trees (30 cm dbh) per hectare. We then plotted the thresholds found for each of the sensitive species in each stand type and fitted curves of expected species richness for each assemblage as a function of canopy closure (Fig. 5a) and density of large trees (≥ 30 cm dbh) (Fig. 5b). Interestingly, the fifth-order polynomial curves indicated that the three species assemblages exhibited a similar response to habitat alteration. All sensitive species were predicted to be present above 70% canopy closure or 80 large trees/ha.

Discussion

Forest Birds and Silviculture

A large proportion of the bird species examined (25/42) responded significantly to habitat alteration, as indexed from forest stand structure. Of the 30 species requiring mature stands for nesting and foraging, nearly half (13) exhibited a significant negative response to the opening of the canopy and a reduction in densities of large trees and snags.

This is one of the first studies identifying thresholds in species response to gradients in habitat alteration at the

local scale. Büttler et al. (2004) also documented thresholds in snag density associated with the occurrence of the Three-toed Woodpecker (*Picoides tridactylus*). Although we sought thresholds for all species responding significantly to stand-level habitat alteration, we focused our attention on those that showed sensitivity to alteration because, in most forest biomes across the world, old forest stands with a high density of snags are rapidly being replaced by younger, more open forest, short-rotation conifer plantations, or nonforest. Finally, with the extensive use of single-tree selection and patch cutting in our study region, there is no shortage of habitat for most bird species associated with early-seral stands (Table 4). These species also use the edges of untreated stands.

Although the bird responses we documented were generally consistent with the results of other studies (Annand & Thompson 1997; Hagan et al. 1997; Rodewald & Yahner 2000), these studies compared either forest stand types or silvicultural treatments. In contrast, our approach explicitly recognizes that, from the perspective of forest birds, different silvicultural treatments can produce stands of comparable suitability or, conversely, that a given treatment can be applied over a broad range of intensities. Thus, we did not compare the effects of silvicultural treatments per se; rather, we assessed bird response to postharvest conditions, in terms of both vegetation structure and composition. Some of our “untreated” stands also exhibited canopy openings, mainly associated with windthrow, past spruce budworm outbreaks, or “high grading” of large specimens of yellow birch, red spruce, and a few other species.

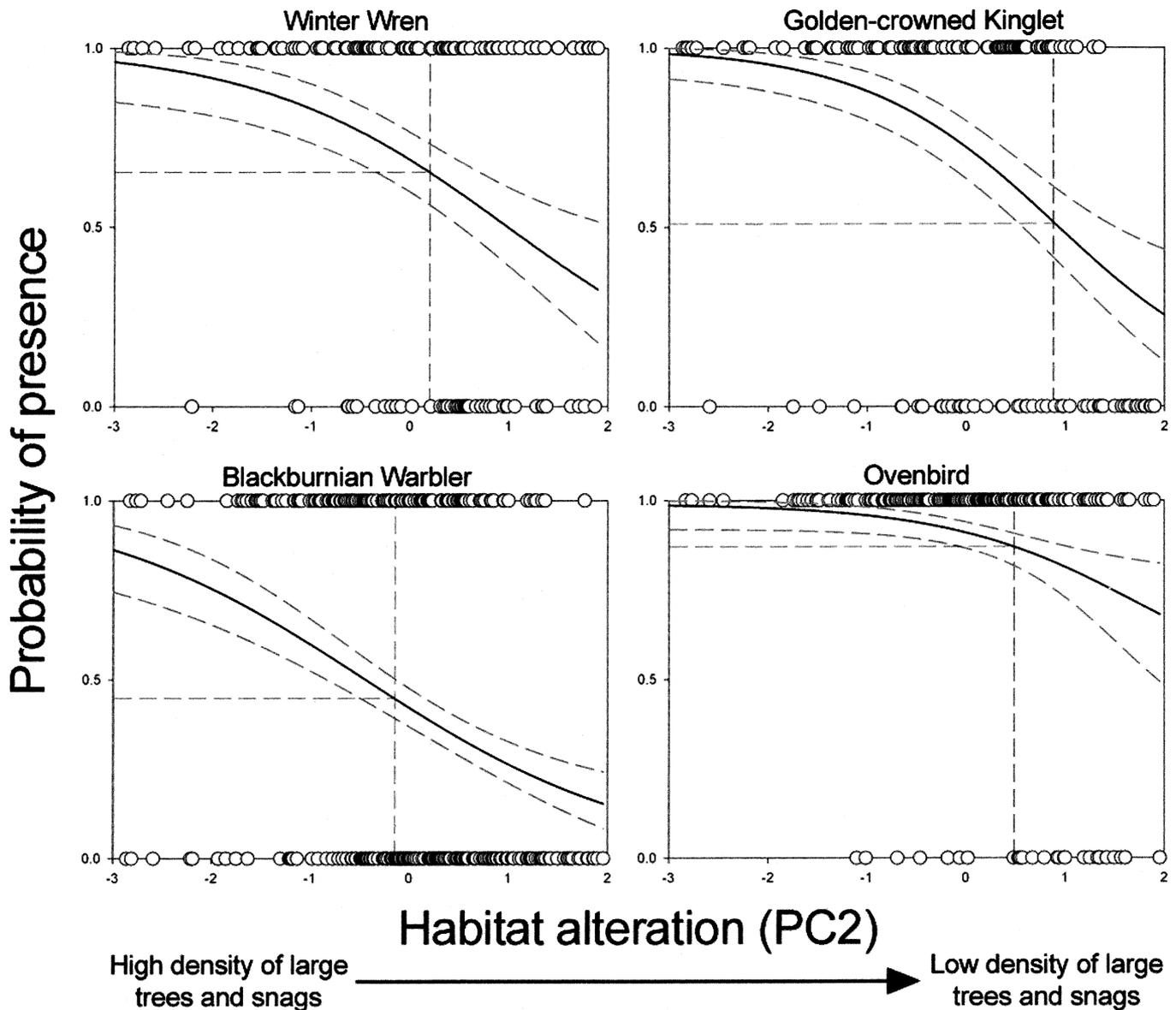


Figure 2. Probability of presence of four bird species sensitive to habitat alteration (PC2). Dashed lines represent 95% confidence intervals. Vertical lines indicate thresholds determined using ROC (receiver operating characteristic) analysis.

Several species showed an occurrence threshold in their response to habitat alteration, but at different levels. These thresholds indicated that some species (e.g., Blackburnian Warbler, Yellow-bellied Flycatcher, Brown Creeper) could tolerate only low-intensity, single-tree selection or patch cutting. At the other end of the spectrum, species such as the Blue-headed Vireo, Golden-crowned Kinglet, and Ovenbird tolerated more intensive silvicultural practices. Because habitat alteration varied widely within a given treatment (Fig. 2), we cannot recommend any specific treatment among those considered to conserve the complete assemblage of sensitive forest bird species. The main issue was the density (or volume) of

trees remaining rather than the silvicultural treatments themselves.

The critical range in stand structure we found when plotting threshold values along the habitat alteration gradient corresponded to stands with a mean canopy closure of 62% and a mean density of 70 large trees (≥ 30 cm dbh)/ha. Stands with values below these means were intensive single-tree selection cuts, intensive patch cuts, or conifer plantations. For critical ranges of single variables associated with PC2, at least 70% mean canopy closure and 80 stems/ha were required to provide suitable habitat for all sensitive species. This indicates that, at the stand level, intensive silvicultural treatments, whether

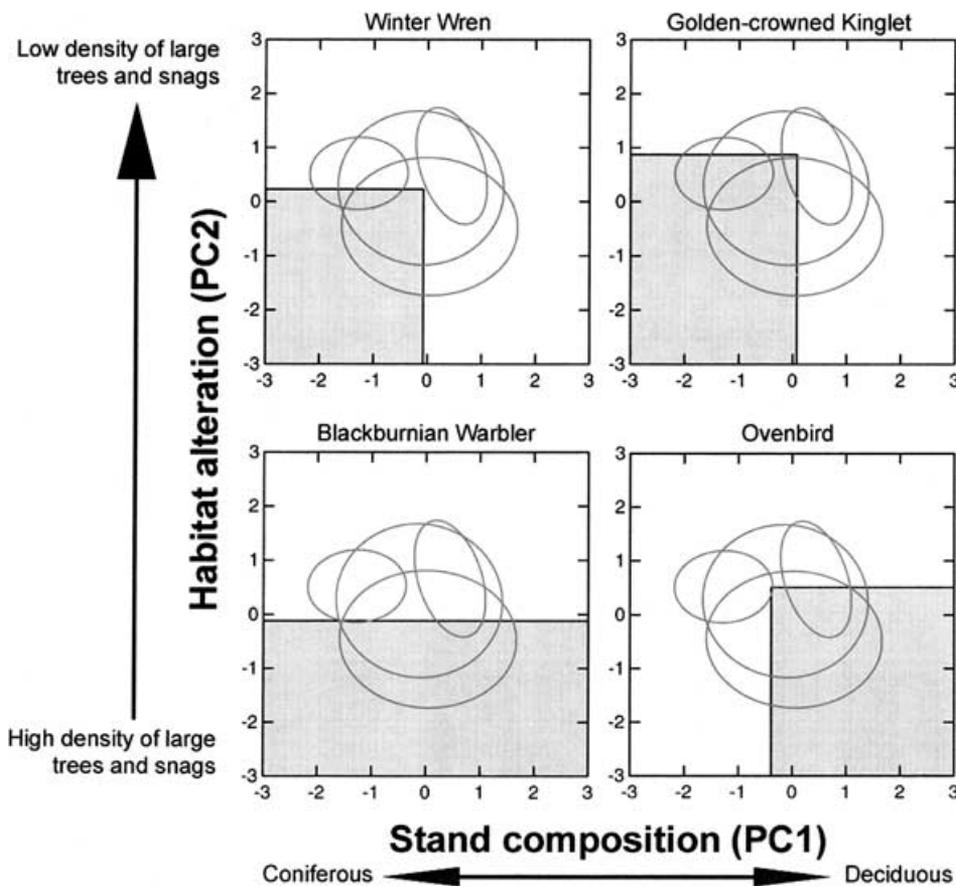


Figure 3. The PCA ordination showing portions of the biplot (conservation target zones) where each species is expected to be present according to thresholds in its response to stand composition (PC1) and habitat alteration (PC2) (shaded areas).

even aged or uneven aged, are incompatible with the conservation of several bird species associated with mature and old forest stands unless harvest entries are separated by sufficient time intervals.

For the most sensitive bird species, even light-harvest treatments may create suboptimal breeding habitat either because these species either require dense canopy and subcanopy foliage to forage efficiently or because they require other conditions associated with closed-canopy stands, such as an open understory, increased soil moisture, or deeper leaf litter (Hansen et al. 1995; Bourque & Villard 2001). Low-intensity harvesting might also increase nest predation (Twedt et al. 2001; Manolis et al. 2002). The few studies documenting reproductive success in lightly harvested stands, however, indicate either that negative effects are mainly associated with density reductions (Bourque & Villard 2001) or that this type of harvesting has no significant effect on reproductive success (Huhta et al. 1998; Robinson & Robinson 2001).

Annand and Thompson (1997) found that some forest songbird species could be more abundant in certain low-intensity, uneven-aged treatments than in uncut stands (e.g., Eastern Wood-Pewee, Red-eyed Vireo). Canopy gaps might increase foraging efficiency for these species or some insect species might be more abundant in gaps because of the greater primary productivity associated with

higher light levels (Blake & Hoppes 1986; Smith & Dallman 1996). In our study, species generally associated with small forest gaps, such as the Eastern Wood-Pewee, Least Flycatcher, Red-eyed Vireo, and Mourning Warbler, did not respond significantly to the gradient in habitat alteration.

By examining patterns in the expected richness of species assemblages sensitive to habitat alteration, we reduced the risk of focusing on a single atypical or ecologically robust species. Managers and conservation planners might choose conservation targets that are lower than the ones we recommend here based on the most sensitive species. This should be done, however, while closely monitoring the response of the species whose thresholds are higher than the conservation target selected. Alternatively, it might be more efficient to meet more stringent threshold values in portions of the land base devoted to conservation while making informed tradeoffs elsewhere.

The fact that many fewer species associated with deciduous stands were sensitive to habitat alteration probably reflects the lower intensity of harvesting in this habitat type in the study area. Indeed, the majority of deciduous stands had received only a first-entry single-tree selection or patch cut. As a result, they had a relatively high canopy closure (mean = 65%, SD = 18) and the density of large trees was higher (mean = 94.7 stems/ha, SD = 48.6) than

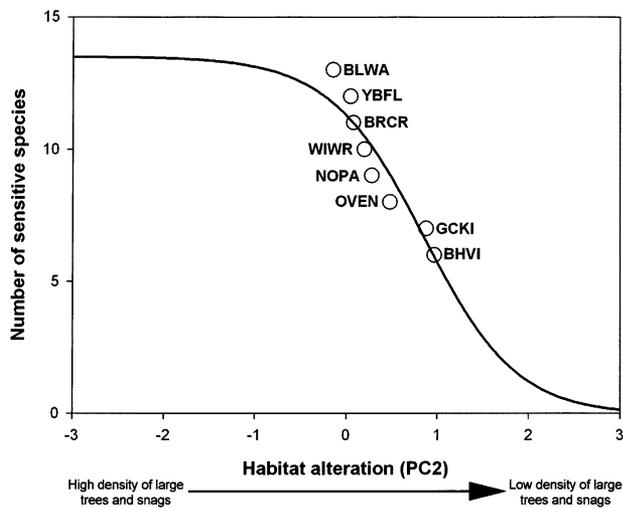


Figure 4. Change in the expected number of sensitive forest bird species as a function of habitat alteration, based on species-specific occurrence thresholds (dots). Bird name codes are defined in Table 1.

in mixed-wood (68.8 stems/ha, SD = 47.5) or coniferous stands (51.2 stems/ha, SD = 56.7). In fact, most of the deciduous stands we surveyed were above the threshold found for the most sensitive species.

Statistical Aspects of Threshold Detection

Our approach allowed us to identify species most sensitive to the alteration of stand structure and composition and the degree of alteration they can tolerate. Thresholds obtained for these species can thus be used to guide the design of treatments (e.g., variable retention or partial cutting) that allow meeting conservation objectives. The next step, however, should be to investigate threshold responses at the landscape scale to assess cumulative or spatial effects.

According to the area under the ROC curve, most of the significant relationships we report with respect to habitat alteration can be characterized as poor (AUC < 0.700; Swets 1988). Relationships were stronger for sensitive species (Table 3), however, and, overall, many relationships (8/15) were close to this arbitrary level. This may reflect the coarseness of the dependent variable we used (presence or absence). Indeed, some noise could be introduced by the detection of transient individuals. Ideally, we should have used a fitness parameter such as an index of reproductive activity (Gunn et al. 2000). Recent calibration experiments, however, suggest this method underestimates true reproductive activity (M.-A.V., F. Paillard & J.-S.G., unpublished data). Nonetheless, ROC analysis is specifically designed to identify thresholds that minimize the noise. Simulations conducted by Guénette and Villard (2004) show that ROC-derived thresholds are surprisingly robust to the introduction of noise in the data.

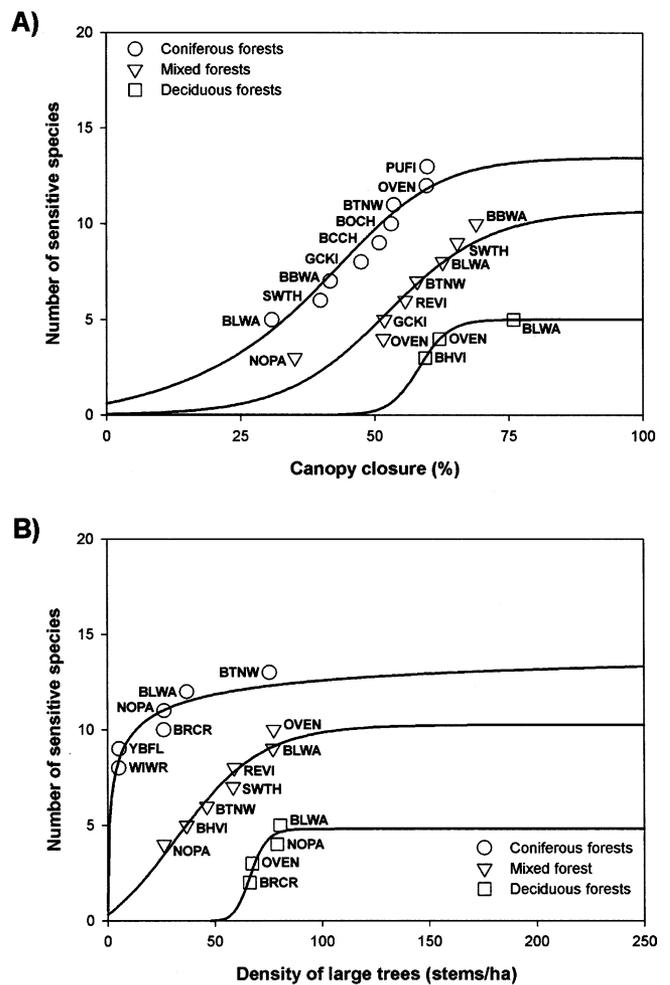


Figure 5. Change in the expected number of forest bird species sensitive to habitat alteration as a function of (a) canopy closure and (b) density of large trees (≥ 30 -cm dbh). Each symbol corresponds to the ROC (receiver operating characteristic)-derived threshold in the occurrence of a given bird species. Each curve was fitted using a fifth-order polynomial. Bird name codes are defined in Table 1.

The portions of multivariate space where certain species are expected to be present can be seen as “conservation target zones” (Fig. 3). Once gradients in habitat alteration and thresholds have been validated and calibrated for a certain region, those target zones can be used to guide forest managers. Calibration may be necessary to account for geographic variation in vegetation types. Scores on gradients in floristic composition and habitat alteration can be easily computed from forest survey data containing all the independent variables used to build the gradients obtained in this study. Then, managers can compare these scores to those corresponding to conservation target zones. This comparison allows determining or simulating the compatibility of specific management

interventions with the occurrence of the most sensitive species.

Instead of using multivariate axes, one could examine thresholds in bird response to specific habitat variables. Our approach makes it possible to adjust threshold values to the study region using basic forest survey data and to determine similar thresholds for other statistically significant variables (e.g., snag density, basal area of large trees).

Finally, pooling thresholds obtained across many species or several taxa will give ecosystem managers a powerful tool to integrate harvest practices and the conservation of forest biodiversity. Future work should compare the responses of various sensitive species to the same habitat alteration gradient.

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Literature Cited

- Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* **71**:355-366.
- Annand, E. M., and F. R. Thompson. 1997. Forest bird response to regeneration practices in central hardwood forests. *Journal of Wildlife Management* **61**:159-171.
- Baker, M. D., and M. J. Lacki. 1997. Short-term changes in bird communities in response to silvicultural prescriptions. *Forest Ecology and Management* **96**:27-36.
- Bélisle, M., and A. Desrochers. 2002. Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. *Landscape Ecology* **17**:219-231.
- Bibby, C. J., N. D. Burgess, and D. A. Hill. 1992. *Bird census techniques*. Academic Press, Cambridge, United Kingdom.
- Blake, J. G., and W. G. Hoppes. 1986. Influence of resource abundance on use of tree-fall gaps by birds in an isolated woodlot. *Auk* **103**:328-340.
- Bonn, A., and B. Schröder. 2001. Habitat models and their transfer for single and multi species groups: case study of carabids in an alluvial forest. *Ecography* **24**:483-496.
- Bourque, J., and M.-A. Villard. 2001. Effects of selection cutting and landscape scale harvesting on the reproductive success of two Neotropical migrant bird species. *Conservation Biology* **15**:184-195.
- Bütler, R., P. Angelstam, P. Ekelund, and R. Schlaepfer. 2004. Dead wood threshold values for the Three-toed Woodpecker presence in boreal and sub-alpine forest. *Biological Conservation* **119**:305-318.
- Chambers, C. L., W. C. McComb, and J. C. Tappeiner. 1999. Breeding bird responses to three silvicultural treatments in the Oregon Coast Range. *Ecological Applications* **9**:171-185.
- Crawford, H. S., R. G. Hooper, and R. W. Titterton. 1981. Songbird population response to silvicultural practices in central Appalachian hardwoods. *Journal of Wildlife Management* **45**:680-692.
- Dale, M. R. T., and M.-J. Fortin. 2002. Spatial autocorrelation and statistical tests in ecology. *Écoscience* **9**:162-167.
- DeLeo, J. M. 1993. Receiver operating characteristic laboratory (ROCLAB): software for developing decision strategies that account for uncertainty. Pages 318-325 in *Proceedings of the second international symposium on uncertainty modelling and analysis*. IEEE Computer Society Press, College Park, Maryland.
- Dutilleul, P. 1993. Modifying the t test for assessing the correlation between two spatial processes. *Biometrics* **49**:305-314.
- Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* **61**:603-610.
- Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* **24**:38-49.
- Fortin, M.-J., and S. Payette. 2002. How to test the significance of the relation between spatially autocorrelated data at the landscape scale: a case study using fire and forest maps. *Écoscience* **9**:213-218.
- Gauthier, J., and Y. Aubry. 1995. *Les oiseaux nicheurs du Québec: atlas des oiseaux nicheurs du Québec méridional*. Association québécoise des groupes d'ornithologues, Société québécoise de protection des oiseaux, Service canadien de la faune, Environnement Canada, région du Québec, Montréal (in French).
- Gobeil, J.-F., and M.-A. Villard. 2002. Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations. *Oikos* **98**:447-458.
- Guénette, J.-S. 2003. *Seuils dans la tolérance des oiseaux forestiers à l'altération de leur habitat*. M.S. thesis. Département de biologie, Université de Moncton, Moncton, NB, Canada (in French).
- Guénette, J.-S., and M.-A. Villard. 2004. Do empirical thresholds truly reflect species tolerance to habitat alteration? *Ecological Bulletins* **51**:163-171.
- Gunn, J. S., A. Desrochers, M.-A. Villard, J. Bourque, and J. Ibarzabal. 2000. Playbacks of mobbing calls of Black-capped Chickadees as a method to estimate reproductive activity of forest birds. *Journal of Field Ornithology* **71**:472-483.
- Gutzwiller, K. J., and W. C. Barrow. 2001. Bird-landscape relations in the Chihuahuan desert: coping with uncertainties about predictive models. *Ecological Applications* **11**:1517-1532.
- Hagan, J. M., and A. L. Meehan. 2002. The effectiveness of stand-level and landscape-level variables for explaining bird occurrence in an industrial forest. *Forest Science* **48**:231-242.
- Hagan, J. M., P. S. McKinley, A. L. Meehan, and S. L. Grove. 1997. Diversity and abundance of landbirds in a northeastern industrial forest. *Journal of Wildlife Management* **61**:718-735.
- Hansen, A. J., W. C. McComb, R. Vega, M. G. Raphael, and M. Hunter. 1995. Bird habitat relationship in natural and managed forests in the west Cascades of Oregon. *Ecological Applications* **5**:555-569.
- Hosmer, D. W., and S. Lemeshow. 2000. *Applied logistic regression*. John Wiley, New York.
- Huhta, E., J. Jokimäki, and P. Helle. 1998. Predation on artificial nests in a forest dominated landscape: the effects of nest type, patch size and edge structure. *Ecography* **21**:464-471.
- Jackson, D. A. 1993. Stopping rules in principal components analysis: a comparison of heuristic and statistical approaches. *Ecology* **74**:2204-2214.
- Jobes, A. P., E. Nol, and D. R. Voigt. 2004. Effects of selection cutting on bird communities in contiguous eastern hardwood forests. *Journal of Wildlife Management* **68**:51-60.

- King, D. I., and R. M. DeGraaf. 2000. Bird species diversity and nesting success in mature, clearcut and shelterwood forest in northern New Hampshire, USA. *Forest Ecology and Management* **129**:227-235.
- Lee, M., L. Fahrig, K. Freemark, and D. J. Currie. 2002. Importance of patch scale vs. landscape scale on selected forest birds. *Oikos* **96**:110-118.
- Lichstein, J. W., T. R. Simons, and K. E. Franzreb. 2002. Landscape effects on breeding songbird abundance in managed forests. *Ecological Applications* **12**:836-857.
- Manel, S., H. C. Williams, and S. J. Ormerod. 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology* **38**:921-931.
- Manolis, J. C., D. E. Andersen, and F. J. Cuthbert. 2002. Edge effect on nesting success of ground nesting birds near regenerating clearcuts in a forest-dominated landscape. *Auk* **119**:955-970.
- Mönkkönen, M., and P. Reunanen. 1999. On critical thresholds in landscape connectivity: a management perspective. *Oikos* **84**:302-305.
- Moser, M., C. Bibby, I. Newton, M. Pienkowski, W. J. Sutherland, S. Ulfstrand, and G. Wynne. 1995. Bird conservation: the science and the action. *Ibis* **137**:S3-S7.
- Peres-Neto, P. R., D. A. Jackson, and K. M. Somers. 2003. Giving meaningful interpretation to ordination axes: assessing loading significance in principal component analysis. *Ecology* **84**:2347-2363.
- Robichaud, I., M.-A. Villard, and C. Machtans. 2002. Effects of forest regeneration on songbird movements in a managed forest landscape of Alberta, Canada. *Landscape Ecology* **17**:247-262.
- Robinson, S. K., and W. D. Robinson. 2001. Avian nesting success in a selectively harvested north temperate deciduous forest. *Conservation Biology* **15**:1763-1771.
- Rodewald, A. D., and R. H. Yahner. 2000. Bird communities associated with harvested hardwood stands containing residual trees. *Journal of Wildlife Management* **64**:924-932.
- Smith, R., and M. Dallman. 1996. Forest gap use by breeding Black-throated Green Warblers. *Wilson Bulletin* **108**:588-591.
- Swets, J. A. 1988. Measuring the accuracy of diagnostic systems. *Science* **240**:1285-1293.
- Tabachnick, B. G., and L. S. Fidell. 1996. Using multivariate statistics. 3rd edition. Harper Collins College Publishers, New York.
- Thompson, F. R. 1993. Simulated responses of a forest interior bird population to forest management options in central hardwood forests of the United States. *Conservation Biology* **7**:325-333.
- Twedt, D. J., R. R. Wilson, J. L. Henne-Kerr, and R. B. Hamilton. 2001. Nest survival of forest birds in the Mississippi alluvial valley. *Journal of Wildlife Management* **65**:450-460.
- Villard, M.-A., M. K. Trzcinski, and G. Merriam. 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. *Conservation Biology* **13**:774-783.
- Zar, J. H. 1999. *Biostatistical analysis*. 4th edition. Prentice Hall, Upper Saddle River, New Jersey.
- Zweig, M. H., and G. Campbell. 1993. Receiver-operating characteristic (ROC) plots: a fundamental evaluation tool in clinical medicine. *Clinical Chemistry* **39**:561-577.

