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P. Vernier and S.G. Cumming

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Sustainable Forest Management Network
G208 Biological Sciences Building
University of Alberta
Edmonton, Alberta, T6G 2E9
Ph: (780) 492 6659
Fax: (780) 492 8160
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Predicting Landscape Patterns from Stand Attribute Data in the Alberta Boreal Mixedwood

by

P. Vernier[1]

and

S. G. Cumming[2]

[1] Centre for Applied Conservation Biology, University of British Columbia, Vancouver BC, V6T 1Z4
[2] Department of Renewable Resources, University of Alberta, Edmonton AB, T6G 2H1

INTRODUCTION

In the boreal mixedwood forest of Alberta, forest practices are an important disturbance structuring the forest landscape. The degree to which the landscape pattern of a managed forest can or should resemble that of the natural forest remains unclear. To address this issue, forest managers need the ability to predict the consequences of changing landscape patterns on wildlife distributions over large areas. One approach that our group is taking to help fill this need is to develop large-scale, coarse resolution habitat models based on existing forest inventory data and empirical studies of wildlife habitat associations, especially of forest birds. In Alberta, two sources of forest inventory data are available for this purpose (Gillis and Leckie 1993): the completed Alberta Phase 3 Inventory (1970–1986) and the ongoing digital Alberta Vegetation Inventory (AVI, 1988–). Both inventories are spatially organized at the township scale. Both consist partly of stand attribute tables which may be used to calculate summary landscape statistics at the township level (e.g., measures of patch sizes and proportional amounts of different patch types). AVI data contains, in addition, higher resolution spatial data, in the form of georeferenced digital forest cover maps (scale 1:15000) that can be used to compute more complex measures of landscape structure (e.g., measures of edge, shape, interpatch distance, patch arrangement, and amount of forest interior habitat). For the purpose of this study we refer to measures of landscape structure obtained from stand attribute tables as **tabular** landscape metrics and those computed from digital forest cover maps as **spatial** landscape metrics. We use townships as our sample landscapes.

Both tabular landscape measures (e.g., habitat area and patch size; Rosenberg and Raphael 1986, Lehmkuhl et al. 1991, McGarigal and McComb 1995) and spatial landscape measures (e.g., edge proximity, core area, and interpatch distance; Johns 1993, Vernier 1995, Schmiegelow et al. 1997) have been shown to influence bird community structure in western North American forests. Moreover tabular and spatial factors may jointly determine the suitability of a patch or a landscape. For example, habitat use by the Northern Spotted Owl (*Strix occidentalis*) is correlated with patch vegetation type, patch isolation, and patch size variability (Lehmkuhl and Raphael 1993). Therefore, both kinds of structural data must be available as predictor variables for habitat models. However, there are two problems which limit the direct use of high resolution spatial data: (1) the incomplete coverage of AVI or similar data in the boreal mixedwood forest and (2) the cost, in terms of model development and execution, of incorporating spatially explicit information (*i.e.*, stand topology) into the structure of habitat models. It would be of interest to determine if it is possible to use tabular data to *estimate* quantitative spatial measures of landscape structure which can only be *computed* efficiently from digital forest cover maps.

The goal of the present study was to determine if landscape patterns, as measured by spatial landscape metrics, can be modelled statistically from highly aggregated stand attribute data alone, without an explicit representation of the underlying stand topology. Ultimately, our goal is to use such statistical relationships in subsequent cross-scale habitat modelling. Our specific objectives are:

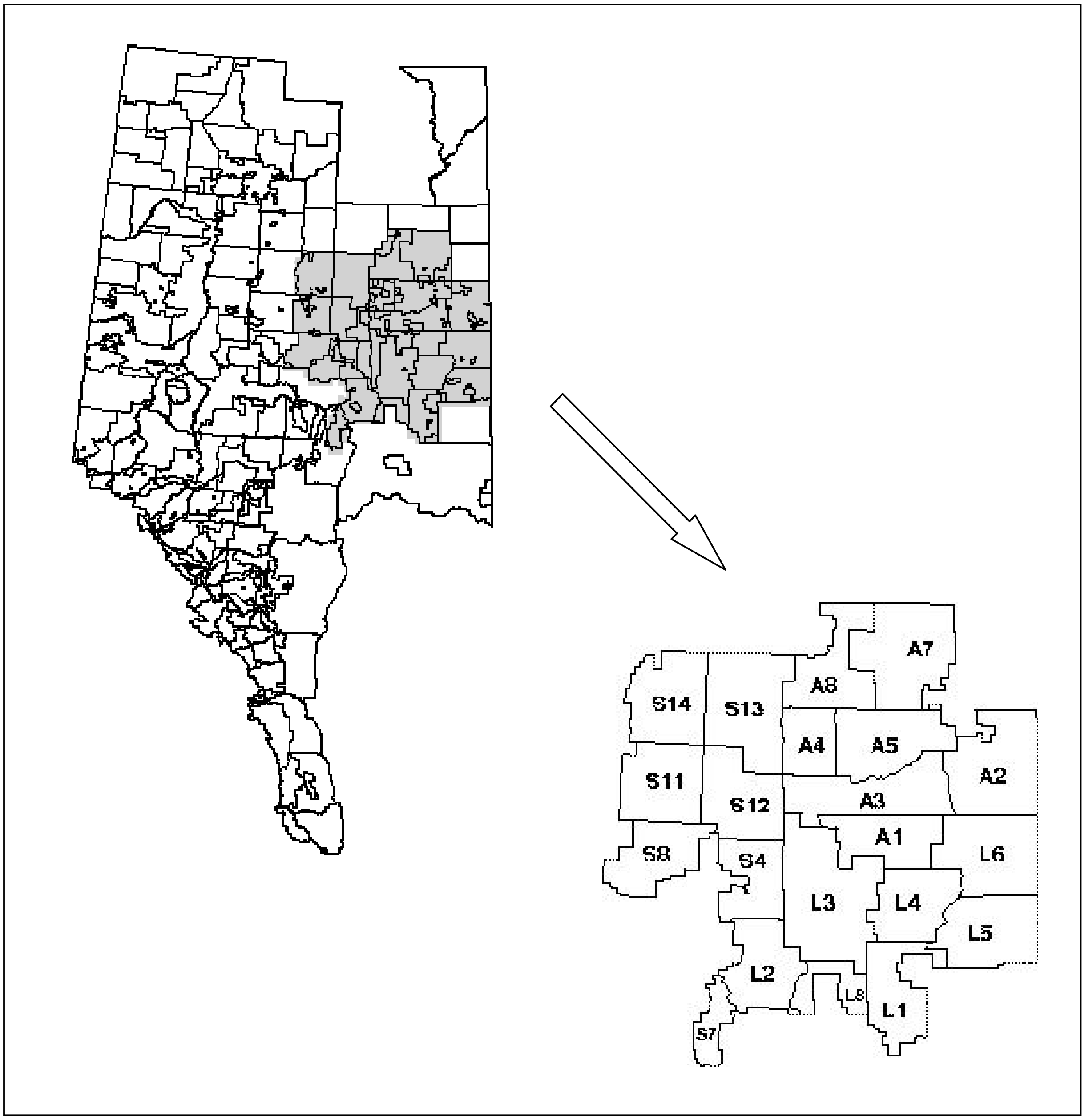
1. To identify representative and interpretable subsets of tabular and spatial metrics from the large set of readily computable candidate landscape metrics (data reduction).
2. To explore the nature and strength of the statistical relationships that exist between these subsets of tabular and spatial landscape metrics (statistical modelling).

METHODS

Study Area

Our study area comprises about 800,000 ha of the boreal mixedwood ecological region of Alberta (Rowe 1972; Figure 1), which is transitional between colder, conifer-dominated forests to the north and warmer, drier aspen parklands to the south (now largely farmland). The regional ecology is described in detail by Moss (1932), Dix and Swan (1971), Kabzems et al. (1986), and Strong (1992). The most abundant tree species are trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), black spruce (*Picea mariana*), jack pine (*Pinus banskiana*), and white spruce (*Picea glauca*). Wetland areas are abundant in the mixedwood, and cover about 50% of the shaded region of the mixedwood in Figure 1, but only 10% of our actual study landscapes. The region has generally low relief, with limited variation in landforms and topography. Historically, stand-replacing fires and insect outbreaks have been the dominant disturbances shaping the forest landscape.

Figure 1. Study area location in northern Alberta (top left) with forest management area (FMA) locations inset (bottom right)



Landscape Data

At the time of the study, digital AVI maps (GIS coverages in ARC/INFO format), were available for four forest management units, L1, L2, S4 and S8 (Figure 1). From these, we selected only complete map sheets (i.e., no missing data due to partial inventories) where the landscape matrix was mostly forested. One complete map was rejected, because it consisted of > 93% lake. The final working set was 84 maps, with a mean size of 9497 ha, ranging from 9397 to 9575 ha. Using the AVI stand-attribute data, we developed a habitat classification system based on the dominant canopy tree species (or genus in the case of *Populus*), estimated stand age, non-forest habitat types, and management history (Table 1). The areal extent of each habitat class per map varied greatly between classes, being highest for young deciduous and black spruce forests and lowest for anthropogenic habitat (e.g., clearcuts; Table 1).

Table 1. Descriptions and summary statistics of derived habitat classes, based on AVI stand attributes. “Leading” species refers to the most abundant species identified in a polygon’s forest cover attribute.

Class	Description	N[1]	Mean	Std. Dev.	Min	Max
WATER	Water (lake, ice, river)	83	414	423	2	1758
NONFOR	Non-forest and wetland	84	990	650	206	3379
Y_DECID	> 70% deciduous and <= 90 years	84	1884	1183	67	5566
O_DECID	> 70% deciduous and > 90 years	84	516	584	2	3406
W_SPRUCE	> 70% white spruce	84	476	393	2	1833
B_SPRUCE	Leading black spruce	84	3443	1445	914	7221
PINE	Leading pine	81	661	844	6	3940
MIXED	Mixed deciduous/white spruce	84	876	526	95	2154
ANTHRO	Anthropogenic (e.g., clearcuts)	79	283	460	1	2024

[1]The number of landscape maps in which the habitat type was present.

We used ArcView to grid each map to a resolution of 1 ha using the derived habitat class attribute, and then used FRAGSTATS (McGarigal and Marks 1995) to compute a suite of spatial landscape metrics from these classified raster maps. FRAGSTATS metrics are computed at one of three levels: the patch-level (individual patches), the class-level (the structure of all patches in one class), and the landscape-level (the structure of the habitat mosaic). Our current focus is on class-level metrics, which measure the aggregate or mean properties of all patches of a particular class within a landscape. We further restricted our analysis to 4 of the 9 habitat classes: Y_DECID, O_DECID, W_SPRUCE, and MIXED. These 4 classes comprise most of the commercially valuable portion of the mixedwood forest, and have attracted the most research effort directed at quantifying avian habitat associations. They are thus of particular interest for future cross-scale habitat modelling. For each of the four focal classes in each of the 84 maps, we computed 29 class-level spatial metrics (all the class-level metrics that FRAGSTATS supports), including a variety of edge, patch-shape and core-area metrics, nearest-neighbor metrics, and contagion and interspersion metrics (Table 2). Algorithms for each metric are listed in Appendix C of the FRAGSTATS report (McGarigal and Marks 1995). Several metrics, such as CWED (contrast-weighted edge density), require a given edge contrast matrix — a matrix of user-defined weights, ranging between 0 and 1, measuring the contrast between different habitat types. We chose weights based on an informal assessment of structural and floristic differences between the different habitat types (Table 3). These metrics constituted our initial set of candidate dependent spatial variables. For our candidate independent variables, we computed 8 tabular landscape metrics for each of the habitat classes, directly from AVI stand attribute tables exported from ArcView (Figure 2).

Variable Reduction

Because many of both the tabular and spatial metrics are strongly correlated, we performed a variable reduction procedure before proceeding to the statistical modelling phase (Figure 2). We first examined all pairwise correlations among the two sets of metrics to identify highly correlated pairs ($r > 0.9$). When pairs of metrics were redundant (100% correlated), we subjectively eliminated one of them. Likewise, we arbitrarily retained standard deviations rather than coefficients of variation to characterize the variability of some the metrics. Following Ritters et al. (1995), one metric was generally selected to represent each group of highly correlated metrics. Selection criteria included the degree of normality, our subjective estimate of interpretability, and the need to have the same reduced set of metrics for each of the four habitat classes. The latter criteria explains why, in a few cases, we retained more than one highly correlated metric for a given habitat class. This procedure reduced the number of tabular metrics to 3 and spatial metrics to 12 (Table 2). Table 4 lists summary statistics, by class, for the 15 selected variables, which are defined in Appendix 1. Among the selected metrics, we log transformed MPS, PSSD, MSI, TCA, MCA2, MNN, and MPI prior to subsequent statistical analyses, to reduce the positive skew in their distributions.

Table 2. Initial set of tabular and spatial metrics computed[1].

Metric group & acronym	Metrics selected (units)
<u>**Tabular Metrics**</u>	
Area metrics	
Not selected: CA, %LAND, LPI	
Patch density, size and variability metrics	
NP	Number of patches (#)
MPS	Mean patch size (ha)
PSSD	Patch size standard deviation (ha)
Not selected: PD, PSCV	
<u>**Spatial Metrics**</u>	
Edge metrics	
CWED	Contrast-weighted edge density (m/ha)
AWMECI	Area-weighted mean edge contrast index (%)
Not selected: TE, ED, TECI, MECI	
Shape metrics	
MSI	Mean shape index
DLFD	Double log fractal dimension
AWMPFD	Area-weighted mean patch fractal dimension
Not selected: LSI, AWMSI, MPFD	
Core area metrics	
TCA	Total core area (ha)
MCA2	Mean area per disjunct core (ha)
CASD2	Disjunct core area standard deviation (ha)
Not selected: C%LAND, NCA, CAD, MCA1 CASD1, CACV1, CACV2, TCAI, MCAI	
Nearest-neighbor metrics	
MNN	Mean nearest-neighbor distance (m)
NNSD	Nearest-neighbor standard deviation (m)
MPI	Mean proximity index
Not selected: NNCV	
Contagion and interspersion metrics	
IJI	Interspersion and juxtaposition index (%)

[1]Those which were eliminated from the first phase of variable reduction are indicated as "*Not selected*". For fuller definitions of the selected spatial metrics, see Appendix 1. The unselected tabular metrics were CA (class area), %LAND (percentage of landscape), LPI (largest patch index), PD (patch density), PSCV (patch size coefficient of variation), TE (total edge), ED (edge density), TECI (total edge contrast index), MECI (mean edge contrast index), LSI (landscape shape index), AWMSI (area-weighted mean shape index), MPFD (mean patch fractal dimension), C%LAND (core area percentage of landscape), NCA (number of core areas), CAD (core area density), MCA1 (mean core area per patch), CASD1 (patch core area standard deviation), CACV1 (patch core area coefficient of variation), CACV2 (disjunct core area coefficient of variation), TCAI (total core area index), MCAI (mean core area index), and NNCV (nearest neighbor coefficient of variation). See McGarigal and Marks (1995) for fuller descriptions of unselected metrics.

Table 3. Edge contrast matrix, used in the computation of several edge contrast metrics (e.g., CWED).

	WATER	NONFOR	Y_DECID	O_DECID	W_SPRUCE	B_SPRUCE	PINE	MIXED	ANTHRO
WATER	0.00								
NONFOR	0.75	0.00							
Y_DECID	1.00	0.75	0.00						
O_DECID	1.00	0.75	0.50	0.00					
W_SPRUCE	1.00	0.75	0.75	0.50	0.00				
B_SPRUCE	1.00	0.25	0.25	0.75	0.50	0.00			
PINE	1.00	0.75	0.50	0.50	0.50	0.25	0.00		
MIXED	1.00	0.75	0.75	0.25	0.25	0.75	0.50	0.00	
ANTHRO	0.75	0.50	0.50	0.75	0.75	0.50	0.50	0.75	0.00

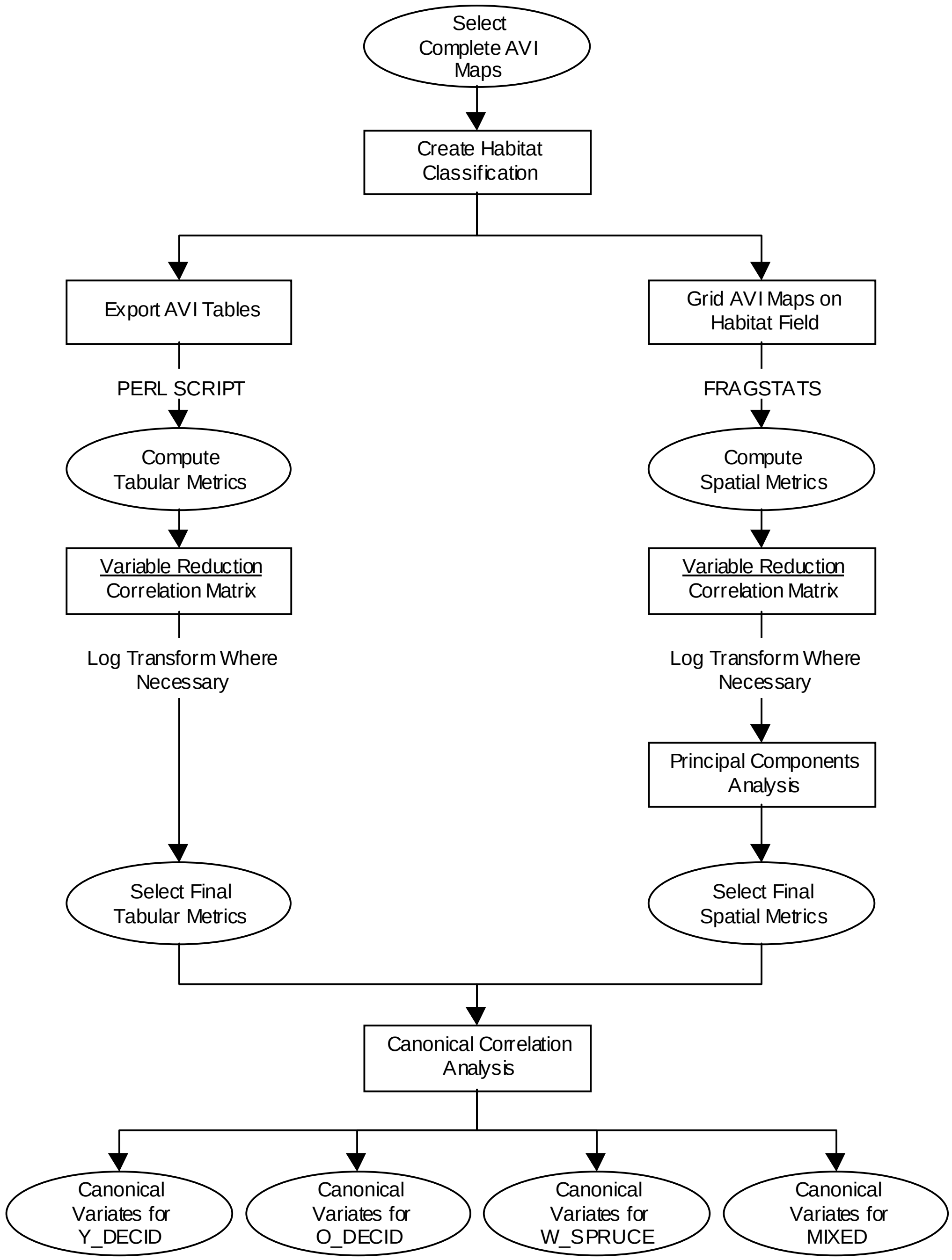


Figure 2. Flowchart of the sequence of procedures used to develop statistical relationships between tabular and spatial landscape metrics. See text for details of procedures.

Table 4. Summary statistics for initial set of selected metrics.

	Variable	Obs	Mean	Std. Dev.	Min	Max
Y_DECID	CA	84	1882.53	1184.14	72.20	5537.76
	MPS	84	7.82	3.52	2.67	19.69
	PSSD	84	16.04	10.18	4.00	57.78
	CWED	84	13.73	6.46	1	27.03
	AWMECI	84	53.02	5.36	42.31	66.86
	MSI	84	1.48	0.12	1.17	1.82
	DLFD	84	1.53	0.05	1.41	1.7
	AWMPFD	84	1.17	0.04	1.07	1.26
	TCA	84	599.54	628.83	2	2956
	MCA2	84	11.52	10.19	1	59.12
	CASD2	84	54.29	63.13	0.47	306.28
	MNN	84	189.16	79.08	113.43	579.41
	NNSD	84	190.72	137.43	40.71	694.77
	MPI	84	218.78	428.51	3.56	2470.17
	IJI	84	77.9	8.43	51.65	93.35
O_DECID	CA	84	515.86	584.26	1.76	3401.53
	MPS	84	7.74	3.93	0.98	20.35
	PSSD	84	11.32	9.92	0.00	58.66
	CWED	84	4.05	3.91	0.05	24.44
	AWMECI	84	51.78	6.19	40.52	69.76
	MSI	84	1.44	0.15	1.03	1.93
	DLFD	83	1.49	0.12	1.17	2.17
	AWMPFD	84	1.11	0.04	1.01	1.22
	TCA	84	129.07	212.3	0	1253
	MCA2	84	5.71	5.53	0	25.7
	CASD2	84	13.66	20.07	0	85.32
	MNN	83	479.21	508.51	117.36	3764.31
	NNSD	83	524.62	460.03	0	3085.63
	MPI	84	30.3	57.19	0	452.33
	IJI	84	73.74	11.36	27.04	90.03
W_SPRUCE	CA	84	473.71	389.44	6.09	1815.32
	MPS	84	4.38	2.06	1.21	12.23
	PSSD	84	5.74	4.58	0.00	23.44
	CWED	84	5.54	3.76	0.04	16.11
	AWMECI	84	54.76	5.82	41.52	69.17
	MSI	84	1.32	0.11	1.1	1.76
	DLFD	83	1.52	0.09	0.96	1.77
	AWMPFD	84	1.09	0.03	1.04	1.17
	TCA	84	50.73	73.48	0	339
	MCA2	84	2.91	2.46	0	11.5
	CASD2	84	5.12	7.06	0	37.49
	MNN	83	333.24	298.08	151.6	2624.88
	NNSD	83	345.27	242.95	0	1363.79
	MPI	84	12.91	18.14	0	108.04
	IJI	84	75.24	8.14	43.29	93.76

Table 4. continued

	Variable	Obs	Mean	Std. Dev.	Min	Max
MIXED	CA	84	876.39	528.14	92.27	2182.98
	MPS	84	5.62	2.86	1.85	17.81
	PSSD	84	7.74	5.34	1.68	33.16
	CWED	84	9.74	4.21	1.63	20.26
	AWMECI	84	59.86	6.77	42.97	72.94
	MSI	84	1.37	0.11	1.14	1.62
	DLFD	84	1.5	0.04	1.37	1.59
	AWMPFD	84	1.11	0.03	1.05	1.2
	TCA	84	148.25	163.83	1	719
	MCA2	84	4.94	3.7	1	25.31
	CASD2	84	11.34	14.71	0	105.43
	MNN	84	226.52	65.59	134.32	443.58
	NNSD	84	216.23	96.94	73.7	454.19
	MPI	84	23.18	27.73	1.1	161.08
	IJI	84	75.85	7.89	49.44	89.38

To further reduce the number of spatial metrics, we performed a principal components analysis (PCA) on each of the four focal habitat classes using the statistical software STATA (StataCorp 1997). PCA produces a linearly independent set of derived variables (*components*) which are linear combinations of the initial (in this case 12) variables. Often, a small number of components will capture most of the variance in the original sample. We used the varimax rotation criteria to aid the interpretation of component loadings (the individual coefficients). From each class, we retained all principal components with an eigenvalue greater than 1 — such components may be interpreted as explaining more variance than any single original variable. From each of these, we selected variables with high loadings (approx. > 0.80) for further analysis.

Statistical Modelling

We performed a Canonical Correlation Analysis (CCA; Johnson and Wichern, 1992) using STATA (StataCorp 1997) to model the relationship between the tabular and spatial landscape metrics. CCA is a generalization of multiple regression in which multiple dependent variables are simultaneously related to multiple independent variables. A canonical correlation is a pair of linear combinations of the dependent and independent variables (initial variables, or *terms*), referred to as *canonical variables*. CCA proceeds iteratively, choosing the first pair of canonical variables by maximizing their correlation: this value is the *canonical correlation*. Subsequent pairs of canonical variables are then chosen subject to the additional condition that they are independent of all previously selected canonical variables. The number of canonical correlations is thus the minimum of the number of dependent and the number of independent initial variables, assuming that these are all linearly independent. The previous dimension reduction methods helps to ensure this independence.

For each habitat class, we performed the following steps. The three tabular metrics surviving the variable reduction step were selected as the set of independent variables. From each principal component retained during the PCA step, we chose the component variables with high loadings as the set of dependent variables for the class. We then performed a CCA on these sets of variables, unless only one spatial metric loaded highly on a given principal component, in which case we performed a multiple regression analysis. The overall modelling strategy, from data assembly to statistical modelling is illustrated in Figure 2.

To assess the resultant multivariate models, we considered the magnitude of the canonical correlation coefficients (*i.e.*, the strength of the overall relationship between the dependent and independent canonical variables), its significance level, and the redundancy indices for each variate. The redundancy index measures the amount of variance in the dependent canonical variate that is explained by the independent canonical variate for each canonical correlation. It is the average of each dependent variables' squared correlation with its corresponding independent canonical variate. It is related to the coefficient of determination (R^2) in a multiple regression analysis and thus provides an index of the predictive ability of the model. The relative importance of each term in each set is indicated by its canonical weight (its coefficients in the canonical variable), its canonical loading (the correlation between the term and its canonical variate), and its canonical cross-loading (its correlation with the opposite canonical variate). When multiple regression was performed, we used the multiple R^2 to measure the strength of the relationship and the standardized regression coefficients to assess the relative importance of each variable.

RESULTS

Principal Components Analysis

For each of the four focal habitat classes, principal components analysis identified 3 uncorrelated linear combinations of the 12 dependent spatial metrics, which accounted for 73.5 to 81.1% of the total sample variation (Table 5). In each case, the first principal component, accounting for 50.0 to 66.8% of the variation, was positively related to measures of patch shape, core area, and patch isolation (AWMPFD, logTCA, logMCA2, CASD2, and logMPI). For the white spruce habitat class, the first principal component was also strongly associated with patch edge (CWED) and patch shape (logMSI). The second principal component, accounting for 12.0–15.5% of the variation, did not consistently measure the same dimensions of landscape structure across habitat classes. For young deciduous and mixedwood habitat, this component was positively related to interpatch distance (logMNN and NNSD), while for old deciduous and white spruce habitat, this component was positively related to patch shape (DLFD). The third principal component, accounting for 8.3–11.6% of the variation, also had inconsistent component loadings across habitat classes. This component had strong positive associations with interspersion and juxtaposition (IJI) for class Y_DECID, with interpatch distance (logMNN and NNSD) for class O_DECID , and with patch shape (DLFD) for class MIXED. It had a strong negative association with patch edge (AWMECI), for class W_SPRUCE. Generally, the second and third principal components describe additional aspects of patch shape, and mean distances between similar patches.

The variables selected for CCA or multiple regression from the principal components are indicated in bold type in Table 5. All variables except for AWMPFD for class Y_DECID had component loadings > 0.79. AWMPFD was retained to allow us to compare results for each habitat class using the same set of metrics. For the same reason CWED was excluded from the W_SPRUCE CCAs.

Table 5. Results of principal components analyses with varimax rotation for 4 habitat classes. Only components whose eigenvalue > 1 are shown. Component loadings in bold typeface were retained for canonical correlation and multiple regression analyses.

Patch type	PC1	PC2	PC3	Commun.[1]	Patch type	PC1	PC2	PC3	Commun.[1]
Y_DECID					**W_SPRUCE**				
Eigenvalue	6.80	1.86	1.08		*Eigenvalue*	6.19	1.83	1.22	
Cum. variance	56.70%	72.18%	81.17%		*Cum. variance*	51.55%	66.83%	76.96%	
Comp. Loadings					*Comp. Loadings*				
logMCA2	**0.955**	–0.035	0.144	0.934	logMCA2	**0.955**	0.014	0.091	0.921
CASD2	**0.893**	–0.154	0.012	0.821	CASD2	**0.915**	0.100	0.177	0.879
logTCA	**0.837**	–0.364	0.300	0.923	logTCA	**0.886**	0.334	0.123	0.912
logMPI	**0.795**	–0.517	0.208	0.942	logMPI	**0.844**	–0.276	0.038	0.791
AWMPFD	**0.684**	–0.615	0.146	0.868	AWMPFD	0.824	0.387	–0.125	0.845
logMSI	0.614	–0.244	0.408	0.603	logMSI	**0.795**	0.021	0.000	0.632
CWED	0.487	–0.740	0.327	0.892	CWED	0.788	–0.277	0.265	0.768
DLFD	–0.387	–0.692	–0.366	0.762	DLFD	–0.644	–0.198	0.205	0.496
logMNN	–0.320	**0.850**	–0.169	0.854	logMNN	–0.591	–0.733	0.102	0.897
NNSD	–0.313	**0.808**	–0.141	0.771	NNSD	–0.245	0.049	**–0.830**	0.751
AWMECI	0.298	0.014	0.738	0.634	AWMECI	–0.106	**0.856**	0.111	0.757
IJI	0.083	–0.299	**0.801**	0.737	IJI	–0.068	0.457	0.611	0.587
O_DECID					**MIXED**				
Eigenvalue	6.00	1.43	1.39		*Eigenvalue*	6.85	1.59	1.00	
Cum. variance	49.97%	61.92%	73.53%		*Cum. variance*	57.11%	70.39%	78.69%	
Comp. Loadings					*Comp. Loadings*				
logMCA2	**0.927**	–0.157	–0.060	0.887	logMCA2	**0.882**	–0.355	0.162	0.931
CASD2	**0.917**	–0.055	–0.282	0.924	CASD2	**0.877**	–0.166	–0.261	0.865
logTCA	**0.872**	0.143	–0.331	0.890	logTCA	**0.875**	–0.028	–0.028	0.767
logMPI	**0.866**	0.358	–0.138	0.897	logMPI	**0.846**	–0.463	–0.037	0.932
AWMPFD	**0.831**	–0.045	–0.139	0.712	AWMPFD	**0.796**	–0.504	–0.223	0.938
logMSI	0.682	0.521	–0.013	0.736	logMSI	0.748	–0.355	0.083	0.692
CWED	0.637	0.174	–0.542	0.730	CWED	0.442	–0.751	0.206	0.802
DLFD	–0.452	0.407	0.006	0.370	DLFD	–0.352	0.508	0.272	0.455
logMNN	–0.342	–0.139	**0.842**	0.846	logMNN	–0.310	**0.900**	–0.038	0.908
NNSD	0.341	0.159	–0.198	0.181	NNSD	–0.221	**0.885**	–0.073	0.838
AWMECI	–0.074	0.105	**0.907**	0.838	AWMECI	0.217	–0.587	–0.045	0.394
IJI	0.030	**0.901**	–0.019	0.813	IJI	–0.071	–0.105	**0.951**	0.920

[1]Communality refers to the amount of variance an original variable shares with all other variables included in the analysis.

Canonical Correlation Analysis

Table 6 shows the results of the CCA on the selected spatial and tabular landscape variables, for each of the four habitat classes. The first canonical correlations were very high in all cases, ranging from 0.934 for old deciduous forest to 0.967 for mixedwood forest. In each case, the canonical correlations were statistically significant at the .01 level. Redundancy analysis shows that tabular landscape variables explained between 73.6% (young deciduous forest) and 77.0% (mixedwood forest) of the variation in the spatial landscape variables. Based on canonical weights and loadings, CA was the most important tabular variable for each habitat class. Among the spatial variables, canonical loadings were high (> 0.76) for all dependent variables. No variable was consistently more important than the other variables. The high loadings for the dependent variables are a consequence of the principal components analysis. Table 6 also includes the cross-loadings for the canonical functions. For the four habitat types, all dependent variables had high correlations with their corresponding dependent canonical variate, ranging from 0.786 to 0.939. By squaring these terms, the results show that 62% to 88% of the variance in the independent variables was explained by the dependent variates. These values are similar to multiple R^2 values that would be obtained by performing a multiple regression analysis on individual dependent metrics.

In the set of second principal components, only classes Y_DECID and MIXED had more than one highly loaded component (logMNN and NNSD in both cases). These variables were also selected from the third principal component for class O_DECID. CCA showed that tabular landscape variables explained < 32% of the variation in these two spatial metrics (results not shown). This is not surprising considering the relatively small amount of sample variation accounted for by the second and third principal components, as measured by eigenvalues and cumulative variance explained (Table 5). Multiple regression analysis was performed on the single highly-loaded variables selected from the remaining principal components. Again, relationships were not nearly as strong as for the first set of canonical functions; tabular landscape metrics explained between 5–24% of the variation in these spatial landscape metrics (results not shown). Only spatial factors with high loadings in the first principal components are good candidates for statistical modelling using the given tabular data.

Table 6. Results of canonical correlation analysis, for the first principal component of each habitat class (see Table 5), showing the relationship between dependent (spatial) and independent (tabular) landscape metrics.

		Canonical Weights	Canonical Loadings	Canonical Cross-Loadings
Y_DECID	Dependent (spatial) variables			
	AWMPFD	–0.262	0.877	0.883
	logTCA	0.951	0.928	0.858
	logMCA2	–0.561	0.793	0.786
	CASD2	0.365	0.764	0.829
	logMPI	0.527	0.960	0.927
	Independent (tabular) variables			
	CA	0.737	0.986	0.925
	logMPS	0.165	0.624	0.611
	logPSSD	–0.011	0.720	0.713
	Redundancy index	**0.736**		
	Canonical correlation coefficient	0.966		
O_DECID	Dependent (spatial) variables			
	AWMPFD	0.121	0.906	0.896
	logTCA	0.588	0.877	0.879
	logMCA2	–0.202	0.856	0.817
	CASD2	0.744	0.908	0.822
	logMPI	0.250	0.944	0.936
	Independent (tabular) variables			
	CA	1.118	0.972	0.937
	logMPS	0.220	0.671	0.616
	logPSSD	0.189	0.780	0.737
	Redundancy index	**0.759**		
	Canonical correlation coefficient	0.934		
W_SPRUCE	Dependent (spatial) variables			
	AWMPFD	0.157	0.880	0.894
	logTCA	1.058	0.844	0.872
	logMCA2	–0.487	0.834	0.809
	CASD2	1.471	0.935	0.827
	logMPI	0.171	0.917	0.934
	Independent (tabular) variables			
	CA	1.663	0.981	0.934
	logMPS	0.163	0.635	0.587
	logPSSD	0.339	0.761	0.706
	Redundancy index	**0.754**		
	Canonical correlation coefficient	0.957		

Table 6. Continued

		Canonical Weights	Canonical Loadings	Canonical Cross-Loadings
MIXED	Dependent (spatial) variables			
	AWMPFD	0.144	0.937	0.902
	logTCA	0.628	0.932	0.892
	logMCA2	–0.075	0.879	0.845
	CASD2	0.438	0.829	0.807
	logMPI	0.614	0.978	0.939
	Independent (tabular) variables			
	CA	1.097	0.948	0.925
	logMPS	0.022	0.694	0.661
	logPSSD	0.616	0.838	0.783
	Redundancy index	**0.770**		
	Canonical correlation coefficient	0.967		

DISCUSSION

Canonical correlation analyses identified strong relationships between landscape metrics measured from stand attribute tables (tabular metrics) and those measured from mapped forest cover polygons (spatial metrics) for four habitat types commonly found in boreal mixedwood forests: young deciduous, old deciduous, white spruce, and mixedwood types. Using the three tabular metrics of total habitat area, and the mean and standard deviation of habitat patch size, we were able to explain more than 73% of the joint variation in spatial metrics of patch shape (AWMPFD), forest interior habitat (logTCA, logMCA2, and CASD2), and patch isolation (logMPI) for each of the four patch types, at a spatial scale of 100 km^2 and a resolution 1 ha. The tabular metrics also explained between 61.8% and 88.2% of the variation in the individual spatial metrics as measured by the canonical cross-loadings. The results were highly consistent across habitat classes, in terms of predictor variables and strengths of association.

Our choices of tabular landscape metrics and spatial scale were based on those that could be calculated from stand attribute tables that are widely available throughout the boreal mixedwood. In fact, similar data are available throughout the boreal forest of Canada at scales ranging from 1:10,000 to 1:20,000 (Gillis and Leckie 1993). Only the habitat classification system would need to be modified to repeat our analyses in different regions. Our selection of spatial landscape metrics followed a procedure similar to that of Riitters et al. (1995), in that we generally selected only a single representative metric from each highly correlated group and then performed a principal components analysis on the selected metrics. Our final set of metrics differed from that obtained by Riitters et al. (1995), in part because our candidate set was quite different; we used FRAGSTATS to calculate all of our spatial metrics whereas Riitters et al. (1995) wrote custom software to calculate their landscape metrics. This underscores the need for a comprehensive evaluation of the many landscape metrics used in ecological studies (Rogers 1995). The current profusion makes it difficult to compare landscape patterns between geographic areas and to generalize from reported relationships between landscape structure and wildlife distributions.

The strong canonical correlations obtained in this analysis have important implications for future habitat modelling in the boreal mixedwood forest. We have demonstrated that stand attribute tables may be used to characterize not only patch sizes and proportional amounts of habitat types, but also several aspects of their spatial structure and distribution within the landscape (*i.e.*, patch shape, core area, and patch isolation). Thus, it is possible to incorporate both tabular and spatial aspects of forested landscapes within large-scale simulation models, without explicit high-resolution representations of the underlying landscape. This will greatly simplify some of the technical aspects of model development and data acquisition, and greatly speed model execution time. Our results also show that spatial factors can be incorporated into models developed for areas where digital maps are unavailable. Linking such landscape-level pattern models to empirically derived patch-level habitat models would then allow us to evaluate the consequences of dynamic landscape processes and management actions over large areas and long time horizons.

Whether such an approach proves fruitful will depend partly on the degree to which landscape structure measured at these coarse scales actually affects forest wildlife (the effective resolution of digital forest inventories is 1–2 ha) and on whether the structural features measured by our present choice of metrics are the important ones. Evidence that landscape structure affects avian populations comes primarily from research conducted in eastern agricultural regions, where landscape changes have been driven by urbanization and agricultural expansion (Freemark and Merriam 1986, Hunter 1990). The applicability of these findings to fire-dominated western boreal forests is uncertain, given that young forest patches created by wildfires and harvesting may not be the impermeable barriers that agricultural or urban areas represent. The strongest available evidence for landscape level effects on western forest birds is provided by McGarigal and McComb (1995). They found that the abundance of many species were positively correlated with total habitat area and measures of fragmentation in some Oregon forest types. Several other studies in western forests, though not specifically designed at the landscape level, have also found that measures of patch size, core area, and patch isolation have a significant effects (e.g., Rosenberg and Raphael 1986, Vernier 1995, Schmiegelow et al. 1997). Schmiegelow et al. (1997) found a significant correlation between patch isolation and bird community composition in the boreal mixedwood forest. Core area, using a 150 m buffer width, was found to be the most important landscape-level predictor of abundance of three songbird species in the montane forests of British Columbia (Vernier 1995). The influence of patch shape may be less direct and related to its interaction with patch size to determine the amount of core area available to forest interior species. None of these studies had replicated samples at the scale of our township level analysis, however. Clearly, more studies designed at the landscape level will be needed to determine the degree to which landscape structure influences wildlife species distribution and abundance.

Our findings and conclusions should be viewed with caution due to several limitations of this study. Our results apply to landscapes that have not yet been greatly modified by clearcut logging (generally less than 5% of a given township). They will need to be refined as a greater proportion of the boreal mixedwood landscape is modified by forest management activities. This is because systematic logging may change the underlying relationships between the tabular and spatial metrics on which our study implicitly relies. At present, we can suggest nothing about the mechanisms responsible for the relations. The sensitivity of our canonical correlations to differences in grid resolution, habitat classification, and spatial extent of the landscape units should also be explored. Our results will be refined concurrently with the development of cross-scale habitat models, as it becomes more clear which spatial metrics have explanatory power with respect to observed species distributions: the present study is just the first step in an iterative process of model development. However, we are encouraged by our results so far, which show that it is possible to model landscape structure metrics that are at least analogous to those few that have been shown to be important in the literature.

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APPENDIX

Definitions of landscape metrics used in PCA and CCA, after McGarigal and Marks (1995).

Acronym	Metric name (units)	Description
Tabular landscape metrics		
CA	Class area (ha)	Total area of landscape within a corresponding patch class.
MPS	Mean patch size (ha)	Average size of patch.
PPSD	Patch size standard variation (ha)	Absolute measure of patch size variability.
Spatial landscape metrics		
CWED	Contrast-weighted edge density (m/ha)	Density of edge involving the corresponding patch type weighted by the degree of structural and floristic contrast between adjacent patches (see edge contrast matrix; Appendix 2).
AWMECI	Area-weighted mean edge contrast index (%)	Mean patch edge contrast weighted by patch area as a percent of maximum contrast; equals 100% when all edge is maximum contrast and approaches 0 when all edge is minimum contrast.
MSI	Mean shape index	Mean patch shape complexity; equals 1 when all patches are square and increases as patches become more complex in shape.
DLFD	Double log fractal dimension	Measures patch shape complexity by regressing log(perimeter) on log(area); sensitive to small sample sizes (e.g., less than 20 patches).
AWMPFD	Area-weighted mean patch fractal dimension	Mean patch shape complexity weighted by patch area based on the fractal dimension of each patch; not sensitive to sample size.
TCA	Total core area (ha)	Total amount of core area of the corresponding patch type; core areas were defined by eliminating a 100 m wide buffer along the perimeter for each patch.
MCA2	Mean area per disjunct core	Average size of core area per patch containing interior forest habitat.
CASD2	Disjunct core area standard deviation	Absolute measure of core area variability.
MNN	Mean nearest neighbor distance	Average distance between neighboring patches of the same type.
NNSD	Nearest neighbor standard deviation	Absolute measure of nearest-neighbor variability.
MPI	Mean proximity index	The degree of isolation and fragmentation of a patch type; all other things being equal, a patch containing more of the corresponding patch type than another patch will have a larger value; similarly, all other things being equal, a patch located in a neighborhood in which the corresponding patch type is distributed in larger, more contiguous, and/or closer patches than another patch will have larger value.
IJI	Interspersion and juxtaposition	The extent to which patch types are interspersed (not necessarily dispersed); higher values result from landscapes in which the patch types are well interspersed (i.e., equally adjacent to each other), whereas lower values characterize landscapes in which the patch types are poorly interspersed (i.e., disproportional distribution of patch type adjacencies).