

Comparing the predictive capability of forest songbird habitat models based on remotely sensed versus ground-based vegetation information

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Abstract: Habitat suitability models allow for predictive modeling of the supply of wildlife habitat through time under various forest harvesting scenarios. These models often rely on remotely sensed data in a forest resource inventory (FRI). However, the level of detail and (or) the accuracy of a FRI may be insufficient to accurately predict habitat suitability for forest birds. We tested if detailed vegetation measurements created habitat suitability models with better predictive power than models that used FRI data alone and if rough estimates of shrub cover were sufficient to supplement FRI data to create models with similar predictive power. For 28 species of forest birds, we found that less of the variation in abundance and (or) occurrence (% deviance explained) could be explained by models using FRI data alone ($34\% \pm 2\%$) than by models using detailed vegetation information ($40\% \pm 2\%$). However, when shrub density rank was included with FRI data, we found no difference in the deviance explained by the two model sets ($39\% \pm 2\%$ vs. $40\% \pm 2\%$). The best-fitting models containing the same vegetation parameters but using different methods of vegetation sampling were similar. These results suggest that coarse habitat classification schemes may be as effective in describing the major variance in bird community structure in the boreal forest as detailed vegetation inventory data.

Résumé : Les modèles de qualité d'habitat permettent de simuler la variation de la disponibilité des habitats fauniques en fonction du temps selon différents scénarios de récolte ligneuse. Ces modèles reposent souvent sur des données d'inventaire des ressources forestières (IRF) obtenues par télédétection. Toutefois, le niveau de détail et (ou) la précision de ces données peuvent s'avérer insuffisants pour prédire la qualité de l'habitat de plusieurs oiseaux forestiers. Nous avons vérifié si des données de végétation plus détaillées que celles de l'IRF pouvaient améliorer le pouvoir prédictif des modèles de qualité d'habitat et si des estimations grossières du couvert arbustif étaient suffisantes pour compléter les données d'IRF. Dans une analyse portant sur 28 espèces d'oiseaux forestiers, nous avons trouvé qu'une moins grande partie de la variation de l'abondance ou de l'occurrence (% des écarts expliqués) était expliquée par les modèles utilisant seulement l'IRF ($34 \pm 2\%$) comparativement aux modèles utilisant des données détaillées de végétation ($40 \pm 2\%$). Toutefois, lorsqu'on ajoutait à l'IRF des données de rangs de densité d'arbustes, il n'y avait plus de différence dans les écarts expliqués par les deux types de modèles ($39 \pm 2\%$ vs $40 \pm 2\%$). Lorsqu'on considérait les modèles les mieux ajustés, basés sur les mêmes paramètres de végétation mais mesurés selon différentes méthodes, on obtenait des résultats semblables. Ces résultats indiquent que des approches de classification grossière de l'habitat peuvent être aussi efficaces que la collecte de données détaillées de végétation pour décrire la majeure partie de la variance dans la structure des communautés d'oiseaux de la forêt boréale.

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Introduction

The last 20 years has seen dramatic increases in the rates of forest harvesting over much of the boreal forest of western Canada (Stelfox 1995; Timoney and Lee 2001; May 2005). This development has raised concerns that some wildlife populations may not be sustained across regions of the commercial forest (Spence 2001; Boutin and Hebert

2002; Work et al. 2003). Consequently, wildlife and forestry managers have developed habitat suitability models that predict the abundance and (or) occurrence of particular species in different forest habitats (Hebert 2004; Schieck and Song 2006; Van Wilgenburg and Hobson 2008). Once developed and validated, habitat suitability models can be used to predict the impacts of future forest harvesting scenarios caused

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by changes in the relative abundance of different forest types and age distributions in the landscape (Hansen et al. 1995; Klaus et al. 2005; Shifley et al. 2006).

The ability to accurately describe habitat variation and to identify those parameters that correlate with wildlife abundance is key to the development of habitat suitability models with strong predictive power. Unfortunately, collecting detailed vegetation data is both time-consuming and expensive, resulting in a lack of spatially explicit vegetation data collected on the ground in most forested areas. This has led to the use of remotely sensed data, such as satellite imagery or forest resource inventory (FRI) data, in habitat suitability models. A FRI is probably the most widely used data source in the forestry sector and summarizes in a geographic information system the stand size, structure, and composition of the forest by using interpreted and digitized aerial photographs. Although remotely sensed data provide information on habitat variability over large spatial extents, such data focus on canopy-level attributes and ignore potentially important ecological information about vegetation attributes below the canopy (Bissonnette et al. 1997). Whether the level of detail in a FRI is sufficient and (or) spatially accurate enough to effectively predict the suitability of forest stands for forest birds in particular is not clear. Dussault et al. (2001) found that FRI and field observations for some important parameters were only weakly correlated (see also Gergel et al. (2007)). FRI data are necessarily reduced to a subset of forest categories that are spatially clustered into distinct polygons, which may or may not represent the natural range of structural and spatial variation in canopy-level attributes that forest birds respond to. As such, efforts are required to determine whether models based on FRI data are as accurate and have the predictive power of models that are based on more detailed assessments of vegetation cover. A recent study conducted in New Brunswick suggests that models of habitat suitability for the majority of forest birds that are based on FRI data are as predictive as those based on detailed vegetation measurements (Betts et al. 2006). Whether this applies to other forested systems or types of FRI data needs to be tested.

For 28 forest passerine species in boreal mixedwood forests of Saskatchewan, we created habitat suitability models using detailed vegetation counts collected in the field versus quick visual estimates of shrub cover combined with canopy-level information derived from FRI data. Our objectives were (i) to determine if the increased information gained from detailed measurement of vegetation in the field would create models with better explanatory power than those created based on attributes from forest inventory maps alone, and (ii) to assess whether rough visual estimates of shrub cover could supplement information from FRI data to generate habitat suitability models with a similar explanatory power to those created based on detailed vegetation data. We predicted that habitat suitability models derived using detailed vegetation measurements taken in the field would explain more of the variation in the data because of a more accurate assessment of variation in forest cover attributes (i.e., absolute tree density rather than percent canopy closure).

Methods

Study area

The data used in this analysis came from a series of studies conducted in the southern boreal ecoregion of Saskatchewan (Hobson and Bayne 2000a, 2000b). Surveys were conducted in and around the Prince Albert Model Forest (Bouman et al. 1996) located about 70 km north of Prince Albert, Saskatchewan (53°50'N, 105°50'W), during the summers of 1993 and 1994. Stands were adjacent to other mature stands and bordered by an access road or trail. Generally, four or five survey stations were located within a single forest stand, with the requirement that these stations were at least 250 m apart and 100 m from an edge, including edges of other stand types. Stands were distributed throughout an area of approximately 400 000 ha and were a minimum of 3 km apart. A total of 204 point count stations were visited in 41 stands.

Vegetation survey techniques

At each bird survey station, vegetation characteristics were recorded in four 0.04 ha (11.3 m radius) circles situated 25 m from the station in each of the four cardinal directions (James and Shugart 1970). In each circle, the number of trees of each species was recorded. Tree height was measured for two individuals of each tree species that reached the canopy. The first tree measured was nearest to the center of the sampling circle, while the second tree was the next nearest neighbor of the same species. Within each circle, two 16 m² subplots were placed at each end of the 22.6 m transect line. Within each subplot, we established four cells that were 4 m² each. In the first cell on the right side of the transect, the stem density of each species of shrub over 1 m in height was determined. In the other cells, shrub density was measured or estimated based on the results of the first cell count. The average shrub height in each cell was estimated for the dominant shrub species. A single vegetation crew working outside the time period when bird censuses were conducted took vegetation measurements. Observers conducting bird censuses collected a second vegetation data set. At each station, observers conducting avian point counts ranked the shrub density into four ordinal classes in a ca. 50 m radius (scattered, low, medium, and high), estimated the proportion of the total shrub layer consisting of different shrub species, and estimated the average height of the dominant shrub species.

Avifauna survey techniques

Breeding bird surveys were conducted twice at each station, once in early June and once in late June. Surveys involved early-morning point counts (0400–0900) at each station (Blondel et al. 1970) and all birds heard or seen during a 10 min count period were recorded. Counts were of unlimited distance, subject to the constraint that only birds estimated to be within the stand were recorded. Observers recorded the approximate location of singing birds on maps and excluded those birds that they believed were detected previously. Four experienced observers performed surveys over the 2 years of the study. Observers were tested in the laboratory and field to ensure similar levels of expertise. To reduce any influence of observer bias, each observer sur-

veyed each station once, and the order of visits was chosen randomly.

Vegetation summaries

The location of each station was recorded using a global positioning system. Based on these coordinates, we located each station in a geographic information system provided by Prince Albert National Park and Saskatchewan Environment and Resource Management. From the FRI data, we derived four variables: (1) stand height (m), (2) canopy closure (%), (3) proportion of canopy consisting of coniferous tree species (%), and (4) tree species richness. Four other variables from the visual estimates of vegetation cover taken during bird censuses were combined with FRI data to create our habitat suitability models. These included (1) shrub density rank (1–4), (2) percentage of shrubs that were coniferous (%), (3) shrub height (m), and (4) shrub species richness. The detailed vegetation data were summarized into eight similar variables: (1) shrub density (stems per 25 m²), (2) percentage of shrubs that were coniferous (%), (3) shrub height (m), (4) shrub species richness, (5) density of trees (stems per hectare), (6) percentage of trees that were coniferous (%), (7) average height of trees (m), and (8) tree species richness. All vegetation variables were standardized to zero mean and unit variance prior to analysis.

Statistical analysis

We created models for only those passerine species that we detected at more than 5% of the stations. The maximum number recorded from the two visits was used as the response variable. This resulted in the development of habitat suitability models for 28 species. Prior to model development, histograms of the abundance of each species were generated to determine if the statistical distribution that we predicted would provide the best fit to the data. For most ($n = 17$) species, the data approached a Poisson distribution. For 11 species that rarely had more than one individual per station (less than 5% of stations with more than one individual), we assumed a binomial distribution would best fit the data. Habitat suitability models were then developed using a generalized linear model. Because sampling stations were spatially clustered within stands, we included a spatial autocovariation term in all models. This term was the weighted average of the number of stations where a species occurred among the set of all stations in that particular stand. The weight given to each station depended on the distance between it and the other stations within the stand (see Augustin et al. 1996).

For each species, we generated 50 different models (Table 1). At the ends of the spectrum were the null and full models for both vegetation data sets. Intermediate models were selected a priori to test various combinations of canopy-level and shrub-level attributes for both vegetation data types. This allowed us to compare how the detailed vegetation measurements versus FRI vegetation estimates influenced the fit of our habitat suitability models. For each model, we calculated the Akaike’s information criterion corrected (AIC_c) for small sample size. We then calculated Δ_{AB} for each species, which was the difference in the AIC_c scores for models sharing common parameters but using the different approaches to vegetation assessment. Pairwise

Table 1. Candidate models examined for each species in this study.

Model No.	Variables in model
1	Null
2	Autocovariation only (AC)
3a, 3b	AC + all shrub-level attributes
4a, 4b	AC + all canopy-level attributes
5a, 5b	AC + all vegetation attributes
6a, 6b	AC + % conifer in canopy (TC)
7a, 7b	AC + tree species richness (TR)
8a, 8b	AC + tree height (TH)
9a, 9b	AC + tree density (TD)
10a, 10b	AC + % conifer in shrub layer (SC)
11a, 11b	AC + shrub species richness (SR)
12a, 12b	AC + shrub height (SH)
13a, 13b	AC + shrub density (SD)
14a, 14b	AC + TC + TR
15a, 15b	AC + TC + TH
16a, 16b	AC + TC + TD
17a, 17b	AC + TC + SC
18a, 18b	AC + TC + SR
19a, 19b	AC + TC + SH
20a, 20b	AC + TC + SD
21a, 21b	AC + TC + SD + TR
22a, 22b	AC + TC + SD + TH
23a, 23b	AC + TC + SD + TD
24a, 24b	AC + TC + SD + SC
25a, 25b	AC + TC + SD + SR
26a, 26b	AC + TC + SD + SH

Note: For each species, we created models based on the vegetation data derived from forest inventory plus rapid visual estimates of the shrub layer (a models) and the vegetation data derived from detailed measurements of forest canopy and shrub layer (b models).

model comparisons with a $\Delta_{AB} > 2$ indicated that the model using the detailed vegetation measurements provided a better fit to the data than the forest inventory or visual estimates of shrub cover, whereas a $\Delta_{AB} < -2$ indicated the reverse. When Δ_{AB} was between 2 and -2 , we concluded that the model fit was similar between methods of collecting vegetation data (Burnham and Anderson 2002).

For each bird species, we also calculated the percent deviance explained by each model. This measure is analogous to a multiple coefficient of determination and measures the proportion of deviance in the independent variables associated with the deviance in the dependent variable (Kleinbaum et al. 1988). We then used the percent deviance from the models that contained common vegetation attributes but that were measured using the detailed vegetation measurement versus FRI data plus shrub estimates as the dependent variable in paired t tests. The proportion of deviance explained by each vegetation sampling approach for each bird species was the dependent variable in this analysis. Our objective was to determine if the explanatory power of the models using detailed vegetation measurements was similar to those using FRI data plus shrub estimates.

To assess whether the model(s) that were selected as having the best fit were similar using the two approaches to measuring vegetation, we generated a series of plausible candidate models and tested how well the resulting model

sets fit the data. Models were ranked based on their explanatory power, with the best-fitting model having the lowest AIC_c score. For the candidate models using a particular vegetation data set, we estimated the Akaike weights (Burnham and Anderson 2002). From these weights, we estimated a 95% confidence set of models (i.e., plausible explanations for the data) from each approach to vegetation measurement for each bird species. By definition, Akaike weights total 1, so derivation of the 95% confidence set of models was calculated by summing the weights from the most parsimonious models until the sum was approximately 0.95. From the 95% confidence set of models, we determined the proportion of models that were common to both confidence sets (i.e., models based on the different vegetation measurement approaches). Since the number of models in each confidence set was not always equal, these proportions were calculated as the proportion of models from the smaller confidence set that was also in the larger confidence set, divided by the number of models in the smaller confidence set. Our objective was to determine whether model selection using the different approaches to vegetation measurement resulted in similar biological explanations to explain the variation in bird abundance. Within each 95% confidence set, we calculated the average percent deviance explained by the models in that set to determine whether the explanatory power of the best-fitting models was similar between the different methods of vegetation measurement.

We also compared the similarity of each station based on the two different approaches to vegetation measurement using a Mantel test with a Euclidean distance similarity matrix. The Mantel test evaluates the null hypothesis of no relationship between two similarity matrices. The probability that the relationships between matrices were significantly correlated was determined by 500 Monte Carlo simulations (McCune and Mefford 1997). These analyses were done for just canopy-level attributes, just shrub-level attributes, and for all vegetation variables combined. In effect, we compared whether detailed vegetation measurements, as a whole, correlated with FRI data plus shrub estimates. These calculations were done in the program PC-Ord. We also calculated individual correlation coefficients between the same vegetation variables measured using the two approaches (detailed vs. FRI).

All data are reported as means \pm standard error unless otherwise reported. A rejection criterion of $P = 0.05$ was used in statistical tests.

Results

Not unexpectedly, the percent deviance explained by the canopy-level attributes derived from just FRI data was less than when all variables collected in the detailed vegetation survey were used to generate bird models ($34\% \pm 2\%$ vs. $40\% \pm 2\%$, respectively; $t = -4.9$, $df = 27$, $P < 0.001$). However, this was not the result of using detailed data on tree density as measured in the field but occurred because shrub layer attributes were incorporated in the detailed vegetation data. When we compared models with vegetation attributes common to both data sets (i.e., all canopy and shrub attributes) we found no difference in the percent deviance explained between FRI and detailed measurements of vege-

tation ($39\% \pm 2\%$ vs. $40\% \pm 2\%$, respectively; $t = -0.6$, $df = 27$, $P = 0.54$; Table 2).

No difference in the percent deviance explained by models created using visual approximations versus absolute measurements of the shrub layer was observed either ($35\% \pm 2\%$ vs. $34\% \pm 2\%$, respectively; $t = -1.3$, $df = 27$, $P = 0.19$). Based on Δ_{AB} , the distribution of 50% of the species modeled was better predicted using detailed shrub measurements, 21% was better predicted using visual estimates of shrub cover, with the remainder showing no difference. Similarly, the way we measured canopy level attributes did not influence the predictive power of our models ($t = -1.4$, $df = 27$, $P = 0.18$). On average, models using only canopy attributes from the detailed vegetation measurements explained $35\% \pm 2\%$ of the deviance in bird abundance while those using FRI explained $34\% \pm 2\%$. Of the 28 bird species modeled, the abundance and (or) occurrence of 39% of the species was better predicted by the detailed canopy measurements taken on the ground, 25% was better predicted by FRI, and 36% showed no difference.

The best-fitting models from the detailed vegetation and FRI data were generally similar. On average, models incorporating variables from the FRI plus shrub data explained $34\% \pm 3\%$ of the deviance in the bird data while the models based on detailed vegetation measurements explained $35\% \pm 2\%$ ($t = -0.5$, $df = 27$, $P = 0.61$). Overall, $82\% \pm 3\%$ of the models selected in a particular confidence set were also selected in the confidence set that used the other approach to measuring vegetation. The model with the lowest AIC_c value based on detailed vegetation data was typically the fifth (mode and median value) best-fitting model in the 95% confidence set from the FRI. This difference indicates that the model selected as being the "best" was influenced by whether detailed vegetation measurements or FRI data were used as the vegetation data (Table 2).

Data from the FRI plus shrub data set were positively correlated with detailed canopy and shrub layer data (Mantel standardized $r = 0.53$, $P < 0.001$). Similarly, our visual estimates of shrub cover were positively correlated with our detailed counts ($r = 0.67$, $P < 0.001$). Canopy-cover attributes, as estimated from the forest inventory maps, were also positively correlated with detailed measures of canopy attributes ($r = 0.42$, $P < 0.001$). Table 3 shows the correlation coefficients between the "same" individual vegetation attribute, as estimated by the FRI plus shrub estimation versus detailed vegetation measurements. There was a positive and significant correlation between all matched variables between the two approaches to vegetation measurement except for tree density and canopy closure. In general, the rapid visual estimates of shrub layer attributes were strongly correlated with the detailed shrub measurements. Canopy-level attributes were less strongly correlated between the two methods. Stand height, as estimated by the FRI, was reasonably correlated with on the ground measurements. The ability of a FRI to capture variation in the percentage of conifers and species richness observed on the ground was not as good, although the correlations were statistically significant at $P < 0.05$.

Discussion

Contrary to our expectations, we found little evidence that

Table 2. The best-fitting models (i.e., lowest AIC_c value) using the detailed vegetation data set and the forest resource inventory plus shrub data, and the percent deviance (r^2) explained by those models.

Species name	Scientific name	Distribution*	Forest inventory model selected†	AIC _c	r^2	Detailed vegetation model selected†	AIC _c	r^2
American Redstart	<i>Setophaga ruticilla</i>	P	5a	127.5	0.70	20b	132.0	0.65
Bay-breasted Warbler	<i>Dendroica castanea</i>	P	4a	114.9	0.50	22b	114.2	0.49
Black-and-white Warbler	<i>Mniotilta varia</i>	B	7a	77.3	0.13	13b	77.3	0.13
Blackburnian Warbler	<i>Dendroica fusca</i>	P	25a	117.8	0.42	22b	123.2	0.39
Black-throated Green Warbler	<i>Dendroica virens</i>	P	14a	149.3	0.31	8b	150.5	0.29
Brown Creeper	<i>Certhia americana</i>	P	4a	147.4	0.33	4b	146.4	0.33
Canada Warbler	<i>Wilsonia canadensis</i>	B	5a	48.5	0.74	13b	62.2	0.44
Cape May Warbler	<i>Dendroica tigrina</i>	P	14a	92.2	0.27	25b	86.9	0.33
Chestnut-sided Warbler	<i>Dendroica pensylvanica</i>	P	3a	94.3	0.63	17b	96.9	0.59
Chipping Sparrow	<i>Spizella passerina</i>	P	14a	149.9	0.39	13b	155.3	0.36
Connecticut Warbler	<i>Oporornis agilis</i>	P	11a	99.1	0.24	2	101.7	0.20
Hermit Thrush	<i>Catharus guttatus</i>	P	12a	168.6	0.32	25b	163.9	0.36
Least Flycatcher	<i>Empidonax minimus</i>	B	6a	70.6	0.41	14b	69.9	0.44
Magnolia Warbler	<i>Dendroica magnolia</i>	P	10a	131.3	0.35	10b	129.2	0.36
Mourning Warbler	<i>Oporornis philadelphia</i>	B	25a	116.1	0.25	15b	113.4	0.26
Ovenbird	<i>Seiurus aurocapillus</i>	P	5a	305.2	0.31	22b	253.4	0.41
Pine Siskin	<i>Carduelis pinus</i>	P	14a	167.1	0.37	20b	164.9	0.38
Red-breasted Nuthatch	<i>Sitta canadensis</i>	P	21a	134.1	0.31	13b	134.3	0.28
Red-eyed Vireo	<i>Vireo olivaceus</i>	P	15a	167.1	0.35	6b	157.1	0.38
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	B	2	124.5	0.33	23b	121.0	0.38
Ruby-crowned Kinglet	<i>Regulus calendula</i>	P	21a	140.6	0.30	20b	127.8	0.36
Solitary Vireo	<i>Vireo solitarius</i>	B	19a	125.4	0.30	14b	121.1	0.31
Swainson's Thrush	<i>Catharus ustulatus</i>	P	10a	162.4	0.37	10b	162.2	0.37
Tennessee Warbler	<i>Vermivora peregrina</i>	P	10a	207.6	0.31	22b	196.1	0.36
White-throated Sparrow	<i>Zonotrichia albicollis</i>	P	21a	167.4	0.37	26b	177.6	0.32
White-winged Crossbill	<i>Loxia leucoptera</i>	B	10a	111.5	0.23	14b	107.2	0.28
Winter Wren	<i>Troglodytes troglodytes</i>	P	17a	68.1	0.33	17b	68.7	0.32
Yellow-rumped Warbler	<i>Dendroica coronata</i>	P	14a	187.3	0.31	24b	182.9	0.38

*The distribution (P, Poisson; B, Binomial) that was used in the generalized linear model procedures for that species.

†See Table 1 for a description of the models.

detailed vegetation measurements generated models that were any more effective at explaining variation in avian abundance than models using FRI plus visual shrub estimates. Prior analyses we have conducted on these data suggest that along this deciduous–coniferous gradient, the two most important variables to measure for predicting bird abundance are percentage of conifers and density of shrubs (Hobson and Bayne 2000a, 2000b). Since the percentage of conifers in the canopy can easily be extracted from forest inventory maps, and shrub density can be effectively estimated at an ordinal level, we feel that detailed vegetation measurements may be unnecessary for deriving effective habitat suitability models in this system. Approximately 400 person-hours went into collecting the detailed vegetation measurements. In contrast, the additional couple of minutes required to estimate vegetation cover after conducting the bird surveys took only 7–10 more person-hours than that allotted to the surveys themselves. Another advantage of measuring vegetation at the ordinal level is that it covers a bigger area and may better represent the area over which birds are surveyed. Detailed vegetation sampling may be less representative of the habitat in which birds are detected if the number of samples taken does not represent the same spatial extent of the point count station.

Part of the difficulty in using FRI data in the development of habitat suitability models is that multiple census locations

are often nested within a single map polygon (i.e., same measure of canopy vegetation used for multiple stations). We found that canopy attributes, as determined by FRI data and detailed measurements of the canopy, were positively correlated, albeit weakly. Even with only a weak correlation between the two vegetation data sets, we found little evidence that the inaccuracy of the canopy-level attributes derived from the FRI influenced the predictive power of our models predicting bird abundance. In contrast, our visual estimates seemed to be quite effective at estimating shrub-level attributes, and the increased accuracy derived by counting shrub stems is likely unnecessary. We believe rapid vegetation assessments that are standardized to identify distinct vegetation assemblages are likely sufficient for the development of effective avian habitat suitability models when bird data are collected by point counts.

Although the explanatory power of the models we created did not differ between the two vegetation data sets, we found that the model with the best fit was not necessarily the same between the two data sets. Instead, we found that many models containing different combinations of variables often had equal predictive power. This occurred because of weak correlations between the dependent variables incorporated into our candidate model sets (Burnham and Anderson 2002). This creates a problem for managers trying to compare habitat suitability models based on statistical equations

Table 3. Correlation coefficient (r) between detailed on-the-ground vegetation attributes and those derived from forest resource inventory (FRI) or rapid visual estimation of shrub layer attributes.

Detailed vegetation measurement	FRI and shrub estimates	Correlation (r)
Tree height	Stand height	0.79
Tree density	Canopy closure	-0.21
% Conifer trees	% Conifer trees	0.56
Tree richness	Tree richness	0.48
Shrub density	Shrub rank	0.72
% Conifer shrubs	% Conifer shrubs	0.91
Shrub height	Shrub height	0.98
Shrub richness	Shrub richness	0.49

from different regions, even when similar descriptions of the vegetation are used in the statistical analyses. This problem can be exacerbated by statistical approaches that use stepwise procedures in model selection. Unlike the approach taken here, stepwise methods generate a single model that is highly dependent on (i) the order in which the dependent variables are entered and (ii) a rejection-inclusion criterion that is based on an arbitrary P value. Although simpler than the a priori model selection approach, models generated by stepwise techniques may not be the most parsimonious explanations of the data and may not reflect the most biologically meaningful explanations of the observed patterns of bird abundance (but see Betts et al. 2006).

Several jurisdictions have developed ecosite classification systems that use site conditions (primarily nutrients and moisture) and both overstory and understory species coverage as the discriminating variables (Jones et al. 1983; Sims et al. 1989; Beckingham and Archibald 1996). Most of these classification systems are based on rapid percentage cover estimates that require considerably less resources to gather than do detailed vegetation measurements (Sims et al. 1995; Bouman et al. 1996; Spence et al. 2008). Ecosite maps that not only classify the structure of the forest canopy but also understory variables would be of great benefit to biologists trying to understand wildlife-habitat relationships. However, techniques for remotely classifying forest stands into ecosite classes may not be accurate enough to be routinely employed (Holopainen and Wang 1998; Nadeau et al. 2004). Employing a standard system of classifying habitats when conducting bird surveys would improve our ability to generalize patterns of avian habitat use across broad regions. Admittedly, the composition of shrub, tree, and bird communities change geographically. However, we suggest that shrub-associated bird species with similar niches and functional roles are present across the boreal forest so that the utility of including the concept of "shrubiness" within bird-habitat models should work in other regions.

The variety of techniques used to estimate vegetation cover, the diverse statistical methods employed, and the fact that few studies examine the same gradients of forest cover are limiting our ability to generalize habitat suitability models among regions for boreal birds. However, given that forest planning should occur at a regional level, it is important that wildlife managers attempt to create habitat suitability models that can be used at broad spatial scales. Few re-

searchers have the resources to comprehensively survey all available forest habitats in a region. Therefore, we suggest pooling of data from different habitat selection studies into a standardized database similar to that of the Breeding Bird Survey (i.e., www.borealbirds.ca). The creation of regional databases would be particularly useful in model validation, which is critical for strong inference yet is rarely done (Hansen et al. 1999). Regardless, our results suggest that vegetation measures based on FRI data with visual estimates of below canopy attributes can be as effective at predicting forest songbird abundance as models based on detailed, time-consuming, and expensive vegetation surveys.

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