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Research Papers, part of a Special Feature on Bird Conservation in the Boreal Forest: Is there a Case for Resilience?

Selecting Focal Songbird Species for Biodiversity Conservation Assessment: Response to Forest Cover Amount and Configuration

Sélection d'espèces de passereaux spécialistes pour l'évaluation de la conservation de la biodiversité : réaction à la configuration et l'étendue du couvert forestier

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ABSTRACT. Conservation of biodiversity is now a firmly entrenched objective of sustainable forest management, and emulating natural disturbance has been widely adopted as a conservation strategy. Yet the foundation for this approach is still very much a hypothesis based on first principles, and there has been little rigorous testing of the approach. In addition, practical constraints mean that the full range and character of natural patterns can never be implemented, so decisions must still be made in setting forest management targets and levels. An alternative, but complementary approach is to select a focal group of species and use their habitat requirements to define the range of conditions that should be maintained on the landscape. In this study, I used a balanced factorial sample design to test the effect of landscape vs. local scale factors for explaining relative abundance of 30 forest songbird species in boreal Ontario, and then examined components of variance, and used multivariate analysis and logistic regression to describe these relationships in more detail. Based on statistically defendable inferences and habitat model coefficients, 13 species were selected, with habitat associations ranging from high to low edge density, homogeneous to heterogeneous forest matrix, hardwood to softwood dominated overstory, young to old stands, and open to closed canopy. I found that variations in amount and configuration of mature forest cover had relatively little influence on the overall boreal forest songbird community, but that individual species differ in their response to these variables. To be successful, biodiversity conservation strategies must emulate the patterns created through natural disturbance by maintaining the full range of forest cover homogeneity and heterogeneity on the landscape. The habitat requirements for Alder Flycatcher, Black-and-white Warbler, Bay-breasted Warbler, Blackburnian Warbler, Brown Creeper, Common Yellowthroat, Chestnut-sided Warbler, Least Flycatcher, Ovenbird, Red-breasted Nuthatch, Red-eyed Vireo, Winter Wren, and White-throated Sparrow describe a broad range of habitat conditions that, at a minimum, describe necessary coarse-filter conditions to sustain the boreal songbird community in Ontario. This suite of species can also serve in developing a "bioassay" to evaluate the effectiveness of forest policy to conserve biodiversity through emulation of natural disturbance.

RÉSUMÉ. La conservation de la biodiversité est maintenant un objectif solidement établi de l'aménagement durable des forêts et l'imitation des perturbations naturelles a largement été adoptée en tant que stratégie de conservation. Toutefois, cette approche, qui se fonde sur une hypothèse établie sur des principes de base, a rarement fait l'objet de tests rigoureux. De plus, des contraintes pratiques font que l'éventail complet et le caractère même des patrons naturels ne peuvent jamais être reproduits, si bien que les décisions doivent encore être prises en fonction d'objectifs et de niveaux d'aménagement forestier. Une approche alternative, mais complémentaire, consiste à sélectionner un groupe d'espèces spécialistes et à utiliser leurs exigences

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en termes d'habitat afin de définir la gamme des conditions qui devraient être maintenues dans le paysage. Dans cette étude, j'ai utilisé un plan d'échantillonnage factoriel équilibré pour tester quels sont les facteurs, à l'échelle du paysage et à l'échelle locale, qui pourraient expliquer l'abondance relative de 30 espèces de passereaux forestiers dans le nord de l'Ontario. J'ai ensuite examiné les composantes de la variance, puis utilisé l'analyse multivariable et la régression logistique afin de décrire ces relations de façon plus détaillée. Treize espèces ont été sélectionnées sur la base d'inférences statistiquement valables et de coefficients de modèles d'utilisation de l'habitat. Les variables de l'habitat et leurs caractéristiques étaient les suivantes : la densité de la bordure (d'élevée à faible), la matrice forestière (d'homogène à hétérogène), la composition de la strate arborescente (de feuillue à résineuse), l'âge du peuplement (de vieux à jeune) et la densité de la voûte (d'ouverte à fermée). J'ai constaté que les variations dans l'étendue et la configuration du couvert forestier des forêts matures avaient relativement peu d'influence sur l'ensemble de la communauté de passereaux, mais que l'effet de ces variables fluctuait selon les espèces. Pour être efficaces, les stratégies de conservation de la biodiversité doivent imiter les patrons créés par les perturbations naturelles, en maintenant l'éventail complet de l'homogénéité et de l'hétérogénéité du couvert forestier du paysage. Les exigences en termes d'habitat requises par le Moucherolle des aulnes, la Paruline noir et blanc, la Paruline à poitrine baie, la Paruline à gorge orangée, le Grimpereau brun, la Paruline masquée, la Paruline à flancs marron, le Moucherolle tchébec, la Paruline couronnée, la Sittelle à poitrine rousse, le Viréo aux yeux rouges, le Troglodyte mignon et le Bruant à gorge blanche correspondent à un vaste éventail de conditions qui, à un seuil minimum, définissent les conditions nécessaires du filtre brut pour soutenir la communauté boréale de passereaux en Ontario. Ce groupe d'espèces peut aussi servir à développer un « test biologique » afin d'évaluer l'efficacité des politiques forestières dans la conservation de la biodiversité au moyen de l'imitation des perturbations naturelles.

Key Words: *boreal; calibration; configuration; discrimination; focal species; forest management; forest songbird; habitat models; niche; Ontario; multiple scale; resilience; resource selection function; spatial*

INTRODUCTION

The trivial hypothesis that boreal forest songbirds are adapted to conditions of the boreal forest carries with it some interesting conditional assumptions. The boreal forest is dynamic, and its pattern and structure is driven by catastrophic disturbance events such as stand-replacing fire and windthrow (Rowe and Scotter 1973). The more subtle disturbance events—such as death of individual trees or groups of trees caused by insects, disease, and simple senescence—drive within-stand structure. Members of the songbird community should be adapted to a complex landscape pattern replete with edges between young and old forest, and mixtures of stand ages and shade-tolerant vs. shade-intolerant tree species (Hunter 1993, Bunnell 1995, Parker et al. 2005, Schieck and Song 2006). Forest management should consider this full range of natural heterogeneity and homogeneity on the landscape if its objective is in part the conservation of biodiversity.

The natural disturbance paradigm suggests that emulating natural disturbance patterns will be sufficient to create this heterogeneity, but practical issues of forest management mean that perfect emulation is never possible. An alternative but complementary approach is to characterize the broad range of habitat conditions associated with the songbird community, and then select a group of focal species that encompasses the broad range of habitat conditions (community niche-space) used by the forest songbird community. Models of the habitat associations for the focal species can then be applied to forest management scenarios. Results of the scenario analyses can be used to assess the relative performance of management options in terms of providing the necessary "coarse-filter" habitat requirements for the songbird community. In this approach, habitat associations of the focal species essentially define the range of variation necessary to sustain the full community.

Complex habitat patterns are not readily characterized by stand-scale resource inventory classifications, whose primary objective is to simplify landscape patterns into homogeneous units for the purpose of accurately estimating merchantable timber volume. Songbirds do not live in the artificial constructs of digitized stand boundaries, and there is no a priori justification to use stand characteristics as the sole means of characterizing a songbird's habitat needs. Stand-scale analyses ignore the influence of adjacent stand conditions and the landscape (matrix) context in which the stand lies, including the influence of local- and landscape-scale homogeneity and heterogeneity on habitat quality. Habitat selection may be occurring at scales much broader than the traditional stand scale of analysis (Villard et al. 1995, 1999, Wiens 1995, Mitchell et al. 2006) so analysis and modeling methods must reflect this ecological possibility.

To achieve these objectives, I took a three-step approach. Using spatially explicit sampling and analysis techniques, I first established relationships between forest pattern and composition variables, at local and landscape scales, with relative density for a suite of forest songbirds. As part of this, I also explored the relative contribution of local- vs. landscape-scale variables in explaining habitat occupancy. I then developed and tested habitat models to quantitatively predict habitat occupancy for individual species. Finally, I selected a suite of focal species based on their relative position within the overall community-niche space, and the relative performance of their predictive habitat models. In a parallel study (Rempel et al. 2007), this suite of species is used to test the effectiveness of alternative forest management policy options for conserving biodiversity.

METHODS

Songbird Sampling and Interpolation

Forest songbirds were identified and counted at forest listening stations by using 10-min. recordings of vocalizations made by singing, territorial males, between sunrise and 10:00 am on calm (<25 km/h wind conditions) and rain-free mornings. Bio-acoustic microphones (Hobson et al. 2002, Rempel et al. 2005) were used to record observations in the Rinker Lake (RL) (2002–2004) and Nipigon Forest (NF) (2005) study areas, and for a subset of the Cochrane Study Area (2002–2003) (Rempel et al. 2007). The microphone range differs slightly among species, with louder species (e.g., White-throated Sparrow (*Zonotrichia albicollis*)) detectable up to 150 m, and higher-pitched species (e.g., Golden-crowned Kinglet (*Regulus satrapa*)) detectable up to about 100 m (Hobson et al. 2002). Density values based on these counts should be interpreted as relative density. Hobson et al. (2002) also found little difference in detectability among habitat types.

Alternative point sample designs were simulated and evaluated in terms of their performance for spatial interpolation (Rempel and Kushneriuk 2003) before sampling was initiated. A modified cluster sampling strategy was selected, where sample points were placed in locally dominant habitat types (based on satellite image analysis) in a clustered design. Sample point locations were selected to provide the spatial dispersion of points that is necessary for spatial interpolation, and to reflect the full range of forested habitat conditions across the study landscape (with the exception of riparian areas). Points were also selected in reasonable proximity (100 m) to secondary roads, tertiary roads, and trails. Travel routes for point-to-point traversing were designed to avoid crossing large streams and cliffs. Stand boundaries and primary forest roads with higher traffic levels were avoided. Point clusters were spaced approximately 2–5 km apart, with individual points within a cluster spaced at least 250 m apart. Point-to-point navigation was facilitated by use of GPS, where waypoints were preselected and digitized on-screen with satellite imagery, Forest Resource Inventory (FRI) digital maps, road layers, and water layers as background, and then uploaded to the GPS. Given these constraints, points were collected without bias with respect to use or non-use by songbirds, but the design cannot be considered truly random.

Songbird sample points were interpolated over a range of just 1 km using ordinary point kriging (Deutsch and Journel 1998) to estimate relative density based on 50 hexagonal analysis cells; thus relative density becomes a function of all points falling within a 50-ha cell, and points adjacent to the cell (Fig. 1). The effective weight of adjacent points in determining the relative density is a function of the proximity of the point, as modeled through the spatial autocorrelation analysis (i.e., semi-variogram). A 50-ha cell corresponds to a radius of ca. 300 m, and cells generally held one to three points, so the relative density reflects the average local condition for an area that is ca. one to two times the effective listening range (ca. 150 m) of points within the cluster. Note that kriging was used only to estimate density within hexagons that contained at least one sample point, and was not used to interpolate densities across the entire study area and disparate cover types (Fig. 1). Multiple point counts are transformed into a surface, so some important effects of this approach are reductions in the autocorrelation of data records, a reduction in total degrees of freedom for analysis, a decrease in the frequency of observations classed as “absent,” and a decreased ability to detect influence of “hard edges” (Fig. 1). Solution of the semi-variogram requires a sufficiently high sample size that is in part dependent upon the number of non-zero data points. Creation of semi-variograms generally failed for species with less than about 30 occurrences. Successful semi-variogram solutions were found for 30 species, and these species were then included in further analyses.

Spatial Data Capture

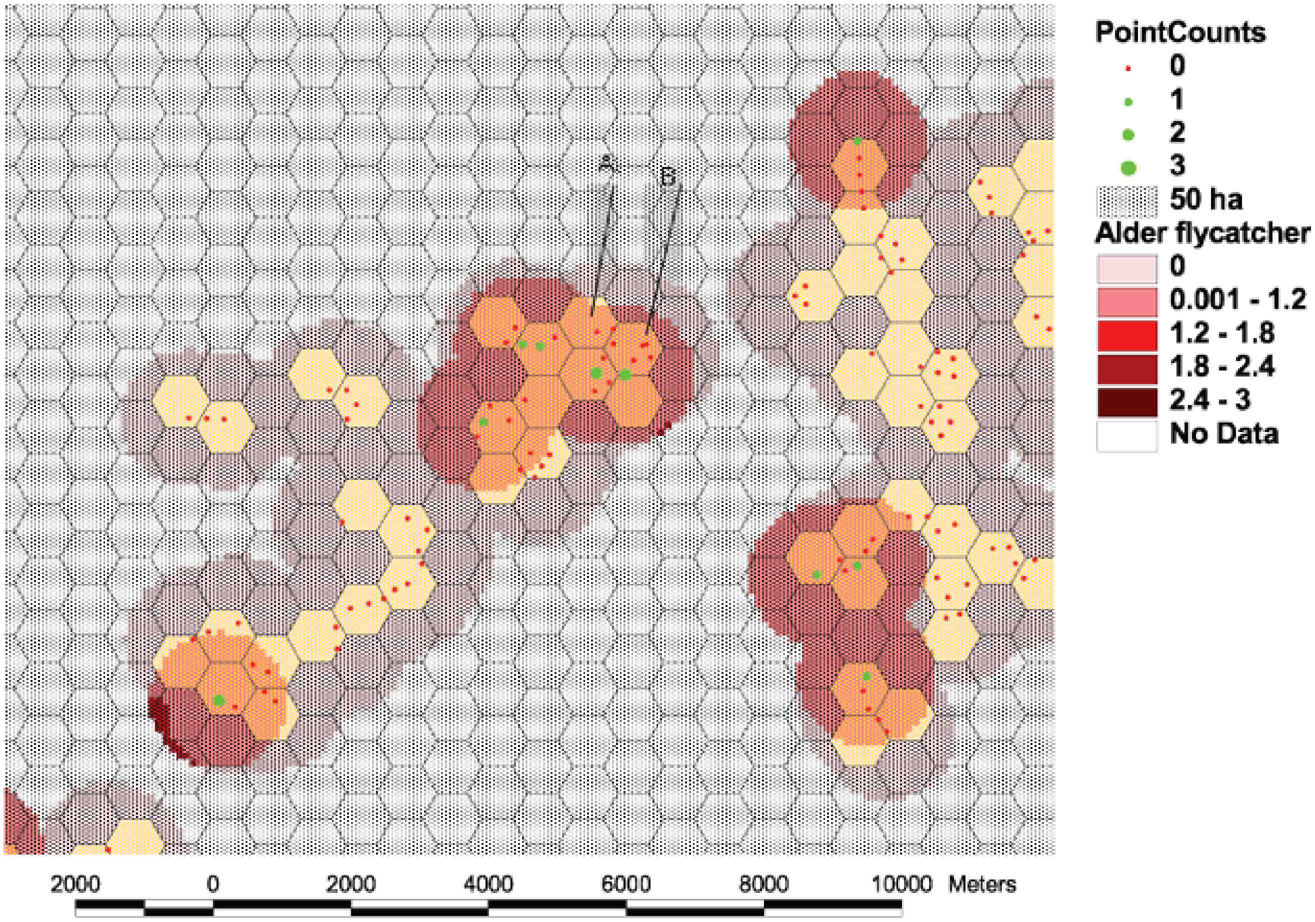
Stand age, height, and standard forest unit (SFU) were captured from the most recent FRI digital maps (1995 photos in NF; 2001 and 2003 photos in CSA), and from these data, percent canopy closure and percent hardwood volume were derived. The FRI maps were first transformed into a raster-like grid of 50- and 5000-ha analysis cells using the newly developed Landscape Scripting Language (LSL) created for specialized spatial modeling (Kushneriuk and Rempel 2004). The weighted average of forest age (AGE), tree height (HEIGHT), percent hardwood volume (HARDWOOD), percent canopy closure (CANOPY) and percent young forest (YOUNG) were calculated at the 50-ha scale, and contrast weighted edge-density (EDGE), and percentage of intact mature and old forest matrix (INTACT) were calculated at the 5000-ha scale (Table 1). Edge-density values were then assigned to each of the 50-ha cells falling within the larger 5000-ha cell. To avoid bias resulting from arbitrary placement of the analysis cells, each gridset was shifted slightly (16 times for the 5000-ha scale, and nine times for the 50-ha scale), and values averaged. This procedure produces a computationally efficient moving-window average.

For each of the three explanatory variables, the inter-quartile range (IQR), based on 25th and 75th percentiles, was calculated for the entire study area, and these limits were then used to assign three factor levels (e.g., high, medium, and low) for the two local-scale variables, AGE class and HARDWOOD class, and for the two landscape-scale variables, EDGE class and INTACT class (Table 2). The IQR is a robust, non-parametric measure of dispersion, and is less sensitive to outliers and non-normal distributions that the standard deviation. Differences in relative abundance were expected among study areas because of differing environmental conditions, so the analysis was cast as a mixed model, randomized block design (Zar 1984), where samples were randomly assigned in each of the RL, NF, and CSA study areas. A study objective was to establish a balanced design, so 564 of 919 data records were randomly selected for analysis based on factor-level groupings using the Complex Samples routine in SPSS (SPSS Inc. 2006). The design was balanced in that all factorial combinations were present, but sample numbers were uneven, with fewer young forest sites relative to the other factors (Table 3). Analysis of variance was used to test effects of the explanatory variables (fixed effects) on square-root transformed songbird densities (statistical significance if $\alpha \leq 0.05$). Untransformed, ln (x+1), square-root (x), and square-root (x + 3/8) transformations were evaluated for their fit with a normal distribution, and the square-root (x) transformed data consistently had the best fit with the normal distribution. Homogeneity of variance and collinearity among variables were evaluated before the analysis. A moderate level of collinearity occurred among tree height, stand age, and canopy closure, so only one of these three, stand age, was used in the ANOVA. All inferential statistical analyses were conducted using SPSS (SPSS Inc. 2006).

Statistical Analyses

Community analysis was performed using Canonical Correspondence Analysis (CCA) (ter Braak and Šmilauer 2002). Its purpose was to estimate components of variance contributed by local- vs. landscape-scale variables, and to visually display species and environmental relationships. This included display of species associations, simple correlations between species occurrence and explanatory environmental variables, and the conditional (partial) correlations between species and environmental variables. Relationships were further visualized by generating isopleths based on generalized linear models (GLM) of species occurrence and individual explanatory variables, and overlaying these on the ordination diagram. All GLM models were significant at $p < 0.0001$. The significance of the direct gradient CCA ordination

Fig. 1. Overlay of 50-ha hexagonal analysis cells on kriged surface of Alder flycatcher point counts. Points with <0 counts are colored green. Interpolation is limited to 1000 m. Only cells that intersect at least one point count (orange and cream colored) are selected for analysis. Note that in cells A and B, estimated relative densities are >0, even though no point counts>0 occurred within the cells. Cell B contributes only one data value to the analysis, even though five point counts occur within the cell; thus cells A and B contribute equal weight to the model.



was tested using Monte Carlo techniques, but CCA was not used to infer statistical significance of environmental relationships with individual species. However, where ANOVA indicated significant main-effects ($p < 0.05$) this information was annotated to the ordination/isopleth diagrams by setting the species name in bold. Partial CCA analysis was used to estimate components of variance contributed by local vs. landscape variables, and methods followed those described in Borcard et al. (1992).

Habitat models were created (trained) using binary Bayesian logistic regression (Genkin et al. 2004, 2005) on the balanced sample data set, and the remaining unselected data were used for model testing. Individual priors were not specified, and the Laplace distribution was specified for the overall priors. Relative songbird density was transformed to a binary (1/0) variable by reclassifying all 50-ha observations with a relative density threshold >0 as 1, and explanatory continuous variables were transformed first to standardized unit variance.

Table 1.. Description of variables (and keywords) used in the habitat models. All variables calculated using hexagonal analysis units generated in LSL

Variable	Scale†	Keyword	Description
Tree height	Local	HEIGHT	Weighted average of Ontario forest resource inventory (FRI) height, as measured from aerial photography using a parallax bar.
Percent hardwood volume	Local	HARDWOOD	A measure of cover type. Percentage of total merchantable timber that is hardwood. Interpolated from yield curves for standard forest units. Low levels indicate softwood cover type, high levels hardwood cover type.
Percent canopy closure	Local	CANOPY	Interpolated from FRI stand age.
Average Stand Age	Local	AGE	Weighted average of FRI stand age. Interpretation based on stand height and texture.
Percent Young Forest	Local	YOUNG	A measure of young forest cover amount. Percentage of total forest <20 years.
Contrast Weighted Edge Density	Landscape	EDGE	A measure of forest cover configuration and age-class interspersion. Contrast weighted density of edge between young (<20 years old), immature, and mature (>60) forest, where young/mature forest has a contrast weight of 1, and immature a weight of 0.5.
Percent Mature and Old Forest	Landscape	INTACT	A measure of mature forest cover amount, and intactness of the mature forest matrix. Percentage of total forest >80 years old.

† Local scale is 50 ha, landscape scale is 5000 ha.

Alternative threshold rates were initially explored, but produced similar results as the >0 threshold. Sample point locations were based on land-cover characteristics, and so sample points were unbiased with respect to expected habitat occupancy. The binary logistic regression models developed from this type of sample protocol are termed resource selection probability functions (RSPFs), and estimate the probability of habitat occupancy (Manly et al. 2002). Logistic regression was selected over linear regression because of its demonstrated performance for habitat classification (Keating and Cherry 2004), its relative robustness to data with non-normal distributions (Manly et al. 2002), and its ability to control the relative rate of errors between false positives and false negatives by setting the classification threshold (Pearce and Ferrier 2000).

Receiver operating characteristic (ROC) curves (and associated 95% confidence limits) were generated to assess model discrimination accuracy (Pearce and Ferrier 2000), where the area under the curve (AUC) integrates both false-positive and false-negative errors and reflects true positives, false positives, and false negatives (hereafter, the term ROC statistic refers to the integrated area under the ROC curve). A completely random association of response variable with explanatory variables would result in an ROC approaching 0.5; values above 0.6 indicate a fair fit of the model to the data; values above 0.7 represent a good fit, and values

Table 2. Definition of classification variables (factors) used in the ANOVA.

Continuous Variable	Factor Name	Factor level		
		1	3	2
Stand age	AGE-class	<25 years	>70 years	All other
Contrast weighted edge density	EDGE-class	<14 m/ha	>20 m/ha	All other
Percent hardwood volume	HARDWOOD-class	<3 %	>33 %	All other
Percent mature and old forest	INTACT-Class	<25 %	>42 %	All other

above 0.8 represent a very good to excellent fit. The ROC is a non-parametric statistic related to the Mann-Whitney statistic and provides a measure of model discrimination. It identifies the probability that an observation will be properly assigned the correct label (i.e., will assign a higher probability of occurrence to a random positive observation than a negative observation) (Bambar 1975, Hanley and McNeil 1982, Pearce and Ferrier 2000).

Model reliability was estimated using calibration curves, which relate observed occurrence in the validation field data set to the predicted probability of occurrence from the habitat model (Pearce and Ferrier 2000). Calibration curves were estimated using logistic regression, where the response variable is the observed presence/absence at each validation site, and the independent variable is the logit of the predicted probability of occurrence for that site. Thus, both dependent and independent variables are logits of observed/expected probabilities, and perfect calibration will result in a 1 to 1 relationship where slope = 1 and constant = 0. Bias occurs when the regression constant deviates from 0, and this may occur because of higher or lower prevalence of the species in the validation data set (Pearce and Ferrier 2000). Model spread occurs when the slope deviates from 1, and is of greater concern because it may indicate model misspecification.

RESULTS

Individual and Community Response

Of the 30 species studied individually through factorial ANOVA, significant habitat associations were found for all species but two (Table 4). Landscape-scale associations were common within the community, as 19 species had at least one significant effect with a landscape-scale variable; 24 species had significant local-scale associations (Table 4).

Where a significant effect occurred, the proportion of variance explained by the landscape variables, EDGE and/or INTACT, was consistently >30% (Table 5), hence both forest cover amount (INTACT) and configuration (EDGE) account for a substantial proportion of the explained variance. The variance-components approach is limited, however, because it does not hierarchically partition independent and shared components of variance.

Partial CCA (Borcard et al. 1992) was used to estimate the independence of local and landscape components of variance at the community level. The variance described by all environmental variables was 0.133, by local variables (after factoring out landscape variables) was 0.095, and by landscape variables (after factoring out local variables) was 0.018. Therefore, only a small component of variance (0.02) was confounded between local and landscape variables. This partial CCA analysis indicates that both local and landscape variables

Table 3. Factorial sample design, with number of samples in each of the four factors, the between-subjects factors, and the randomized block (study area).

Factor	Categories	N
Study area	COCH	194
	NIP	166
	RL	204
AGE-class	1.00	79
	2.00	313
	3.00	172
EDGE-class	1.00	155
	2.00	230
	3.00	179
HARDWOOD-class	1.00	135
	2.00	290
	3.00	139
INTACT-class	1.00	177
	2.00	225
	3.00	162

contribute independent information, but that local-scale variables account for about five times more variance than landscape-scale variables (0.095 and 0.018, respectively).

The relationships between environmental variables and species occurrence was described by overlaying the vectors of environmental variables that explain the patterns of co-occurrence (Fig. 2). The continuous local-scale variables (HARDWOOD, CANOPY, HEIGHT, AGE, and YOUNG) and landscape-scale variables (EDGE, INTACT) were cast as explanatory variables, and arrows on the CCA biplot depict the direction and strength of the relationship between the explanatory variables and species occurrence.

The CCA reveals four distinct explanatory “factors” associated with species occurrence patterns (p = 0.0020; F = 15.91). The intact forest matrix vector is opposite that of the forest cover type (HARDWOOD) vector, and is separate from that for edge density. The edge density variable, however, is correlated with the local disturbance variable (YOUNG). Finally, the internal stand structure variables CANOPY, HEIGHT, and AGE tend to track together. These responses can be interpreted as four separate factors: (1) overstory

Table 4. Significance (ANOVA p values) of songbird relative abundance response to local- and landscape-level effects. Values <0.05 are set in bold.

Common Name	AOU Code	Latin Name	Local (50 ha)		Landscape (5000 ha)		Random Block (Study Area)	DF Error†
			AGE Class	HARDWOOD Class	EDGE Class	INTACT Class		
Alder Flycatcher	ALFL	*Empidonax alnorum*	**0.000**	**0.007**	**0.000**	0.184	**0.004**	537
American Redstart	AMRE	*Setophaga ruticilla*	0.172	**0.002**	**0.000**	**0.011**	0.267	537
Black-and-white Warbler	BAWW	*Mniotilta varia*	**0.028**	0.429	0.953	**0.004**	0.970	380
Bay-breasted Warbler	BBWA	*Dendroica castanea*	**0.004**	0.195	**0.004**	0.674	0.480	537
Blue-headed Vireo	BHVI	*Vireo solitarius*	0.349	0.457	0.051	0.624	**0.000**	537
Blackburnian Warbler	BLBW	*Dendroica fusca*	0.109	**0.005**	0.211	0.054	0.286	352
Brown Creeper	BRCR	*Certhia americana*	0.551	0.215	0.128	0.084	**0.000**	195
Common Yellowthroat	COYE	*Geothlypis trichas*	**0.000**	0.361	**0.048**	**0.005**	**0.044**	195
Chestnut-sided Warbler	CSWA	*Dendroica pensylvanica*	**0.001**	0.879	0.519	0.203	**0.000**	537
Dark-eyed Junco	DEJU	*Junco hyemalis*	**0.047**	0.071	0.294	0.115	**0.017**	537
Golden-crowned Kinglet	GCKI	*Regulus satrapa*	**0.000**	0.542	0.498	0.071	0.393	537
Hermit Thrush	HETH	*Catharus guttatus*	0.302	**0.006**	**0.029**	0.376	0.246	537
Least Flycatcher	LEFL	*Empidonax minimus*	0.374	**0.000**	**0.002**	0.228	0.223	537
Magnolia Warbler	MAWA	*Dendroica magnolia*	0.131	0.458	0.381	**0.031**	0.070	380
Mourning Warbler	MOWA	*Oporornis philadelphia*	**0.008**	**0.006**	0.610	**0.026**	**0.025**	537

(con'd)

Nashville Warbler	NAWA	*Vermivora ruficapilla*	0.088	**0.000**	0.223	0.346	**0.007**	537
Ovenbird	OVEN	*Seiurus aurocapilla*	0.404	**0.000**	0.062	0.290	**0.011**	352
Palm Warbler	PAWA	*Dendroica palmarum*	0.449	**0.002**	**0.000**	**0.027**	0.451	537
Pine Siskin	PISI	*Carduelis pinus*	0.072	**0.000**	0.327	0.967	**0.003**	537
Pileated Woodpecker	PIWO	*Dryocopus pileatus*	0.373	**0.003**	**0.012**	0.152	**0.000**	195
Red-breasted Nuthatch	RBNU	*Sitta canadensis*	0.220	**0.005**	**0.030**	0.659	**0.000**	537
Ruby-crowned Kinglet	RCKI	*Regulus calendula*	0.098	**0.012**	0.666	0.443	0.209	537
Red-eyed Vireo	REVI	*Vireo olivaceus*	0.069	**0.000**	**0.002**	**0.000**	**0.001**	537
Swainson's Thrush	SWTH	*Catharus ustulatus*	0.203	0.132	**0.028**	0.672	**0.009**	537
Veery	VEER	*Catharus fuscescens*	0.682	0.552	**0.001**	0.412	0.121	352
Winter Wren	WIWR	*Troglodytes troglodytes*	**0.003**	**0.001**	0.587	**0.015**	**0.005**	537
White-throated Sparrow	WTSP	*Zonotrichia albicollis*	**0.000**	0.719	**0.002**	**0.001**	**0.043**	537
Yellow-bellied Flycatcher	YBFL	*Empidonax flaviventris*	**0.023**	0.091	0.356	**0.022**	**0.000**	537
Yellow-rumped Warbler	YRWA	*Dendroica coronata*	0.453	0.213	0.109	0.068	**0.002**	537
Yellow Warbler	YWAR	*Dendroica petechia*	**0.024**	**0.025**	**0.003**	**0.005**	0.735	352

† For all model factor tests, number of factor levels = 3, and factor (numerator) df = 2.

composition (HARDWOOD), (2) forest cover configuration (EDGE), (3) intactness of the forest matrix (INTACT), and (4) development of stand internal structure (AGE/CANOPY/HEIGHT). The ANOVA used classification variables directly related to these four factors, thus it is reasonable to accept the notion that the four ANOVA classes represent distinct ecological factors useful for explaining patterns of species occurrence.

The ordination analysis supports the notion that the landscape-scale variable, INTACT, contributes explanatory information that is independent from local-scale variables. INTACT is a measure of intactness of the mature forest matrix, and is only weakly correlated with the local-scale variable AGE. However, EDGE is highly correlated with the local-scale variable YOUNG. YOUNG is a measure of the relative amount of young forest at the 50-ha

Table 5. Proportion of variance explained (PVE†) by the four environmental variables (ANOVA main-effects only). Variance components based on partial eta-square (PES) analysis. Significant ($p < 0.05$) effects are set in bold.

Species	Proportion of Variance Explained Local		(Randomized Block ANOVA) Landscape	
	AGE	HARDWOOD	EDGE	INTACT
Alder Flycatcher	**0.47**	**0.14**	**0.34**	0.05
American Redstart	0.09	**0.30**	**0.39**	**0.22**
Black-and-white Warbler	**0.36**	0.09	0.00	**0.55**
Bay-breasted Warbler	**0.42**	0.13	**0.42**	0.03
Blue-headed Vireo	0.20	0.15	**0.56**	0.09
Blackburnian Warbler	0.19	**0.44**	0.13	0.25
Brown Creeper	0.09	0.23	0.31	0.37
Common Yellowthroat	**0.62**	0.04	**0.12**	**0.21**
Chestnut-sided Warbler	**0.74**	0.01	0.07	0.17
Dark-eyed Junco	**0.34**	0.29	0.14	0.24
Golden-crowned Kinglet	**0.68**	0.05	0.06	0.21
Hermit Thrush	0.11	**0.47**	**0.33**	0.09
Least Flycatcher	0.05	**0.54**	**0.32**	0.08
Magnolia Warbler	0.28	0.11	0.13	**0.48**
Mourning Warbler	**0.35**	**0.36**	0.04	**0.26**
Nashville Warbler	0.18	**0.62**	0.11	0.08
Ovenbird	0.03	**0.81**	0.10	0.05
Palm Warbler	0.04	**0.31**	**0.48**	**0.18**
Pine Siskin	0.22	**0.68**	0.09	0.00
Pileated Woodpecker	0.08	**0.45**	**0.33**	0.14
Red-breasted Nuthatch	0.14	**0.49**	**0.33**	0.04
Ruby-crowned Kinglet	0.29	**0.55**	0.05	0.10
Red-eyed Vireo	0.06	**0.59**	**0.16**	**0.19**
Swainson’s Thrush	0.21	0.27	**0.47**	0.05

(con'd)

Veery	0.04	0.07	**0.79**	0.10
Winter Wren	**0.33**	**0.40**	0.03	**0.24**
White-throated Sparrow	0.46	0.01	0.24	0.29
Yellow-bellied Flycatcher	**0.34**	0.22	0.09	**0.35**
Yellow-rumped Warbler	0.11	0.21	0.31	0.37
Yellow Warbler	**0.20**	**0.20**	**0.31**	**0.29**

† $PVE_i = PES_i/Sum\ (PES_{age,hwd,edge,mature})$, where PVE is proportion of variance explained, PES is the partial eta-squared value, and i is one of the four explanatory variables.

scale, whereas EDGE is a measure of the configuration of young and old forest at the 5000-ha scale.

Both the ANOVA and the ordination indicate that individual species within the boreal songbird community are associated with a range of cover type, stand age, disturbance intensity, and forest matrix conditions. Individual species have specific environmental needs, but the overall community requires a broad range of environmental conditions. Overlaying isopleths that model the relationships between individual environmental variables helps give concrete meaning to the rather abstract ordination. Isopleths of equal edge density are illustrated in Fig. 3, and reveal that Veery (*Catharus fuscescens*), Yellow Warbler (*Dendroica petechia*), Alder Flycatcher (*Empidonax alnorum*), and Common Yellowthroat (*Geothlypis trichas*) are all associated with high edge density (>20 m/ha), whereas Bay-breasted Warbler (*Dendroica castanea*), Brown Creeper (*Certhia americana*), Ovenbird (*Seiurus aurocapilla*), and Red-breasted Nuthatch (*Sitta canadensis*) are associated with low edge density (<18.5 m/ha) (Fig. 3). Those species responding significantly to the edge variable are highlighted in bold in the figure.

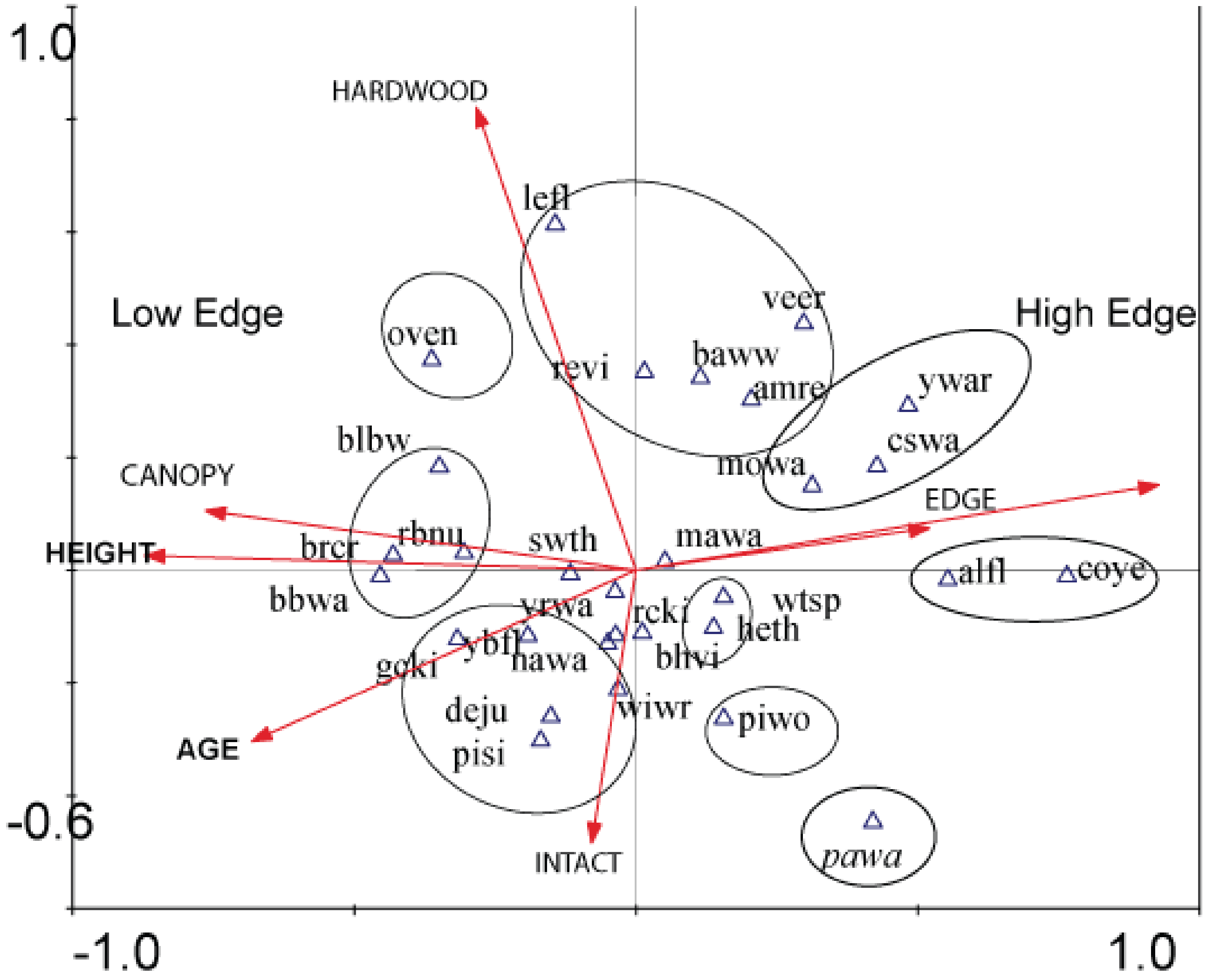
Likewise, there are patterns of discrimination for intact forest at the landscape scale. Species such as Red-eyed Vireo (*Vireo olivaceus*), Veery, and Chestnut-sided Warbler (*Dendroica pennsylvanica*) are associated with low levels of intact mature forest cover (<32%), whereas Dark-eyed Junco (*Junco hyemalis*), Pine Siskin (*Carduelis pinus*), Pileated Woodpecker (*Dryocopus pileatus*), and Winter Wren (*Troglodytes troglodytes*) are associated with a forest matrix with higher levels of intact mature and old forest (Fig. 4). At the local scale, patterns of discrimination are evident for both cover type and average stand age. Note that the ordination pattern for HARDWOOD (Fig. 5) vs. AGE (Fig. 6) is almost orthogonal; hardwood conditions are important for both young and old stands, and do not simply represent an early successional condition.

When conditional (partial correlation) environmental vectors are overlaid (Fig. 7), five relatively strong and orthogonal groupings of explanatory variables (factors) emerge: HARDWOOD, HEIGHT, CANOPY, INTACT/AGE, and YOUNG/EDGE. A consequence of modeling partial correlation is that the importance of forest configuration (EDGE) becomes much smaller relative to the amount of young forest (YOUNG). Interpretation of the ordination figure and the ANOVA results reveals at least ten natural groupings of species that collectively define a broad range of environmental conditions on the landscape:

1. Older, tall, closed canopy hardwood, with little interspersion of young and old forest: Ovenbird.

2. Immature to younger hardwood, with relatively open conditions: Least Flycatcher (*Empidonax minimus*), Red-eyed Vireo, Black-and-white Warbler (*Mniotilta varia*), American Redstart (*Setophaga ruticilla*), and Veery.

Fig. 2. Simple correlations of environmental variables with species occurrence. Arrows show positive correlations only, and points in proximity correspond to species often occurring together. Length of the arrow represents the strength of the association with overall community structure. Species close to the origin show no strong discrimination patterns for the measured environmental variables. Species codes are defined in Table 4.



3. **3.** Younger hardwood, open canopy, interspersion of young and old forest: Yellow Warbler, Chestnut-sided Warbler, Mourning Warbler (*Oporornis philadelphia*).

4. **4.** Young mixedwood, open canopy, interspersion of young and old forest: Alder Flycatcher, Common Yellowthroat.

5. **5.** Old, open, conifer bogs: Palm Warbler (*Dendroica palmarum*).

6. **6.** Older, open, softwood stands in a mature forest matrix: Pileated Woodpecker.

7. **7.** Older, closed, softwood forest, in a mature forest matrix: Winter Wren, Dark-eyed

Fig. 3. Species ordination (CCA), with overlay of isopleths (GLM) for contrast weighted edge density (EDGE) in m/ha. Species with a significant effect (ANOVA *p* < 0.05) are highlighted in bold. Isopleths delineate species predicted to occur in areas of low to high density of edge.

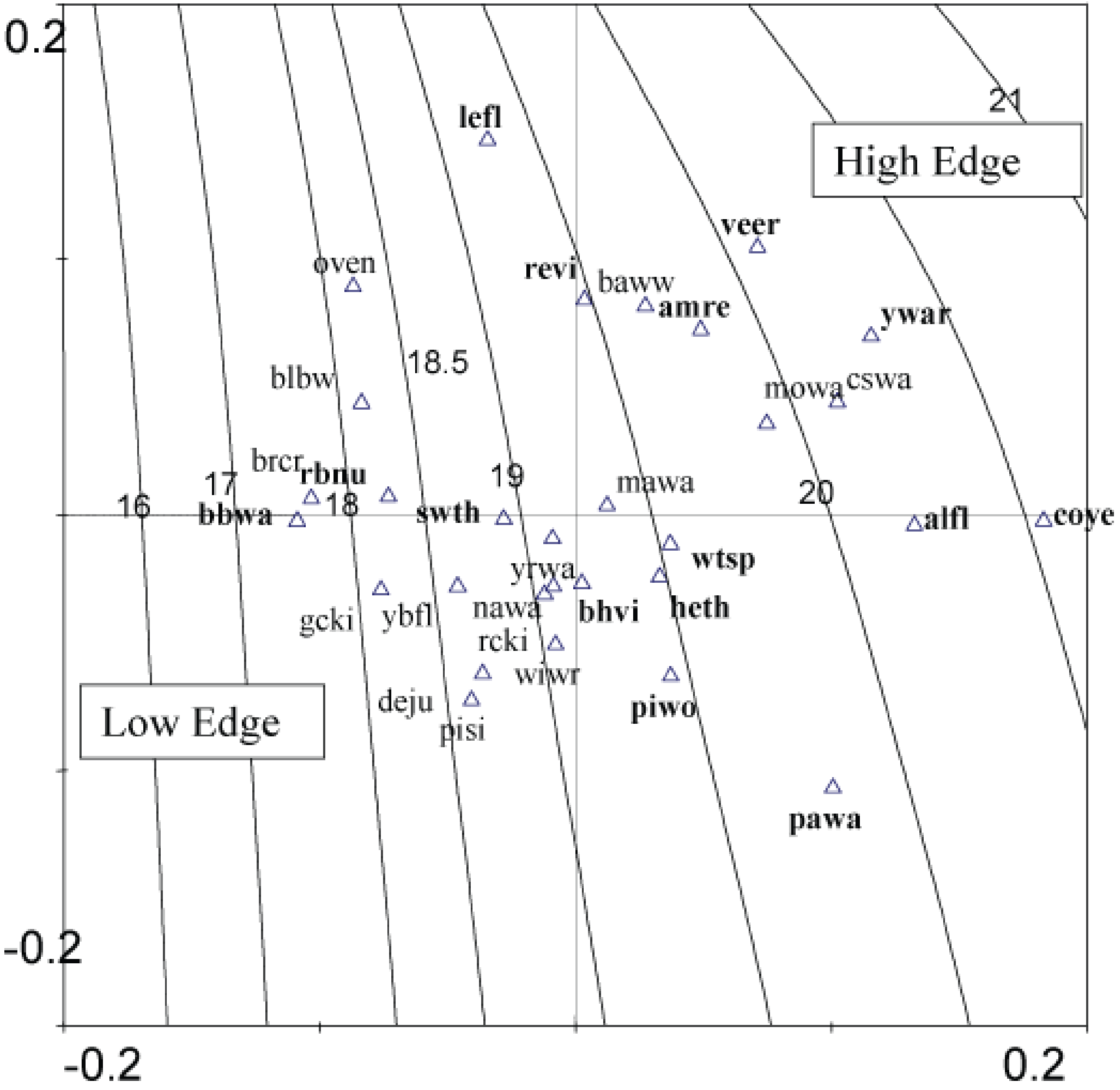


Fig. 4. Species ordination (CCA), with overlay of isopleths (GLM) for proportion mature and old forest (INTACT). Species with a significant effect (ANOVA $p < 0.05$) are highlighted in bold. Isopleths delineate species predicted to occur in areas of low to high proportions of intact mature forest.

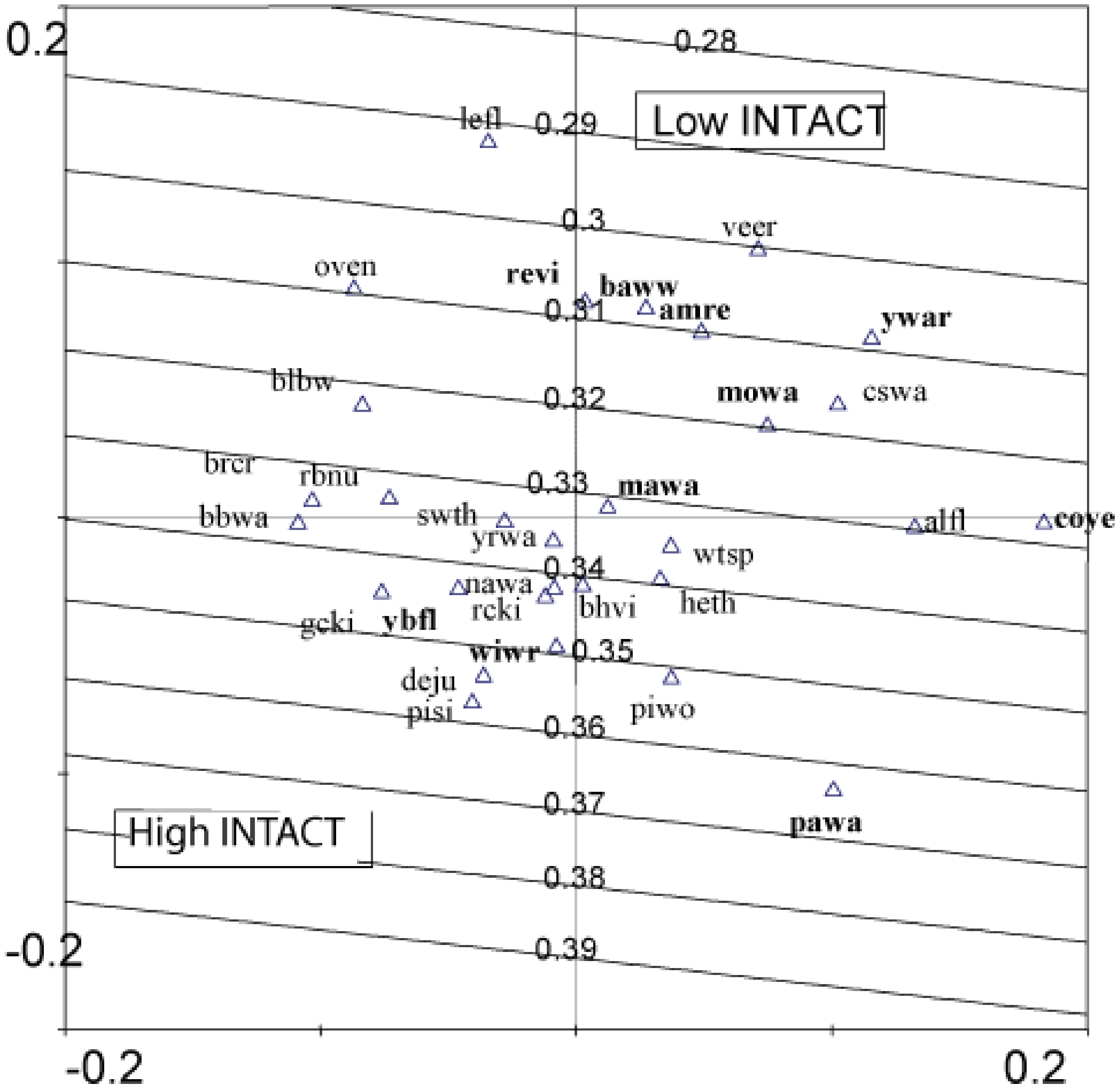


Fig. 5. Species ordination (CCA), with overlay of isopleths (GLM) for percent hardwood volume (HARDWOOD). Species with a significant effect (ANOVA $p < 0.05$) are highlighted in bold. Isopleths delineate species predicted to occur in areas of low to high proportions of hardwood forest.

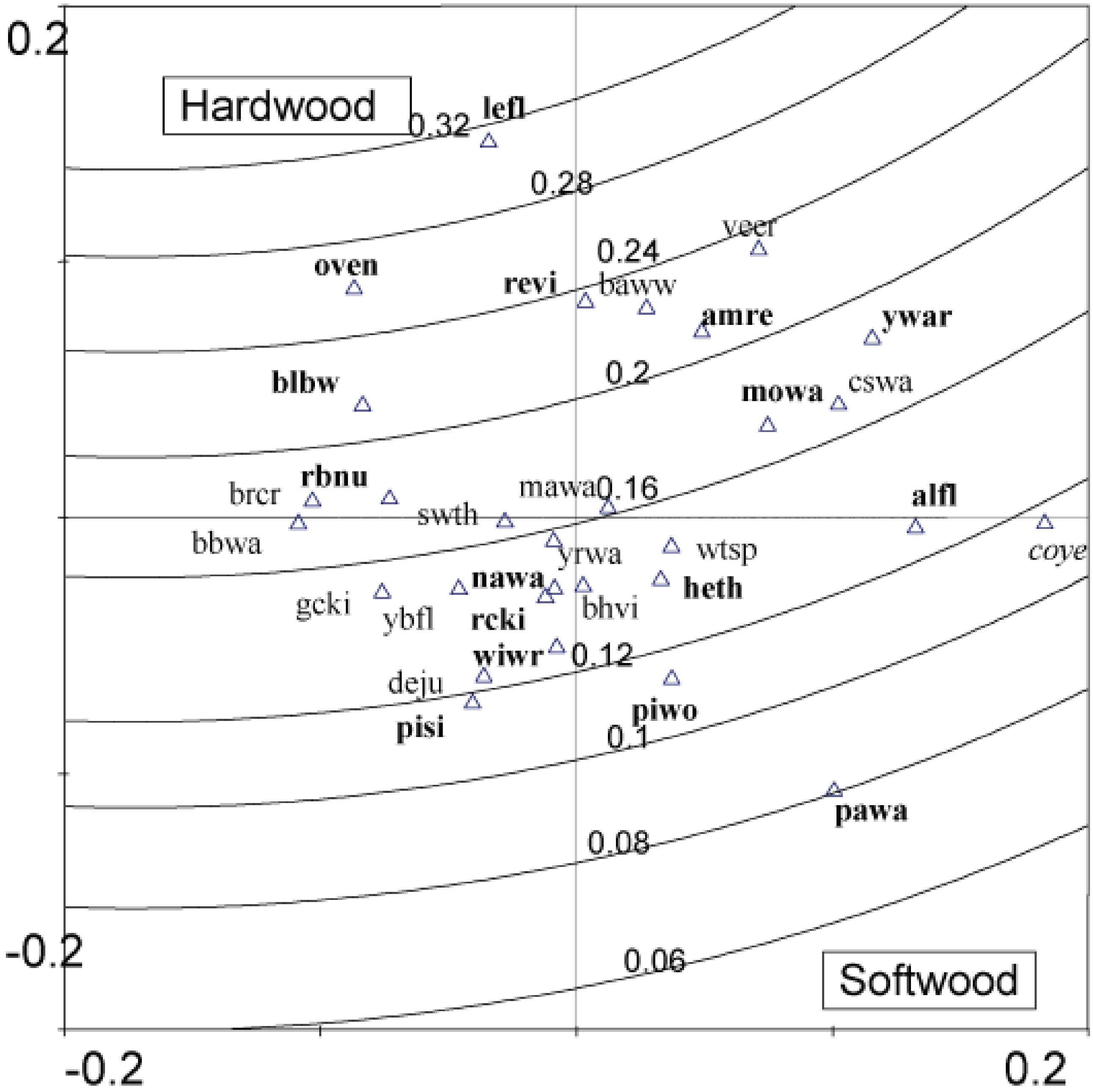


Fig. 6. Species ordination (CCA), with overlay of isopleths (GLM) for stand age (AGE) in years. Species with a significant effect (ANOVA $p < 0.05$) are highlighted in bold. Isopleths delineate species predicted to occur in areas of young to old forest.

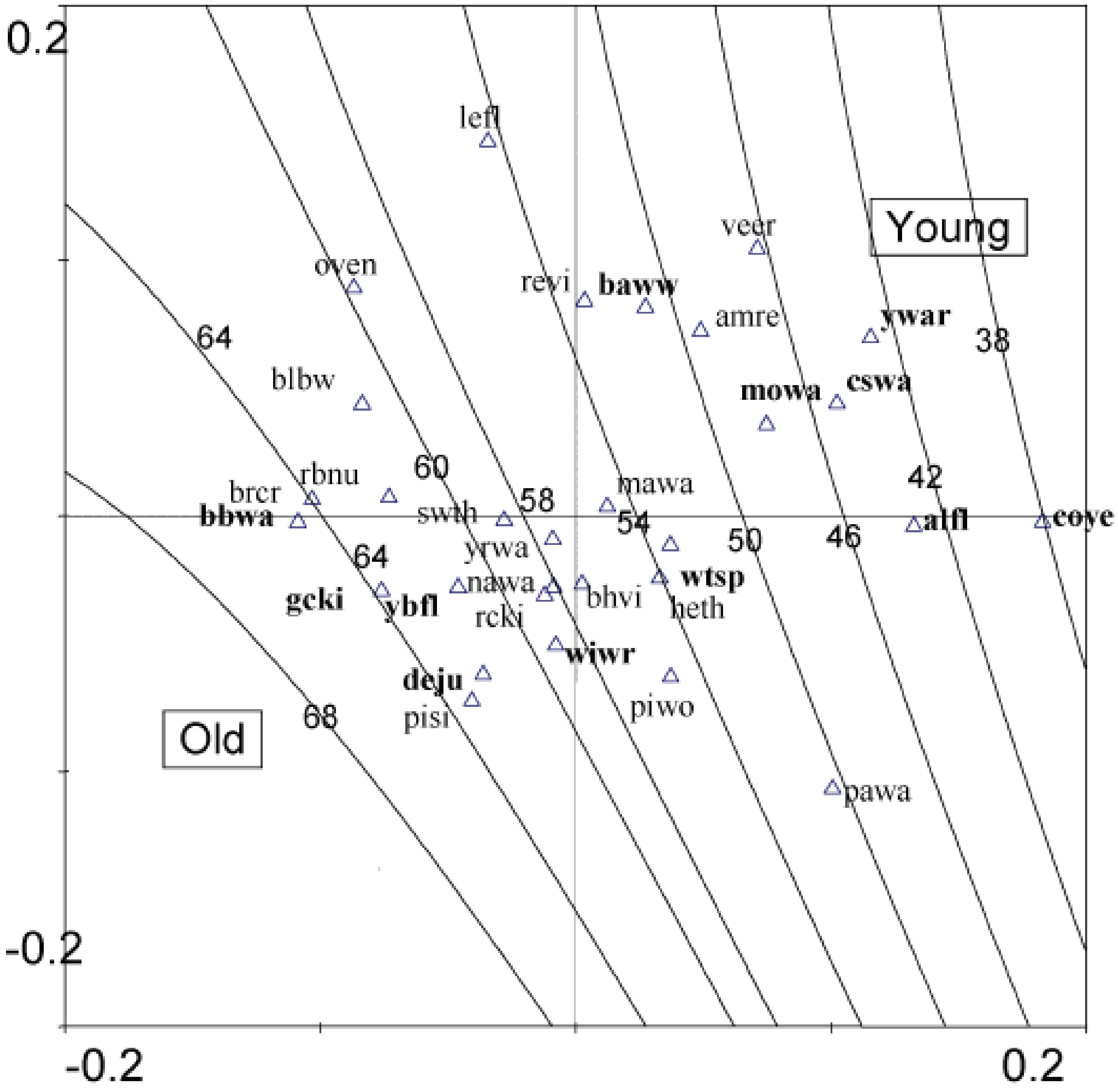
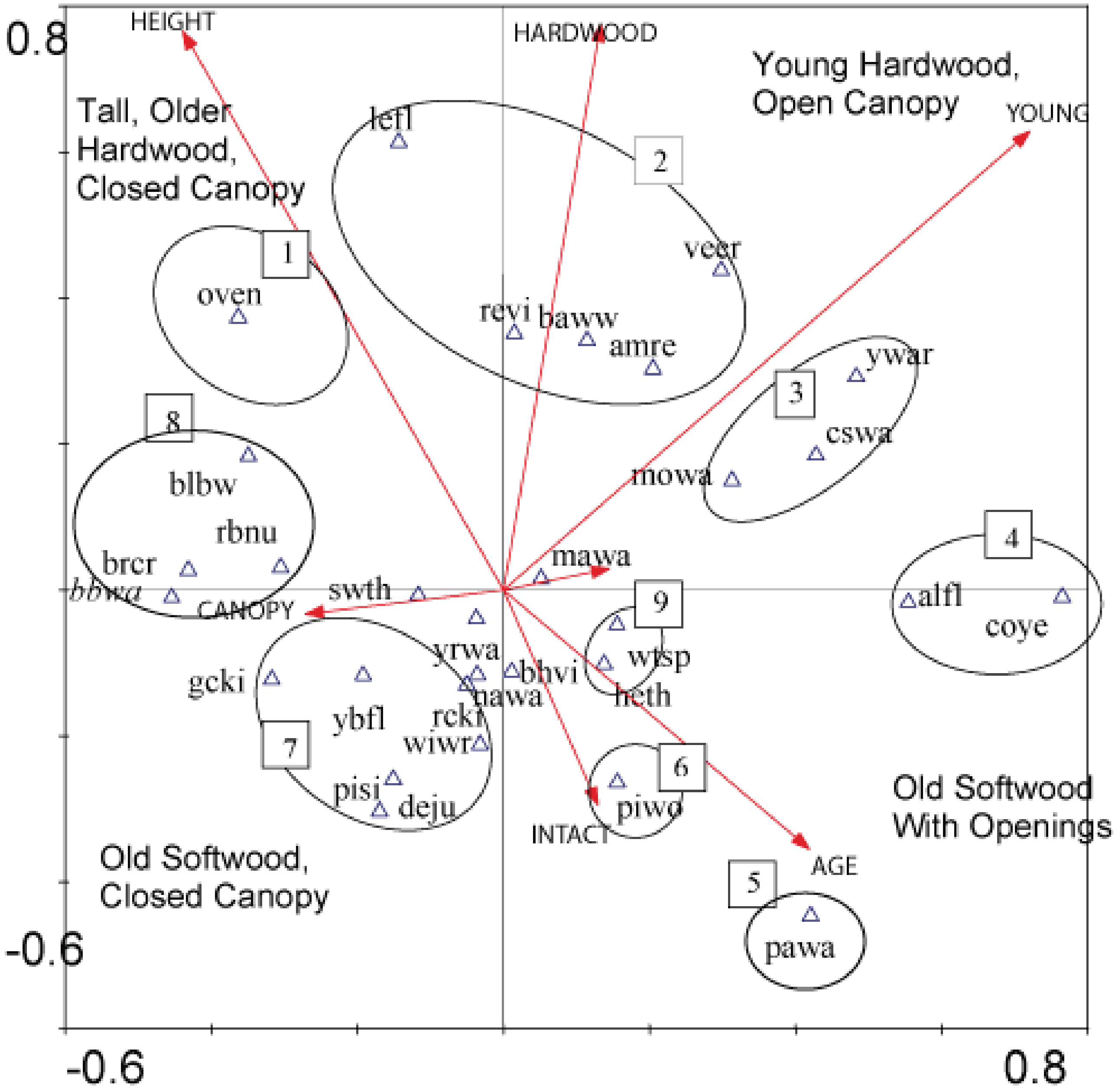


Fig. 7. Partial correlations (conditional effects) of standardized environmental variables with species occurrence, where conditional effects are represented by arrows pointing in the direction of positive associations, assuming the other environmental variables are held at their mean values. Length of the arrow represents the component of variance accounted for by that factor in predicting overall community structure.



Junco, Pine Siskin, Yellow-bellied Flycatcher (*Empidonax flaviventris*), Golden-crowned Kinglet.

8. Older, closed, mixedwood (hardwood and softwood dominated types), with little interspersion of young and old forest: Bay-breasted Warbler, Brown Creeper, Red-breasted Nuthatch, Blackburnian Warbler (*Dendroica fusca*).

9. Open mixedwood, high edge density: White-throated Sparrow, Hermit Thrush (*Catharus guttatus*).

10. Species without strong patterns of discrimination for the measured variables: Magnolia Warbler (*Dendroica magnolia*), Swainson's Thrush (*Catharus ustulatus*), Yellow-rumped Warbler (*Dendroica coronata*), Blue-headed Vireo (*Vireo solitarius*), Nashville Warbler (*Vermivora ruficapilla*), Ruby-crowned Kinglet (*Regulus calendula*).

This grouping of species provides critical information for making an informed and unbiased selection of focal species for modeling and monitoring environmental effects of forest management. If species are selected from only one quadrant of the ordination figure, then management assessment would be biased toward a restricted set of environmental conditions and species response.

Habitat Model Performance and Focal Species Selection

Canonical correspondence analysis ordination figures do not easily translate into testable management objectives, so RSPF habitat models were developed to predict the probability of habitat occupancy based on local- and landscape-scale variables. The habitat models essentially translate forest cover amount and configuration into probabilities of habitat occupancy, and consequently are of great value for evaluating alternative forest management options (and resulting forest configurations) for biodiversity conservation. In general, the logistic regression model coefficients reflect the direction of partial correlations (Fig. 7), but there were a few exceptions. For example, CCA analysis suggested Yellow-bellied Flycatcher would be associated with older forest with greater canopy closure, but the logistic regression resulted in an opposite association.

Model discrimination was tested using ROC values, and for training data these ranged from 0.6 to 0.85 (Fig. 8). The ROC values were also calculated for model test (validation) data to evaluate consistency of model discrimination. Models with the highest ROC values (i.e., >0.8) almost always had test ROC values lower than the 95% confidence limit (Fig. 8). This suggests that model discrimination was inconsistent for these species.

Model reliability was tested using calibration curves (Table 6), and model spread ranged from 0.47 to 1.12. Models where the slope approaches unity (i.e., the 95% C.L. for the slope brackets 1) indicate the model is reliable in terms of systematically predicting relative species occurrence. Models with low reliability (e.g., American Redstart, Golden-crowned Kinglet, Nashville Warbler, and Pileated Woodpecker) also had inconsistent discrimination, where ROC test values fell well below the 95% C.L. (Fig. 8). Model bias was estimated by the model constants, and 11 of 30 models had constants where the 95% C.L. did not encompass 0, indicating some level of bias. This probably occurs because the species is either more prevalent or less prevalent in the test data relative to the training data. This can lead to a consistent over or underestimation of the probability of occurrence. Model spread, however, is of greater concern because it indicates model misspecification.

The selection of focal species is based on a combination of study objectives and evaluation of species' model performance. Overall model performance was considered high when: (1) CCA analysis agreed with logistic regression analysis, (2) model discrimination among observations was >0.7, (3) model discrimination was consistent among training and testing sites, and (4) model predictive reliability was high, with model spread (i.e., slope) approaching unity. Where the objective is to select species that represent a broad range of forest diversity (niche-space) as revealed through the CCA analysis, then Hermit Thrush, Veery, Brown Creeper, Pine Siskin, Alder Flycatcher, Ovenbird, and Palm Warbler all represent this diversity and have models that perform well in terms of consistency, discrimination, and reliability.

In contrast, study objectives may be focused on more specific forest attributes, such as forest cover

Fig. 8. Accuracy assessment (ROC) and 95% confidence limits for the habitat models. Values are area under the ROC curve, and represent the probability of correctly assigning the correct label (occupied/ unoccupied) for new observations. Closed symbols are for model development (training), and open symbols for independent test of the models.

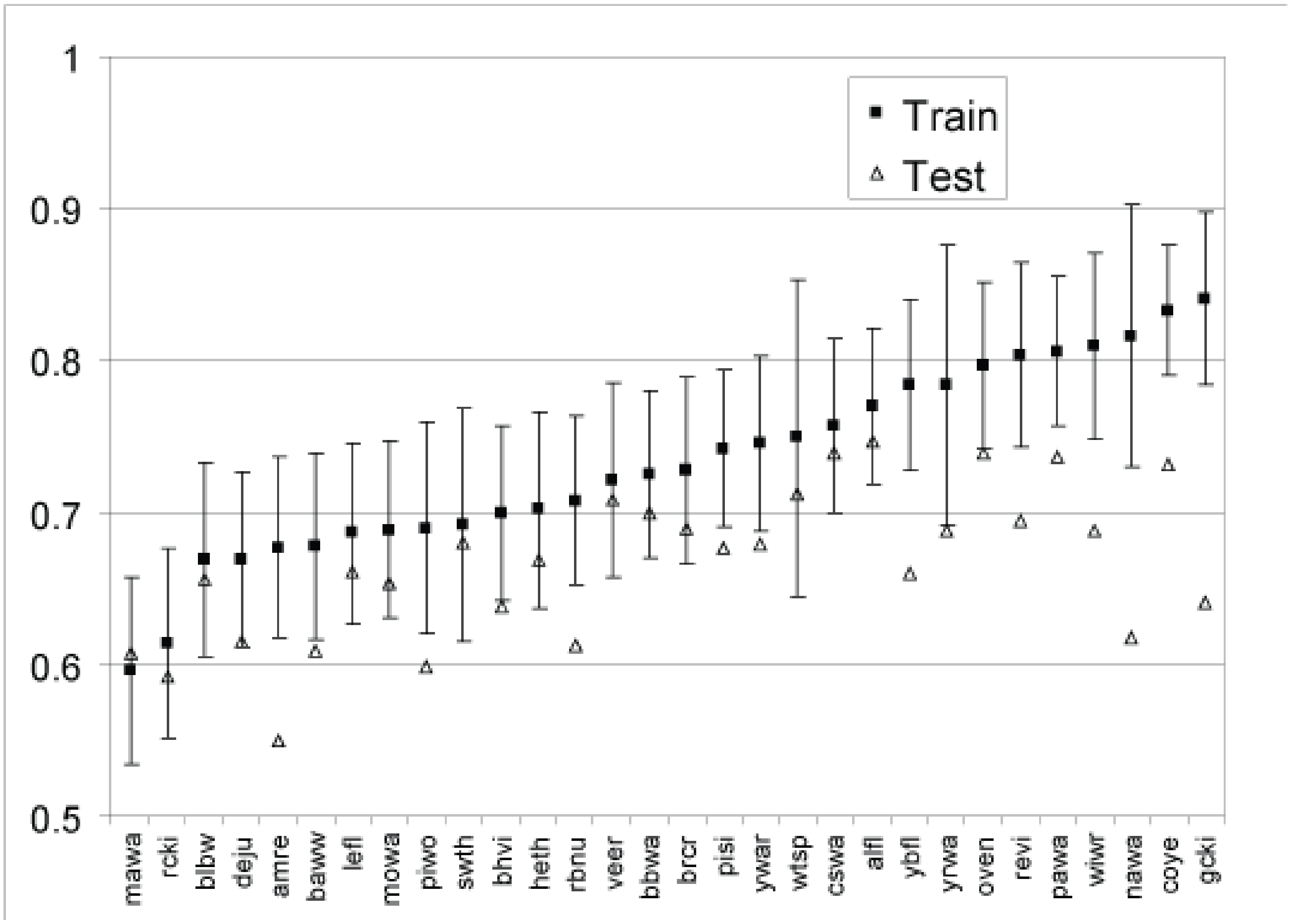


Table 6. Model reliability estimates, based on logistic-regression calibration curves of (logit) predicted probability vs. presence/absence in validation test site. Well-calibrated models have a slope approaching 1, and constant approaching 0.

Species	Slope (Spread)	95% CL	Constant (Bias)	95% CL
ALFL	1.08	(1.34, 0.82)	-0.28	(-0.07, -0.48)
AMRE	0.27	(0.58, -0.04)	0.12	(0.32, -0.09)
BAWW	0.56	(0.90, 0.22)	-0.44	(-0.08, -0.80)
BBWA	1.03	(1.33, 0.72)	0.09	(0.35, -0.17)
BHVI	0.72	(0.99, 0.46)	0.07	(0.27, -0.13)
BLBW	-0.06	(0.10, -0.22)	-0.96	(-0.75, -1.17)
BRCR	1.07	(1.49, 0.64)	-0.55	(-0.11, -0.99)
COYE	0.73	(0.95, 0.51)	-0.50	(-0.19, -0.80)
CSWA	1.04	(1.34, 0.73)	-0.36	(-0.01, -0.71)
DEJU	0.65	(0.95, 0.35)	0.12	(0.31, -0.07)
GCKI	0.45	(0.64, 0.27)	0.52	(0.87, 0.18)
HETH	1.06	(1.41, 0.72)	-0.01	(0.34, -0.37)
LEFL	1.21	(1.66, 0.77)	0.24	(0.67, -0.19)
MAWA	0.54	(0.80, 0.28)	-0.27	(0.02, -0.56)
MOWA	0.81	(1.13, 0.48)	-0.16	(0.18, -0.50)
NAWA	0.57	(0.80, 0.33)	0.55	(1.11, -0.01)
OVEN	0.79	(1.01, 0.57)	0.32	(0.59, 0.04)
PAWA	0.97	(1.24, 0.70)	-0.15	(0.25, -0.56)
PISI	0.75	(0.97, 0.53)	-0.06	(0.14, -0.27)
PIWO	0.47	(0.73, 0.21)	-1.07	(-0.65, -1.49)
RBNU	0.63	(0.92, 0.34)	-0.06	(0.13, -0.26)
RCKI	0.95	(1.57, 0.32)	0.03	(0.38, -0.32)
REVI	0.60	(0.82, 0.37)	0.69	(1.01, 0.37)
SWTH	1.16	(1.58, 0.75)	-0.36	(0.25, -0.97)
VEER	0.78	(1.05, 0.51)	-0.11	(0.26, -0.48)

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WIWR	0.60	(0.80, 0.39)	0.62	(0.93, 0.31)
WTSP	1.12	(1.61, 0.63)	0.08	(1.11, -0.94)
YBFL	0.63	(0.86, 0.41)	0.09	(0.41, -0.22)
YRWA	0.64	(0.90, 0.37)	0.63	(1.28, -0.03)
YWAR	0.55	(0.87, 0.24)	-0.69	(-0.35, -1.04)

amount and configuration at the landscape scale. In such cases, evidence of a significant response to those attributes, as revealed through factorial ANOVA, becomes a dominant factor in the selection of focal species. This imposes restrictions on model selection, and can lead to compromises on setting acceptable model performance. The selection of focal species suggested for assessing (in part) the sustainability of proposed forest management policy options was based on a species' position within the environmental ordination (Fig. 2), the presence of a least one significant effect at the landscape scale (Table 4), and the assessment of model performance. Thirteen species were selected as focal species for this second objective, and their RSPF model coefficients (Table 7) define a broad array of habitat conditions that reflect the diversity of forest conditions expected at the landscape scale. This selection of focal species, however, includes a few models that performed relatively poorly. Those models were selected only because the species revealed a significant ($p < 0.05$) response to either forest cover configuration or amount of intact forest at the landscape scale, and there was no other alternative species with a better performing model. To reflect the variability of confidence in habitat models, the influence of the model in assessing policy options can be weighted by the model discrimination test score (Rempel et al. 2007).

DISCUSSION

In this study, I ignored stand boundaries, and instead characterized habitat at local (50 ha), and landscape (5000 ha) scales, and found that for 19 of 30 species the area of influence on songbird habitat use extended up to 5000 ha. Forest configuration, i.e., the edge between young and old forest, and the homogeneity of the intact forest matrix had significant effects on habitat use. Partial CCA analysis revealed that both local- and landscape-scale variables contributed independently to explained variance. At the local scale, the stand-structure effects of average stand age and percent hardwood volume had strong and predictable effects, but for 19 species, significant additional components of variance in songbird relative abundance were accounted for by including landscape-scale variables. However, unlike the partial CCA analysis, the component of variance approach used in ANOVA does not hierarchically partition the variance components. In simple terms, the value of a local site as habitat to a bird is influenced by the composition and homogeneity (or heterogeneity) of the surrounding landscape. This has implications for forest management, in that broad landscape-scale patterns of forest disturbance may indeed influence habitat use by songbirds. Development of biodiversity conservation strategies must consider landscape-scale patterns such as the relative area of mature forest cover, and the configuration of cover in terms of forest edge.

Modeled gradients of habitat association for the 13 species selected as focal species for evaluation of forest policy options (Alder Flycatcher, Black-and-white Warbler, Bay-breasted Warbler, Blackburnian Warbler, Brown Creeper, Common Yellowthroat, Chestnut-sided Warbler, Least Flycatcher, Ovenbird, Red-breasted Nuthatch, Red-eyed Vireo, Winter Wren, and White-throated Sparrow), all generally agree with previously published findings. For example, on relatively moderate forest-cover gradients I found Alder Flycatcher, American Redstart, Black-and-white Warbler, Common Yellowthroat, Chestnut-sided Warbler, Least Flycatcher, Mourning Warbler, Red-eyed Vireo, Veery, and White-throated Sparrow are associated with higher disturbance intensities, with less intact

Table 7. Model coefficients and constant (C) for logistic regressions, where additive sum is probability of habitat occupancy.

Species	AGE	AGE^2	HEIGHT	HEIGHT^2	PYF	PCC	PCC^2	PHV	PHV^2	CWED	CWED^2	PMOF	C†
Alder Flycatcher	0.020	0.000	0.236	-0.014	-0.132	-0.173	0.002	0.464	0.169	0.131	-0.003	1.331	0.594
Black-and-white Warbler	0.006	0.000	-0.096	-0.001	0.000			0.827	0.218	-0.011		-3.596	0.584
Bay-breasted Warbler	-0.002	0.000	0.314	-0.017	-3.111	-0.066	0.000	0.000	-0.707	-0.262	0.006	1.512	3.189
Blackburnian Warbler		0.000	0.070	0.000	-1.052		0.000	0.564				1.110	-1.631
Brown Creeper	0.003	0.000	0.265	0.002	0.450	-0.001	0.000	-4.358	5.306	0.046	-0.002	1.418	-3.578
Common Yellowthroat	0.056	0.000	-0.706	0.022	0.862	-0.087	0.001	4.880	-6.184	0.552	-0.013	-0.543	-3.352
Chestnut-sided Warbler	0.050	0.000	0.507	-0.009	0.928	-0.156	0.000	-1.461	3.874	0.022	-0.001	0.387	-2.383
Least Flycatcher	-0.002			0.003		-0.020		2.118	-0.643	-0.021		-1.388	0.066
Ovenbird	-0.012		0.134	-0.002	-2.258	-0.051	0.000	9.001	-9.145	-0.186	0.003	-0.657	4.340
Red-breasted Nuthatch	0.019	0.000	0.189	-0.004	0.000	0.020	0.000	2.401	-3.530		-0.001	1.866	-2.138
Red-eyed Vireo		0.000	-0.686	0.032	-3.141	-0.088	0.001	9.011	-8.072	0.159	-0.003	-2.085	5.855
Winter Wren	0.027	0.000	-0.073	-0.006	-1.964	-0.023		-2.330	3.131	0.081	-0.001	5.494	0.487
White-throated Sparrow			-0.086					1.262	-2.589		0.001	4.642	1.343

† Constant

mature forest cover, and higher levels of age-class interspersion. Webb et al. (1977) studied a gradient of disturbance intensity (0, 25, 50, and 75% harvest removal) over 7 years in the Adirondacks and, even though the ecoregion is markedly different, also found American Redstart, Chestnut-side Warbler, Black-and-white Warbler, and Veery all tended to increase with harvest intensity. Similarly, in Ontario, Freedman et al. (1981) found Chestnut-sided Warbler, Common Yellow-throat, and White-throated Sparrow to be associated with younger forest, and Welsh (1987) found White-throated Sparrow, Chestnut-sided Warbler, Mourning Warbler, and Alder Flycatcher to be associated with early successional habitat.

In contrast, I found that Bay-breasted Warbler, Blackburnian Warbler, Brown Creeper, Golden-crowned Kinglet, Ovenbird, Red-breasted Nuthatch, and Winter Wren are associated with conditions of lower disturbance intensities, including greater levels of intact mature forest cover and less age-class interspersion. Webb et al. (1977) also found Blackburnian Warbler, Least Flycatcher, Ovenbird, and Winter Wren tended to decrease with harvest intensity, and for all but Least Flycatcher, agreed with results here. Likewise, Welsh (1987) found Bay-breasted Warbler, Golden-crowned Kinglet and Ovenbird to be associated with late-successional habitat. The results for Least Flycatcher disagreed with those of Webb et al. (1977); however Holmes and Sherry (2001) found

Least Flycatcher to be strongly associated with early successional habitat.

Habitat fragmentation generally refers to two factors, the loss of habitat and the breaking apart (configuration) of habitat, and consequently requires at least two separate measures to quantify area-sensitive vs. edge-sensitive responses (Fahrig 1997, Schmiegelow and Monkkonen 2002). Although INTACT-class was used to measure amount of mature forest cover, and EDGE-class to measure configuration of forest cover, the study design did not allow complete separation of these factors. For example, a decline in INTACT will generally result in some increase in age-class edge (EDGE) because the area of forested land does not change temporally or spatially. Regardless of the partial dependencies, the data were only weakly collinear, and the ordination revealed almost orthogonal responses, with species like Bay-breasted Warbler and Red-breasted Nuthatch responding negatively to the configuration of mature forest (EDGE), and Winter Wren responding negatively to forest cover loss (INTACT). There was also considerable overlap in the ordination, with many species responding to both EDGE and INTACT. For the ordination and regression, YOUNG, a measure of the relative abundance of young forest at the local scale, was used to characterize loss of mature forest (or gain in young forest). Logistic regression analysis was used to assign relative weights of the model variables for predicting habitat occupancy, and in general, the results are similar to those found by Trzcinski et al. (1999) in that relative amount of mature forest cover was a stronger predictor of habitat occupancy than the configuration of forest cover. Similar to Villard et al. (1999), the gradient of response to forest cover and configuration was only moderately strong, and without steep thresholds.

A factorial, randomized block design was used to compartmentalize the components of variance resulting from local- vs. landscape-scale variables. This approach helps strengthen the conclusion that landscape-scale effects were important; however, they leave unaddressed whether 5000 ha is the most appropriate scale for assessing forest edge and matrix conditions. The CCA analysis suggested strong correlation between the landscape-scale variable EDGE, and the local-scale variable YOUNG. The terms local and landscape have no intrinsic meaning, and 50 ha may be considered by some to be a landscape-scale variable. Regardless, both these variables will increase with greater disturbance intensity. Future studies should explore this relationship by characterizing the two variables over a greater division of scales. In contrast, the landscape-variable INTACT did not have any strong correlation with local-scale variables.

The factorial ANOVA was not used to test for interactions among factors (e.g., EDGE-class * HARDWOOD-class), rather the ANOVA was used to test only for simple and unambiguous main effects (but, of course, where randomized block interactions with main effect variables were included in the model design). This limited the overall power for hypothesis testing because, for example, EDGE may have been insignificant as a main effect, but significant as an interaction effect where an effect is observed at only the lower HARDWOOD-class levels. With four factors and three factor levels each, the model complexity becomes quickly overwhelming for a fully specified model. Instead, variable interactions were explored through CCA and logistic regression analysis.

The CCA ordinations help translate the statistical inferences (ANOVA) into more tangible interpretations. For example, Fig. 3 identifies which species are associated with high vs. low edge (in m/ha) by identifying the general associated levels of edge density, and Fig. 4 does likewise for the intactness of the forest matrix. From a songbird community perspective, species are associated with a broad range of landscape patterns, ranging from high to low edge and intactness of the forest matrix, and at the local scale, high to low levels of forest disturbance, canopy closure, and early successional tree species.

The songbird community requires disturbance to provide the range of habitat conditions to which the species are adapted. For example, some species such as Bay-breasted Warbler and Red-breasted Nuthatch are associated with conditions found in low levels of disturbance, including low levels of edge, low levels of hardwood, older forest, and closed canopy. Other species such as Common Yellowthroat, Alder Flycatcher, and Yellow Warbler are associated with higher level of disturbance, and these species apparently require disturbance for the creation of quality habitat.

CONCLUSION

To be successful, biodiversity conservation strategies must emulate the patterns created through natural disturbance by maintaining the full range of forest cover homogeneity and heterogeneity on the landscape. This variation in landscape pattern can be achieved by creating habitat conditions to support a range of focal species that collectively describe the wide range of niche-space occupied by the forest songbird community. The combination of community-level and species-level analyses help to identify the set of focal species that land managers should consider when developing forest management plans. Providing the habitat needs for all members within this focal group will ensure important “coarse-scale” habitat needs are not lost on the landscape. Defining the habitat needs for individual species within the focal group provides the basis of a concrete strategy for identifying appropriate levels and combinations of landscape patterns required to conserve biodiversity for a broad range of forest songbirds, and perhaps even the invertebrates and other food-web species associated with these birds. In a parallel study (Rempel et al. 2007), the focal species habitat models developed here are applied to forest simulation models, where the goal is to select policy options that will succeed in both conserving biodiversity and maintaining current harvest levels. Future studies need to evaluate these predications at different times and places because habitat associations may be influenced by as yet unidentified causal factors (e.g., distributions in insect prey abundance). Although many of the local-scale habitat associations are relatively well known, most of the landscape-scale habitat associations are less well understood. Further study is required to evaluate the robustness of habitat associations at the broader landscape scales.

Responses to this article can be read online at:
http://www.ace-eco.org/vol2/iss1/art6/responses/

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