A MULTI-SCALE ANALYSIS OF FOREST STRUCTURE AND VERTEBRATE DIVERSITY

by

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Abstract

Predicting the occurrence of species is a central problem in ecology and conservation. The ability to accurately predict species occurrence requires an understanding of the relations among species and the environment defined at appropriate spatial and temporal scales. Through my research, I test the hypothesis that forest structure can reliably predict the occurrence of vertebrate species and vertebrate-species assemblages using logistic regression models and classification and regression tree (CART) analysis. With the results, I assess the potential of using forest structure as a surrogate measure for monitoring species diversity. I also investigate how deriving species presence from different types of detection data (i.e., audio and visual detections versus sign) and using different measures of forest structure affect prediction accuracy and model selection. To assess prediction accuracy, I use the area under the receiver-operating characteristic curve (ROC) for logistic regression models and a classification matrix of predicted and observed group membership for CART analysis. In addition, I use spatially and temporally independent data to validate single-species models. Models constructed using presence derived from detections of sign resulted in higher prediction accuracy, probably due to lower spatial uncertainty. Models for single species (n = 101) had good prediction accuracy (ROC ≥ 0.70) only 56.4% of the time and few models retained good accuracy when validated with spatially and temporally independent data. Only spatial uncertainty appeared to systematically affect ROC values when sources of uncertainty (i.e., identification, spatial, or temporal) were examined with ANOVA. CART analysis successfully predicted 45.8% of group membership of plots. Together these results suggest that spatial uncertainty and measuring structural characteristics of forests at the appropriate spatial scale, for the species being modelled, have the largest effect on model outcome.

Models developed cannot be assumed to be transferable to different areas or applicable in different years. Overall, forest structure did not accurately predict species presence or species groups well and, therefore, is not a suitable surrogate measure for species occurrence or monitoring diversity of vertebrate species.

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Chapter 1. Introduction

Background

Activities driven by anthropogenic values have contributed to habitat loss and fragmentation resulting in a global decline of many species (Hunter, 1990; Harper and Hawksworth, 1995). Protecting biodiversity in reserves will not fully mitigate the effects of anthropogenic activities on biodiversity loss (Lindenmayer and Franklin, 2002; Beazley et al., 2005). In addition, many species are adapted to various levels of disturbance that should allow human use concurrent with conservation objectives. Therefore, biodiversity assessment and monitoring have become an important part of management planning, such as for forest harvesting (Hunter, 1999; Noss, 1999).

Forests provide habitat necessary for approximately 65% of terrestrial taxa (World Commission of Forests and Sustainable Development, 1999), as well as considerable economic and social resources to humans. With estimates of less than 12% of the world's forests remaining intact outside the boreal forests (Bryant et al., 1997), a better understanding of the relations among species distribution and forest structures, both in the short and long term, will provide the knowledge to help mitigate the loss of species from forest environments. This understanding is a relevant and necessary component of efforts that will lead to an improved balance between economic, social, and ecological values, which includes the conservation of biodiversity.

Measuring and monitoring biodiversity

Biodiversity is a relatively new word in the scientific and political arenas and holds several meanings, often dependent on perspective. In the scientific community it is generally considered synonymous with 'biological diversity' defined as encompassing all genetic, species, and ecosystem variability (Norse et al., 1986). Because this definition is so broad, researchers must state explicitly the component(s) of biological diversity of interest, as the focus of research is rarely, nor practically, inclusive of all three levels of biodiversity. Even species diversity is difficult to quantify, as accurately measuring all species in an area is not easily done. Most studies, therefore, focus on a subset of species for estimates of species richness (i.e., the number of species within an area) or other surrogate measures of biodiversity.

Surrogate approaches

A good surrogate measure of biodiversity is sensitive to environmental change, both physical and biological, and data are reasonably easy to sample and analyse. Surrogates may also be selected because of economic importance or because of their usefulness as a planning or management tool (Hannon and McCallum, 2001). Surrogate measures can broadly be categorised into coarse-, medium-, and fine-filter approaches.

Coarse-filter approaches focus at the level of ecosystems, processes, or habitats with the goal of maintaining biodiversity within them across broad areas (Hunter, 1990; Noss and Cooperrider, 1994). The assumption of a coarse-filter approach is that complete representation of environmental variability and the preservation or emulation of processes that contribute to this variability will maintain species diversity. Less emphasis is placed on full knowledge of species biology and species richness and, therefore, this approach recognises that for many species this knowledge is unknown. In forest management, measurements of structural diversity, including stand complexity, composition, connectivity, and heterogeneity, are proposed as suitable surrogate measures of species diversity in a coarse-filter approach (Kimmins, 1997; Önal, 1997; Lindenmayer et al., 2000). Structural diversity increases as variation in tree-species composition and tree size, across both horizontal and vertical spaces, increases (Zenner and Hibbs, 2000; Staudhammer and LeMay, 2001; McElhinny et al., 2005). If a relationship exists between structural diversity and vertebrate-species diversity, measures of structural diversity should be correlated with measures of species richness when the unit of area is the same for both measures (Araújo et al., 2001).

Medium-filter approaches (meso-filter, *sensu* Hunter, 2005) focus at a stand scale and centre on specific elements of habitat (Bunnell et al., 1999). For example, several studies have identified the importance of dead and dying trees, coarse-woody debris, riparian areas, and deciduous species to forest-dwelling species in western forests (e.g., Zabel and Anthony, 2003). The retention and enhancement of these structural elements may contribute to the maintenance of species diversity. Monitoring the distribution and abundance of these habitat elements may thus be a sufficient means to ensure that sensitive species are maintained in an industrial landscape (Bunnell et al., 1999; Lindenmayer et al., 2000).

Fine-filter approaches focus on the population dynamics, presence and absence, or the specific needs of a plant or animal species (Hunter, 1991; Hansen et al., 1999). Changes in the population or distribution of a fine-filter surrogate should indicate changes to medium- or coarse-filter objectives (e.g., loss of a certain ecosystem type or habitat elements) and are, therefore, not exclusive of other approaches. Designation of indicator species, keystone species, umbrella species, and rare or endangered species can all be categorised as fine-filter approaches. The selection of the fine-filter surrogate depends upon the context, goals, and objectives of the study or problem (Caro and O'Doherty, 1999).

The general disagreement of the success of fine-filter approaches (Simberloff, 1998; Caro and O'Doherty, 1999) and a concern that coarse-filter approaches will not be sensitive enough (Reyers et al., 2000) have resulted in the recommendation that a combination of approaches is necessary (Hansen et al., 1999; Sarakinos et al., 2001). Regardless of the approach, or complement of approaches, the task remains to test and validate indicators and surrogates to ensure they are telling us what we think they are (Lindenmayer, 1999; Noss, 1999).

Modelling the occurrence of species

Single species

Niche, island-biogeography, and metapopulation theories have all played important roles in predicting species occurrence at various spatial and organisational scales. Niche theory predicts species occupancy at a site given specific habitat conditions relative to the species' physiology, morphology, behaviour, and ecology (Wiens, 1989). In this context, habitat is defined as the area that provides the resources (e.g., food, water, and cover) and environmental conditions (e.g., temperature and precipitation) that support an individual or population of a given species, its survival, and successful reproduction (Morrison et al., 1998). The set or range of environmental features that allow a species to survive and reproduce is one way to describe a species' niche (Grinnell, 1917). Other definitions of a species' niche include defining the functional role of a species in a community (Elton, 1927) or as a multidimensional hypervolume where numerous axes represent individual resources or other important factors (Hutchinson, 1957). In investigations of the relations among species and physical aspects of habitats, assumptions about the existence of, or role of, a species within a community should be avoided (Morrison, 2001). Therefore, delineating the physical habitat and biological components of a species' niche allows independent focus on the interactions among species and habitat, and species with other species (Leibold, 1995).

Predictions of species occurrence may be based on both the physical and biological components of the species' environment. Predictions relative to the physical components of habitat, described in terms of spatial extent, vegetation structure, and vegetation species composition (Morrison and Hall, 2002), are traditionally approached through a variety of single-species models that build on knowledge of life history, habitat selection, and / or foraging theory (reviewed in Morrison et al., 1998).

Multiple species

Predictions of species occurrence relative to the biological component of a species' niche require an understanding of the presence or absence of prey species, predators, facilitators (i.e., a species dependent on another species for the efficient acquisition of resources), or competitors. To determine the importance of biological contributors to species distributions, a multi-species approach to predictions and analyses is necessary. Multi-species approaches include categorising species into guilds, compiling species-habitat matrices, and community-structure models (reviewed in Morrison et al., 1998, Root et al., 2003).

To avoid assumptions based on species interactions, species groups can also be defined based on their occurrence together in space and in time. These groupings are simply defined as assemblages (Fauth et al., 1996). Assembling species into groups that share similar characteristics is a compromise to deal with the impracticality of considering all species at the same time or all species individually. The general aim of forming species groups, regardless of how the group is defined, is to make predictions that are more general than for individual species, but not so general, or unrealistic, as making predictions for all species combined (Wilson, 1999). Species selected as representatives of the species categorised within groups may then be monitored with fine-filter approaches.

Scale

Measures of species diversity are inherently scale-dependent (Magurran, 2003). For example, species-area curves (i.e., species richness plotted against area; Arrhenius, 1921; Coleman, 1981) repeatedly plotted for data collected at different spatial scales do not produce constant slopes, but rather show systematic variation dependent on spatial scale of measurement (Crawley and Harral, 2001). Thus, for any study examining biological diversity, the specific level of diversity being studied and the scale must be defined. Determining the appropriate spatial and temporal scale of measurement should coincide with the goals and objectives relevant to the study, ecological processes, and the physical and behavioural traits of an organism. How a habitat patch is defined in space (i.e., pattern, area, and isolation) depends on the ecological scale at which the species uses the habitat patch (Vos et al., 2001). For example, an ideal habitat patch situated 500 m from a similar habitat patch is very isolated for a terrestrial mammal with a home range of less than a hectare. For a terrestrial mammal with a home range of several 100 ha, however, this habitat patch is not isolated. The assessment of isolation is further confounded by the structure of the vegetation that surrounds the habitat patch and the flexibility of the organism to tolerate sub-optimal conditions. The probability of a species occurring in a suitable habitat patch will, therefore, relate to the effective isolation distance, juxtaposition of habitat types, the combined area of the suitable habitat in relation to the species' area needs, and the ability of the species to exploit resources in the surrounding habitat matrix. Determining the scale that is ecologically relevant for the species is an important step in the classification of the landscape and subsequent prediction of species occurrence; therefore, forest structure should also be described at multiple scales.

Frequentist versus Bayesian approaches

There are several statistical approaches to modelling the prediction of species' occurrence, many of which have been applied only in recent years. Review articles (e.g., Guisan and Zimmerman, 2000; Rushton et al., 2004) summarize approaches and how advances in new technologies have made ecologists play a "catch-up game" to determine how characteristics of data may affect accuracy and interpretation of model results. Although a review of individual techniques is beyond the scope of this introduction, a brief overview of two paradigms, frequentist and Bayesian, is important.

The debate between frequentist (i.e., classical) and Bayesian statisticians is not new (Clark, 2005). Frequentist statistics are those typically thought of as probabilistic techniques that rely on falsification of hypotheses, whereas Bayesian approaches use prior information to develop the formulation of competing hypotheses. Recently, information-theoretic approaches, a paradigm rooted in Bayesian statistics, have become more prevalent in ecological studies (Rushton et al., 2004). Comparison studies have reported that information-theoretic approaches (Burnham and Anderson, 2002) often had a better ability than a frequentist approach to fit the data and furthered ecologic understanding of the system studied (e.g., Greaves et al., 2006). In instances, however, where the system is not well studied, or the investigator cannot use prior knowledge to formulate competing hypotheses, information-theoretic approaches are undermined. Therefore, there are situations where frequentist or a combination of Bayesian and frequentist approaches are appropriate (e.g., Boone and Krohn, 1999; Rushton et al., 2004).

Summary and outline of chapters

Accurately predicting the occurrence of species is a central problem in ecology. As well, predicting species occurrences based on surrogate measures for biodiversity is an important aspect of sustainable forest management. Overall, our ability to predict species occurrence requires an understanding of the relations among species and the environment defined at appropriate spatial, temporal, and organisational scales relative to the goals and objectives of the study. In forest management, approaches such as ecosystem representation and objectives aimed at mimicking natural-disturbance regimes, contribute to coarse-level biodiversity objectives. This study focuses on determining the relationship between the presence of a species or group of species (fine-filter) and structural elements of the stand (medium-filter). The results of my research are intended to contribute to both ecological and conservation problems.

My dissertation is divided into 3 main chapters. In Chapter 2, I investigate the effect of detection method and different sources of structure data on model selection and validation. Different methodologies can result in different ways of determining species presence. Further, forest managers maintain databases of forest-inventory measures that are commonly derived through photo interpretation, whereas species may be responding to structure at local scales. It is, therefore, important to understand if these differences affect model results and inferences that are drawn. My specific objectives include determining: 1) the effect that detection type (i.e., sign, audio, visual) has on selection of model variables and predictive accuracy; and 2) how data sources (i.e., local or photo interpreted measures) affect prediction accuracy.

In Chapter 3, I examine the role that physical aspects (i.e., forest structure) of a species' environment play in determining the presence or absence of individual vertebrate species. If forest structure predicts species occurrence well, then there is the potential for efficiently incorporating its use as a surrogate measure in species-diversity monitoring programs. Because species use landscapes at different scales (i.e., small or large territories and a range of mobility), this approach may be more appropriate for a subset of species with specific life-history traits. Therefore, my specific objectives include determining: 1) the viability of using attributes of forest structure to predict the occurrence of vertebrate species; 2) the prediction accuracy of models when validated with spatially and temporally independent data; and 3) if statistical artefacts (e.g., prevalence or detection uncertainty) or specific traits of species (e.g., mobility or territory size) systematically affect prediction accuracy.

In Chapter 4, I examine how the physical aspects of the environment explain presence or absence of assemblages of vertebrate species. If biological aspects of species occurrence, which are not accounted for by structural aspects of habitat, can be accounted for by grouping species, forest structure may still be useful as a surrogate measure for monitoring. Specifically, in this chapter my objectives include determining: 1) the reliability of plot groupings based on species co-occurrence and forest structural characteristics of plots; 2) the correlation among species-based and structure-based plot groupings; and 3) whether forest structure can be used to predict group membership.

Examining these objectives in a multi-scale framework will contribute to the fields of community ecology, landscape ecology, and conservation biology as well as the management goal of assessing a potential surrogate approach to monitoring species. By taking a multi-scale approach to predicting the occurrence of species and analysing the relations among species and structural elements of forests, my research will contribute to an improved understanding of the complexity and variation of species responses to the physical and biological environment.

Chapters are presented as individual, stand-alone manuscripts intended for submission for peer-review publication; therefore, there is a certain amount of overlap among chapters, particularly in the methods sections. I conclude with a brief summary (Chapter 5) of the results from the preceding chapters.

Chapter 2. Considerations for the validation of species-habitat models[1]

Abstract

The multitude of approaches to wildlife-habitat modeling reflect the broad objectives and goals of various research, management, and conservation programs. Validating models is an often overlooked component of using models effectively and confidently to achieve the desired objectives. Statistical models that attempt to predict the presence or absence of a species are often developed with logistic regression. In this paper, we review principles of validating logistic regression models, measures of prediction accuracy assessment, and potential sources of prediction errors in a forest-management context. Based on our work in central British Columbia, Canada, we use two species, Red Squirrel (*Tamiasciurus hudsonicus*) and Pileated Woodpecker (*Dryocopus pileatus*), to examine the prediction accuracy of logistic regression models. Because different types of detections may increase spatial or temporal uncertainty in empirical models, we use either audio and visual observations or sign (e.g., forage, nests) as the response variable to compare model results. We also compare models using data from Vegetation Resource Inventory (VRI; the regional inventory used by the Province of British Columbia for timber quality and quantity developed from photo interpretation and ground measurements), local plot measurements collected as part of this study, and a combination of the two as explanatory variables in the statistical models. Using detections of sign as the dependent variable resulted in models with higher predictive accuracy for both species, but the difference was not as great for Red Squirrel, with small home-range sizes, as for Pileated Woodpeckers, that use landscapes at

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[1] This chapter is written in the first person plural to recognize the contribution of others to the work. It has been submitted for publication with the authorship Psyllakis, J.M and M.P Gillingham to the Proceedings for Monitoring the Effectiveness of Biological Conservation, Richmond, BC.

much larger scales. The final models selected, based on low Akaike's Information Criterion (AIC) and predictive accuracy, included a combination of locally measured independent variables and VRI data as explanatory variables. Our results suggest that detection type may affect model outcomes and relatively small investments in data acquisition can improve predictive accuracy. We discuss considerations for the development and validation of statistical models intended for use in biodiversity monitoring.

Introduction

The worldwide rate of species decline has resulted in international agreements (e.g., Convention on Biological Diversity; United Nations Environment Programme, 1992), national strategies (e.g., Canadian Biodiversity Strategy; Minister of Supply and Services Canada, 1995), and provincial guidelines (e.g., Landscape Unit Planning Guide; Province of British Columbia, 1999a) aimed at preserving species diversity in reserves, as well as landscapes managed for industrial purposes. Forests provide habitat necessary for thousands of species, as well as considerable economic and social resources to humans. Activities driven by anthropogenic values have contributed to habitat loss and fragmentation resulting in a global decline of many species from forest environments (Hunter, 1990; Harper and Hawksworth, 1995). A strategy for conserving, or minimizing impacts on, biodiversity is also required as part of most sustainable forest certifications (e.g., Sustainable Forestry Initiative, 2004; Forest Stewardship Council, 2005).

Models that build on the relationships between species and their environments provide an important tool for biodiversity monitoring. To be effective, however, species-habitat models need to be explicitly tested (Guisan and Zimmerman, 2000; Scott et al., 2002) and model validation is a vital component to confidently implement monitoring objectives

(Ottaviani et al., 2004). The process of validation can increase the understanding of species-habitat relationships (Fleishman et al., 2002), the limitations of the statistical model application, and whether or not the model is appropriate for its intended use (Rykiel, 1996).

Statistical approaches to species-habitat modeling vary with modeling objectives and available types of data (Guisan and Zimmermann, 2000). Logistic regression is often the preferred method to model species presence or absence in relation to habitat variables (Manel et al., 1999; Pearce and Ferrier, 2000). The resulting logistic equation predicts the probability of species presence given independent variables and parameters (i.e., the intercept and β coefficients). Validation of logistic regression models usually focuses on the accuracy of predictions (Fielding and Bell, 1997; Johnson, 2001) and is judged on: 1) reliability – the accuracy of the predicted likelihood of occurrence; and 2) discrimination – the ability of the model to accurately distinguish between occupied and unoccupied sites (Pearce and Ferrier, 2000).

Calculating the area under the receiver-operating characteristic curve (ROC) is a favoured measure used to assess the predictive accuracy of logistic models, when presence and true absence data are available (Fielding and Bell, 1997; Pearce and Ferrier, 2000). The ROC value is calculated by plotting the number of sites where presence is correctly predicted divided by the total number of positive sites (sensitivity), against the fraction of incorrect cases where presence is predicted (1-specificity; Table 2.1) across available thresholds. The area under the resulting curve is an estimate of predictive accuracy not biased by threshold probabilities (i.e., $p > 0.5$ designated as presence; Fielding and Bell, 1997) or species prevalence (i.e., one outcome greatly outnumbers the other; Manel et al., 2001). A ROC value is interpreted as the percentage of time that a random selection from the positive class

Table 2.1. Matrix of prediction classifications describing the possible outcomes of presence or absence and the associated indices that can be used to describe predictive performance.

Classification matrix			Definitions of the four indices of performance	
	Recorded Present	Recorded Absent	Sensitivity	= A / (A + C)
Predicted Present	A	B	Specificity	= D / (B + D)
Predicted Absent	C	D	False positive fraction	= B / (B + D)
			False negative fraction	= C / (A + C)

will have a higher predictive score than a randomly drawn case from the negative class (Deleo, 1993). ROC values of 0.5 indicate the explanatory variables do not improve discrimination beyond random assignment and 1.0 indicates perfect discrimination. A value below 0.5 indicates the model performs more poorly with the explanatory variables than without them. Values between 0.5-0.7 are considered to have low discrimination ability, 0.7-0.9 are good, and >0.9 are considered excellent (Manel et al., 2001).

Statistical models developed to monitor biodiversity are often applied to areas beyond the location where data were collected (Mac Nally, 2002). To have the highest confidence in the reliability and discrimination of the model, an external data set (independent from the data used to build the model) should be used in validation (Guisan and Zimmerman, 2000; Fleishman et al., 2002). Obtaining an independent data set, however, is often not feasible. Withholding data to test the model or using a resampling technique are alternatives to using an independent data set (Fielding and Bell, 1997; Boyce et al., 2002), but will still result in optimistic prediction accuracy (Verbyla and Litaitis, 1989; Fielding and Bell, 1997; Pearce and Ferrier, 2000).

Further assessment of the sources of prediction error can lead to improved understanding of the ecological associations between the species and its habitat as well as the utility of the model. Prediction errors can occur because of errors in specifying the model, inappropriate statistical assumptions, measurement errors, and uncertainty related to natural variation (Elith and Burgman, 2002; Fielding, 2002). Two potential sources of error related to specification error come from bias in detection type and misappropriate inclusion or exclusion of explanatory variables.

Species presence can be established from a variety of detection types including visual detections, auditory detections, tracks, scat, and forage sign. Visual detections have little or no spatial or temporal uncertainty associated with them. In contrast, auditory detections are temporally certain, but potentially can have a high degree of spatial uncertainty given that, for some species, calls can travel several hundred meters. Mobile species may call while in flight adding additional uncertainty as they may be in transit between activity areas of their home ranges. Feces, tracks, dens, and nests are all exact in space, but vary in their temporal certainty. Some signs (e.g., cavity nests, dens) are very persistent on the landscape and habitat structure can change significantly around the sign. It may be unclear if the location is still useful to the species it is associated with, because individuals may not be present at the time of detection. Uncertainty in the response data potentially leads to unexplainable variation in the model and reduced reliability and discrimination (Pearce and Ferrier, 2000). Determining species absence is more ambiguous, and may require that an alternative modeling and validation approach is adopted for presence-only data (e.g., ecological niche factor analysis, see Hirzel et al., 2002; MacKenzie et al., 2002; Ottaviani et al., 2004).

Misappropriate inclusion or exclusion of explanatory variables also leads to prediction error of species presence or absence. Factors that influence species distribution often include variables that are not typically measured in association with studies of species-habitat relationships (e.g., intra- and inter-species interactions). In the context of forest management, habitat data for use as predictor variables may be obtained from data that are available for forest-harvest inventories. Vegetation Resource Inventory (VRI) is an inventory methodology adapted by the British Columbia (BC) Provincial government (Province of British Columbia, 2002); the primary objective of the inventory is to assess the quantity and quality of timber. These data are available for much of the forested landbase of BC. The limits associated with the type of environmental data available or acquisition of appropriate data, both for statistical model construction and its use in monitoring activities may, however, influence the effectiveness of achieving the desired model objective(s).

Statistical model assessment also includes an evaluation of the variation explained by the independent variables. In the logistic model, this cannot be calculated in the same way as for other regression models and there are several alternative measures. Pseudo-R^2 is the recommended measure to describe variance explained for logistic regression (Menard, 2002) and is measure of proportional reduction in the absolute value of the log-likelihood when variables are included (Nagelkerke, 1991). What constitutes a “good” pseudo-R^2 value is unclear, but it can be useful when comparing across models that do not have the same response data (e.g., comparing between detection types). A model with a low pseudo-R^2 may still have high predictive accuracy.

In this paper we investigate how two types of potential model error affect the predictive accuracy and evaluation of species-habitat models: 1) the type of detection used to determine species presence and, 2) different sources of data for explanatory variables. We use two species as examples of how differences in the response variable and habitat data source may affect model selection and discrimination, Red Squirrel (*Tamiasciurus hudonicus*) and Pileated Woodpecker (*Dryocopus pileatus*). We selected these species for examples because they are relatively common in our study area, their sign is distinctive (i.e., there is little uncertainty in species identification from sign), and the Red Squirrel uses the landscape at small-spatial scales and is not highly mobile in short-time periods, whereas the Pileated

Woodpecker uses the landscape at relatively large scales and is highly mobile in short-time periods.

Methods

Study area

The data were collected from May 2001 through January 2004 near the northern extent of the Interior Douglas-Fir (IDF) Biogeoclimatic zone (Meidinger and Pojar, 1991). The study area was located approximately 30 km south of Williams Lake, British Columbia, hereafter the Williams Lake Study Area (Figure 2.1). Elevations within the study area ranged from 800-1200 m above sea level and was characterised by stands of closed- and open-canopy Douglas-fir (*Pseudotsuga menziesii*). At high elevations, or where crown fires have occurred in the past, Lodgepole Pine (*Pinus contorta*) was common and at low elevations forest stands were intermixed with non-forested grassland and wetland communities. There were localised stands of hybrid White Spruce (*Picea engelmannii* x *glauca*) and Trembling Aspen (*Populus tremuloides*) throughout the study area. Fire was an important disturbance process in our study area historically, but is now actively suppressed. Insect outbreaks continue to influence stand dynamics. Forest harvesting and cattle grazing are the predominant anthropogenic disturbances.

Habitat data

We established 243 plots to encompass a range of variation in structural characteristics over a breadth of spatial scales (Figure 2.1). Plots were connected by 150-m or 300-m transects for a total of nearly 42 km of transects. Each transect was flagged to ensure that the same route was followed on successive visits. We collected extensive vegetation data

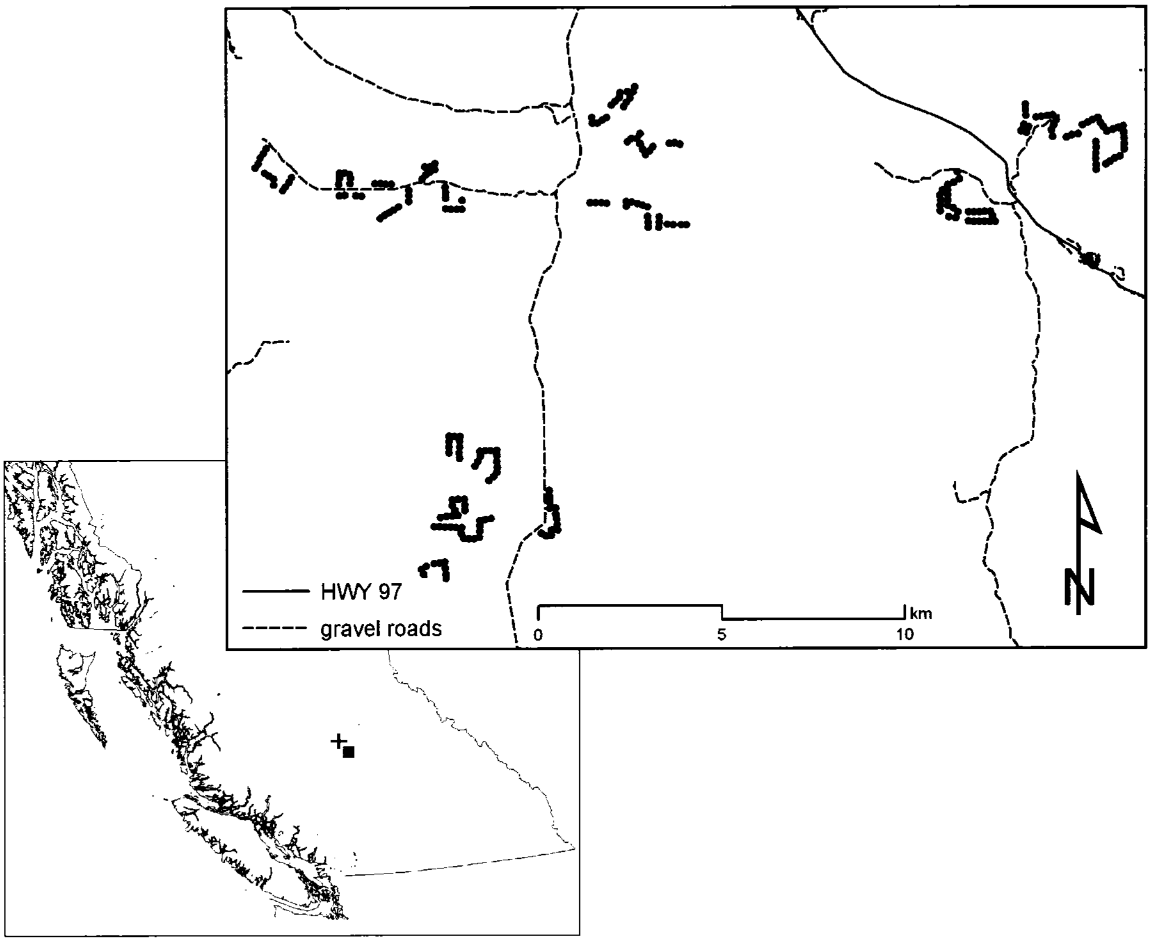

Figure 2.1. The location of the Williams Lake Study Area (▪) in central British Columbia, Canada. Williams Lake is mapped for reference (+). We established 243 plots (•) across a range of variation in structural characteristics and surveyed them for species presence from May 2001-January 2004.

for all plots using standardised methodologies modified from several sources (summarized in Gillingham and Parker, 2001). Modifications to the standard inventory were made so that data were relevant from both the perspectives of wildlife and forest inventory, as well as for the examination of spatial variation.

We used surveyor tapes, laid out on perpendicular axes through plot centre, to measure shrub species and cover, canopy gaps, and coarse-woody debris along the intercept. For coarse-woody debris, we recorded the diameter of the piece perpendicular to where it crossed the axis, the tree species, decay class (Maser et al., 1979), and any sign of use by wildlife. At 5, 2-m radius plots located 11.28 m from plot centre on each axis and at plot centre, we measured coverage for litter, coarse-woody debris, herb species, moss and lichens, shrub species, sapling species, bare ground, and rock. Within a 5.64-m radius plot (0.01 ha) around plot centre, we tallied all trees and stumps. Within an 11.28-m radius (0.04 ha) we tallied all trees >30 cm diameter at breast height (dbh) and snags. For trees, we recorded dbh, height, species, health, evidence of wildlife use, and whether or not the tree was standing or not rooted. We recorded general information for each plot including canopy closure around plot centre (average of 4 measurements taken on each axis; Robert E. Lemman model C densiometer, Bartlesville, Oklahoma), aspect, slope, canopy stratification and complexity, disturbance history (evidence of fire, cattle grazing, logging), any wildlife species detected while taking vegetation measures or their sign, and the elevation above sea level. We were supplied Vegetation Resource Inventory (VRI) data by the forest company that operates in our study area (Tolko Ltd., Vernon, British Columbia).

Species detections

Vocal and visual detections of Red Squirrels were recorded during point-count surveys and encounter-transects surveys. We also recorded foraging sign, middens, and nests during encounter transects and intensive-plot searches. Vocal and visual detections were recorded for Pileated Woodpeckers during playback surveys, point counts, and encounter transects. Foraging sign and nest cavities were recorded during encounter transects and intensive-plot searches.

Red Squirrels frequently vocalise and are often recorded during point-count surveys (Mattson and Reinhart, 1996; Bayne and Hobson; 2000). Therefore, during point-count surveys, which began no earlier than 30 min before sunrise and were ceased no later than 4 h after sunrise (Ralph et al., 1993) from late-May until early-July, we recorded visual and vocal presence of Red Squirrels. Point counts lasted 6 min and began 1 min after arriving at the centre of a plot. Distance and direction to detection from plot centre were estimated and recorded as either <50 m, 50-75 m, or >75 m. One visit per plot was made over a 7- to 10-day period by a different observer. Direction of travel along the transect was changed on successive visits to reduce bias associated time of day.

We conducted playback surveys, broadcasting recordings of calls and drumming, for the 7 species of woodpeckers expected to occur in the study area, including Pileated Woodpecker. The call playback technique attempts to solicit woodpecker responses to broadcasted recordings (Johnson et al., 1981). Woodpecker surveys began no earlier than 30 min before sunrise and ended by 1100 h from mid-May until mid-June at every other plot (minimum distance of 300 m between playback stations). When a woodpecker was detected, distance and direction to bird from plot centre were estimated and recorded as for point counts. When point counts were conducted in conjunction with playbacks, playbacks were always conducted after the passive listening period of the point count. Poor weather, such as high winds, rain, and fog can inhibit both bird behaviour and observer ability; therefore, point-count and playback surveys were only conducted in appropriate weather conditions. Each plot was surveyed by point count and playback 3 times per year for a total of 9 visits.

Along the transects connecting plots, we conducted encounter-transect surveys of unlimited width. If a species was detected along the transect, a Global Positioning System (GPS) waypoint was recorded with species ID, distance and bearing from waypoint, as well as a sign code (singing, call, visual, den/nest, track, remains, browse, or feces). In addition, extensive searches were made around all plots for animal sign. Each plot was searched intensively, to a 50-m radius, for all sign of vertebrates (i.e., visuals, calls/song, nests, dens, feeding, feces, remains). Detections from all methods were entered into a database and georeferenced.

Model construction and predictive evaluation

We used logistic regression (Hosmer and Lemshow, 2000) to examine the relationship of species occurrence to vegetation structure and composition. Candidate variables were selected from potential variables measured and supplied (i.e., VRI data). We considered a variable a candidate if it was, or was related to, an aspect of the species' habitat requirements (Table 2.2). If variables existed that were measures of the same characteristic, but from a different data source (e.g., plot percent gap and VRI sum of crown closure), the variable with the highest correlation coefficient with the species presence was included in a candidate model. Therefore, the final candidate model set included combinations of variables expected to influence the occurrence of Red Squirrel and Pileated Woodpecker. We only

Table 2.2. List of candidate variables used to construct competing models for Red Squirrel (*Tamiasciurus hudonicus*; TAHU) and Pileated Woodpecker (*Dryocopus pileatus*; PIWO). A structural variable was considered a candidate if it related directly to known associations between the species and its habitat.

Data Source	Variable	Species
Plot Measures	Main canopy height	TAHU, PIWO
	Percent gap	TAHU, PIWO
	Percent shrub cover	TAHU
	Percent herb cover	TAHU
	Coarse-woody debris volume (m^3)	TAHU, PIWO
	Percent suspended CWD	TAHU
	Live tree basal area	TAHU, PIWO
	Dead tree basal area	TAHU, PIWO
	Diameter breast height ≥30cm basal area	TAHU, PIWO
	Deciduous stems per ha	TAHU, PIWO
	Frequency Douglas-fir	TAHU, PIWO
	Frequency Spruce	TAHU, PIWO
	Coniferous stems ha^{-1}	TAHU, PIWO
Vegetation Resource Inventory	Shrub crown closure	TAHU
	Adjusted live basal area	TAHU, PIWO
	Herb cover percent	TAHU
	Adjusted canopy closure	TAHU, PIWO
	Douglas-fir cover	TAHU, PIWO
	Aspen cover	TAHU, PIWO
	Spruce cover	TAHU, PIWO
	Adjusted leading species height	TAHU, PIWO
	Structure class (categorical)	TAHU, PIWO

considered plots in which structure was not altered (e.g., harvested) over the duration of the study (*n* = 228).

To test for collinearity among independent variables, we calculated variance inflation factor values for all variables in the model after linear regression (Neter et al., 1985). Variation inflation increases with increasing collinearity among variables and results in overestimates of variance explained. Although there is no set rule for a variance inflation factor indicating a collinearity problem, we adopted a value of 5 or above, which corresponds with a tolerance score of 0.2, a recommended threshold (Menard, 2002). If collinearity was indicated, we reran our model using only one of the indicated problem variables and compared outcomes. We retained the variable that resulted in the highest pseudo-R^2 and predictive accuracy. We calculated the pseudo-R^2 (Nagelkerke, 1991) as our measure of variation explained and ROC values to estimate predictive accuracy. We classified ROC values between 0.5-0.7 as low, 0.7-0.9 as good and >0.9 as high model prediction accuracy (Manel el al., 2001). For comparing models with different response variables (i.e., audio or visual detections versus sign detection), we considered the highest pseudo-R^2 and highest ROC value as the best model.

Once we determined which detection type resulted in the best model (i.e., highest pseudo-R^2 and highest ROC value), we then assessed competing models (i.e., different combinations of independent variables). Competing models were ranked using Akaike's Information Criteria (AIC; Akaike, 1973; Burnham and Anderson, 2002). AIC model selection estimates the information loss between the probability distribution with the true and the probability distribution associated with the model that is to be evaluated. Choosing the model with the lowest expected information loss between the true model and the approximating model is asymptotically equivalent to choosing a model that has the lowest AIC value (Burnham and Anderson, 2002). We applied a correction to the AIC value to account for small sample sizes (AIC_c) and determined the Akaike weight (w_i), the likelihood of the model given the data (Burnham and Anderson, 2002). For those competing models, the lowest AIC_c value and highest Akaike weight defined the best model for each set of predictor variables. After the final models were selected, we reviewed cases for high leverage and studentised residual values to determine if any cases were disproportionately driving the model relationship (Menard, 2002). We used the program Stata (version 8.2; StataCorp, 2003) for all statistical analyses and employed the DESMAT procedure (Hendrickx, 2001) for design matrices involving categorical variables.

Results

Red squirrel

We recorded audio and visual detections of Red Squirrel at 178 plots and detected sign at 205 plots (219 plots in total). Audio and visual detections were primarily made during point-count surveys. Sign detections included foraging sign, middens, remains, and nests. The best model was constructed with sign as the response variable (Table 2.3). This model explained approximately 16% more variation and the prediction accuracy improved by 8%, but both the sign and audio visual models had good predictive accuracy (sign ROC = 0.88, audio and visual ROC = 0.80; Table 2.3). Several of the same variables were included in both models, specifically, structure class, percent gap, and frequency Spruce. Comparing the results of competing models for only sign as the response variable, the best model was constructed with a combination of plot-level data and VRI data (AIC_c = 181.55; Table 2.4).

Table 2.3. Model results predicting the occurrence of Red Squirrel (*Tamiasciurus hudonicus*) in the Williams Lake Study Area using audio and visual detections or sign detections. Using sign as the response variable resulted in the highest pseudo-R^2 and highest ROC value.

Response variable	Independent variables	Pseudo-R^2	ROC
Audio Visual	Structure Class Percent Gap Frequency Spruce	0.20	0.80
Sign	Structure Class Percent Gap Frequency Spruce Dead trees basal area Shrub crown closure	0.36	0.88

Table 2.4. Models predicting occurrence of Red Squirrel (*Tamiasciurus hudonicus*) in the Williams Lake Study Area using different sources for independent data variables. The model using plot measures and Vegetative Resource Inventory (VRI) data resulted in the lowest AIC_c and highest ROC value.

Data Source	Independent variables	AIC_c	ΔAIC	w_i	ROC
VRI and Plot	Structure class Percent gap Spruce stems ha^{-1} Dead tree basal area Shrub crown closure	181.55	0	0.93	0.88
VRI	Adjusted canopy closure Structure class Spruce cover	187.31	5.28	0.067	0.86
Plot	Percent gap Spruce stem ha^{-1}	212.36	29.28	<0.01	0.76

The multi-source model was highly favoured as the best model with an Akaike weight of 0.93, or a 93% likelihood of being the best model; however, prediction accuracy did not improve dramatically (VRI ROC = 0.86, multi-source ROC = 0.88; Table 2.4).

Pileated woodpecker

We recorded audio and visual detections for the Pileated Woodpecker at 63 plots and sign at 33 plots (85 plots in total). Sign detections included foraging and nest cavities. The best model was constructed using sign as the response variable (Table 2.5). There was little overlap among explanatory variables included in the two models. Sign detection as the response variable dramatically improved model performance over audio and visual measures. The variation explained improved by 14% and predictive accuracy improved from poor (ROC = 0.66) to good (ROC = 0.82; Table 2.5). Comparing the results of competing models using only sign as the response variable, the best model was constructed with a combination of plot and VRI data (AIC_c = 179.55; Table 2.6). The likelihood of the multi-source model being the best approximating model was 66% and predictive accuracy improved by 10% (Table 2.6).

Discussion

For both the Red Squirrel and Pileated Woodpecker, logistic models using sign detections outperformed those with audio and visual detections. Measurement uncertainty from several sources may explain this result. Firstly, it is sometimes difficult to associate vocalisations to specific locations because of the distance over which sound travels and measurement error assigning the detection to a spatial location. Secondly, vocalisations may be made while the individual is in transit between parts of its home range, as is the case for

Table 2.5. Model results predicting the occurrence of Pileated Woodpecker (*Dryocopus pileatus*) in the Williams Lake Study Area using audio and visual detections or sign detections. Using sign as the response variable resulted in the highest pseudo-R^2 and highest ROC value.

Response variable	Independent variables	Pseudo-R^2	ROC
Audio Visual	CWD volume Percent gap Douglas-fir stems ha^{-1} dbh ≥0cm basal area	0.06	0.66
Sign	Percent Gap Structure class Douglas-fir cover Main canopy height Adjusted live basal area	0.21	0.82

Table 2.6. Models predicting occurrence of Pileated Woodpecker (*Dryocopus pileatus*) in the Williams Lake Study Area and different sources for independent data variables. The model using plot measures and Vegetative Resource Inventory (VRI) data resulted in the lowest AIC$_c$ and highest ROC value.

Data Source	Independent variables	AIC$_c$	ΔAIC	w_i	ROC
Multi-Source	Percent Gap Structure class Douglas-fir cover Main canopy height Adjusted live basal area	179.55	0	0.66	0.82
VRI	Adjusted canopy closure Douglas-fir cover Adjusted live basal area	181.16	1.611	0.30	0.72
Plot	Main canopy height	185.21	5.66	0.04	0.65

the Pileated Woodpecker. Finally, the observer must be at the location at a moment in time when the individual is near the same location. For species with large home ranges, the probability of an observer being in the same location, in space and time, is lower than that for a species with a smaller home range. It is possible, therefore, that we may have not detected presence. Given our survey methods for sign, it was unlikely that we would not detect presence if it was there.

Sign detections are often associated with a specific component of a species' habitat requirements (e.g., foraging or nesting sites). Logistic models with sign data as the response variable likely had higher predictive efficiency because foraging and nesting substrates are often selected for at smaller scales, within the context of a home range. For example, Red Squirrels have home ranges of 1-3 ha (Obbard, 1987), easily within a single stand of similar habitat characteristics. Audio and visual detections are likely recorded within the same stand as foraging and other life history activities take place; therefore, it is not surprising that model results are similar for the different detection types for Red Squirrel. The additional variables included in the sign model for Red Squirrel, shrub cover and dead wood basal area, may be more related to the associated effects of middens on ground vegetation and the availability of cones. Potential temporal uncertainty associated with changes to vegetation structure and composition from disturbance (e.g., alteration because of harvesting practices) around sign detections may prove a greater issue in long-term monitoring studies.

The Pileated Woodpecker has a large home range; pairs in the Pacific Northwest use between 300 and 600 ha, while unpaired birds used up to 1400 ha (Bull and Holthausen, 1993). Pileated Woodpeckers select large snags and logs to forage on and large diameter trees for nesting (Bull and Holthausen, 1993; Carey et al., 1991). These structural components may be localised or clustered within a highly variable home range, resulting in better predictive accuracy of models for sign. Further, because we employed a survey methodology that was designed to solicit responses from individuals if they were in the area (i.e., to minimise false absence detections) we may have inadvertently attracted an individual from its original location and the associated characteristics of that original location. It is unclear which is more detrimental to the predictive efficiency of logistic species-habitat models and their use in a biodiversity monitoring program, false absence or spatial uncertainty related to an individual's movement.

Overall, differences in logistic-model results, and the potential difference in a monitoring program designed around them, emphasize the importance of assessing sources of potential model error and the predictive efficiency. For a species that uses landscapes at relatively small scales (e.g., Red Squirrel), sign and visual or audio detections are likely to be within the same area and not have a large effect on a monitoring program. In contrast, there was little overlap among variables included in the different statistical models for Pileated Woodpecker and the predictive efficiency varied greatly. It may be more appropriate to use complementary models over a general model that has weak predictive accuracy and to give careful consideration to the biology of the species. Ultimately, the decision of which is the most appropriate approach will depend on what poses the highest risk to the species (e.g., loss of critical habitat features) and the goals and objectives the statistical model is intended to help achieve.

In this paper we examined the effects of two kinds of potential model error: detection type and availability of structure data. We showed that: 1) different types of detection can potentially affect model results and assessment of accuracy; and, 2) that adding a small amount of locally measured data can improve predictive efficiency dramatically. Measuring these data may have relatively low costs. We conducted our analyses using our original data set; using independent data to validate models is the preferred approach to address all aspects of validation. It is, therefore, likely that we have reported optimistic predictive accuracy (Chatfield, 1995). Additionally, although the area under the ROC curves is a robust measure of prediction accuracy, its use in the biological sciences is relatively recent. Some caution should be taken when using the method outside of its original development (Kraemer, 1988) although the approach is highly recommended for presence and absence data (Ottaviani et al., 2004).

Overall, assessing prediction accuracy is only one component of model validation. Validation needs to be an iterative process so that confidence is maintained in the model's usefulness through continued monitoring (Johnson, 2001). Other factors, outside of those used in predictive-habitat models, may ultimately have greater impact on the presence of species (e.g., invasive species, climate change). A better understanding of the relations among species distribution and forest characteristics, both in the short- and long-term, will provide knowledge to help mitigate the loss of species from forest environments. Ultimately, assessing model performance will allow for informed trade-offs and lead to improved effectiveness of biodiversity monitoring. In conclusion, every monitoring program for biodiversity that uses species-habitat models should make effort to ensure that models are valid for their intended use. Clear articulation of model objectives and a thorough consideration of appropriate types of data collection, a standard of acceptable error, and independent data for evaluation of error will improve the effectiveness of biodiversity monitoring programs.

Chapter 3. Using forest structure to predict the occurrence of vertebrate species[1]

Abstract

In forested environments, mitigating negative impacts of forest-harvesting activities and monitoring biodiversity are common requirements of sustainable-use certification and of various laws and regulations. Managers require an understanding of how species respond and persist within the dynamics of changing forest environments so that management strategies can retain and recruit structural aspects necessary for the persistence of populations. We tested several structural models to predict the presence or absence of a range of vertebrate species (n = 55) and to determine the potential of using forest structure to monitor species distributions. We validated models with temporally and spatially independent data. Some of the models had good predictive accuracy that was retained when validated and thus have application in terms of implementation as management tools. Modelling success varied, however, depending on whether plot or stand data were used; many models included variables related to spatial relationships of structures. Few models were reliable when applied to the independent data; therefore, our results indicate that models cannot be assumed to be applicable in different years or applied outside the area where the model was developed, even with similar spatial and temporal contexts. We did not find robust relationships necessary to guide management targets for retention and recruitment of specific forest structures. Therefore, using these structural models as surrogates for monitoring species occurrence is limited. Monitoring of structure should still be included as part of biodiversity monitoring programs because preservation of structures known to be negatively affected by harvesting (e.g., dead wood, large trees, closed canopies, continuous forests) contributes to local and

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[1] Throughout this chapter the first person plural is used to reflect the contributions of others to this research. The manuscript will be submitted with the authorship: Psyllakis, J.M. and M.P. Gillingham.

landscape heterogeneity and has been shown to affect species presence in this study and others.

Introduction

Industrial forest-management activities can contribute to the loss and fragmentation of habitat, change in tree-species composition, and the introduction of non-native species. These factors are linked to the decline of species from forest environments at local to global scales (Groombridge, 1992; Berg et al., 1994; Harper and Hawksworth, 1995; Noss, 1999; Hunter, 2001). Protecting biodiversity in reserves is not sufficient to mitigate the decline (Hunter, 1990). Therefore, efforts to mitigate loss of biodiversity are also included in plans for the sustainable use of natural resources (Rosenzweig, 2003). Through sustainable forest-management policies and certification, protection of biodiversity and ecological integrity are mandated (e.g., United Nations Environment Programme, 1992; Province of British Columbia, 1995; Montreal Process Working Group, 1999; Canadian Council of Forest Ministers, 2003), thus forest-land managers require tools to assess biodiversity and to ensure that operational activities have minimal effects on biodiversity.

Biodiversity is a broad concept that spans spatial, temporal, and organizational scales (see Chapter 1; Bunnell and Huggard, 1999; Purvis and Hector, 2000; Willis and Whittaker, 2002; Magurran, 2003). Species diversity is a commonly measured component of biodiversity (Purvis and Hector, 2000; Magurran, 2003). Even the narrow focus on the measurement of species diversity is problematic as it is impossible to measure or monitor all species. To overcome the difficulty of measuring all species directly, surrogate measures are used with an assumption that whatever is being measured is representative of a larger aspect of diversity (Noss, 1990; Caro and O'Doherty, 1999; Margules and Pressey, 2000).

Approaches to surrogate measures may be habitat-based, species-based, or a combination of the two, and will vary depending on the spatial scale of the conservation goals (Poiani et al., 2000; Groves et al., 2002). To reflect the scale of the approach, both spatially and biologically, surrogate measures are often characterised as fine-, medium-, or coarse-filter (see Chapter 1; Hunter, 1990; Noss, 1996; Lindenmayer and Franklin, 2002; Hunter, 2005). In the context of forest management, fine-filter approaches are typically species-based and applied at local scales; medium- and coarse-filter approaches are typically habitat-based and applied at stand to landscape scales (Noss, 1996; Hunter, 2001; Lindenmayer and Franklin, 2002; Hunter, 2005).

Examples of fine-filter approaches include monitoring or managing population trends or distribution of single species (Hansen et al., 1999; Hunter, 2001). Fine-filter species may be rare or endangered or be representative of other aspects of the ecosystem or community (e.g., indicator, flagship, keystone, or umbrella species; Hunter, 2001). Fine-filter approaches have been criticised because of a general lack of knowledge and understanding of the relationships among species and species diversity, the expense and time that is required to monitor or manage single species, and the questionable contribution that protecting the identified species has on the rest of the ecosystem (Simberloff, 1998; Ricketts et al., 2002; Caro et al., 2004).

Medium-filter (also mesofilter *sensu* Hunter, 2005) surrogate approaches focus on specific elements of forest stands that represent critical habitat for the persistence of some species (Bunnell et al., 1999; Lindenmayer et al., 2000; Hunter 2005). For example, in forested environments several studies have identified the importance of dead and dying trees, coarse-woody debris, riparian areas, and deciduous species to forest-dwelling species (e.g., Bunnell et al., 1999; Martin and Eadie, 1999; Bowman et al., 2000; Zabel and Anthony, 2003; Mazurek and Zielinski, 2004). The retention and enhancement of these structural elements may, therefore, contribute to reducing the risk of extirpation of species dependent on these structures for some aspect of their life history from managed forests (Lindenmayer and Franklin, 1997; Bunnell et al., 1999; Lindenmayer et al., 2000).

Coarse-filter surrogate approaches centre on the preservation of representative habitats and ecosystems on the landscape through time. An underlying assumption is that complete representation of environmental variability, and the preservation or emulation of processes that contribute to this variability, will maintain species diversity and thus their processes and functions (Hunter, 1990; Noss and Cooperrider, 1994; Hunter, 2001). Coarse-filter approaches are criticised because of a lack of congruence between environmental and species diversity (Reyers et al., 2000; Araújo et al., 2001) and a sensitivity to missing rare, endemic, and sensitive species (Margules and Pressey, 2000; Hunter, 2001; Noon et al., 2003). The general disagreement of the success of fine- and coarse-filter approaches (Simberloff, 1998; Caro and O'Doherty, 1999) has resulted in the recommendation that a combination of approaches is necessary (Noss, 1990; Noss and Cooperrider, 1994; Poiani et al., 2000; Sarakinos et al., 2001; Lindenmayer and Franklin, 2002).

The use of habitat-based surrogates at the coarse- and medium-filter level has been encouraged because complete knowledge of species' biology is not required and it is usually less costly to assess characteristics of habitats than species and populations (Noss, 1996; Bunnell et al., 1999; Lindenmayer et al., 2000; Ricketts et al., 2002). Habitat-based approaches are particularly appealing to forest managers because measures such as forest cover, vegetation species composition, and stand age are intuitive and directly linked to harvest-based forest inventories. Regardless of the approach, the surrogate measure should have a strong relationship with its intended non-measured counterpart.

Linking species presence to forest structural elements for the purpose of biodiversity monitoring incorporates aspects of both species-based and habitat-based surrogate approaches and is a compromise between the expense of monitoring a single species and the possibility of missing species needs in coarse-filter approaches. Using forest structure as a predictor of species richness has received considerable recent attention (e.g., Lahde et al., 1999; Díaz et al., 2005; Loehle et al., 2005; Oxbrough et al., 2005). Generally, however, forest structure remains relatively untested as a surrogate measure for biodiversity monitoring. The development of statistical models linking species occurrence to structural characteristics of forests may also provide clear targets for management that have direct impacts on structural aspects of forests. Further, predictions on how species will respond to changing structure need to be made if a better understanding of the causal effects of management on diversity, an important aspect of adaptive management (Walters, 1986), are to be incorporated into management. If linkages are strong and predictions of species presence are accurate, monitoring forest structure could contribute to assessing the effects of management on species diversity.

Examining the linkages between species presence and forest structure can be approached with statistical modelling. Before implementing the use of statistical models as part of management programs, however, the models should be validated with spatially and temporally independent data (Rykiel, 1996; Guisan and Zimmerman, 2000; Ottaviani et al., 2004; Guthery et al., 2005). Validation of logistic regression models, a common method of modeling species presence and absence data, usually involves assessment of two aspects of prediction accuracy: 1) reliability – the accuracy of the predicted likelihood of occurrence; and, 2) discrimination – the ability of the model to accurately distinguish between occupied and unoccupied sites (Fielding and Bell, 1997; Pearce and Ferrier, 2000; Johnson, 2001). Statistical artefacts (e.g., sample prevalence; Manel et al., 2001; McPherson et al., 2004), as well as biological attributes of species (Karl et al., 2000; Scott et al., 2002; McPherson et al., 2004; Seoane et al., 2005) are linked to prediction accuracy. An assessment of systematic biases in model predictions is, therefore, required if models are to be compared among different species.

The overall goal of our study was to examine the possible use of structure-based measures as explanatory variables to predict the presence and absence of vertebrate species, as a surrogate approach to monitoring species diversity. Although vertebrates represent a relatively small portion of species diversity in most ecosystems (Redak, 2000; Spence, 2001), several standardized protocols exist for their measurement (Province of British Columbia, 1991; Heyer et al. 1994; Wilson et al., 1996) and there is a wide range of studies linking the presence of vertebrate species to structural elements of habitat (e.g., snags, basal area, large trees, coarse-woody debris; Keisker, 2000; Bull, 2002). Specifically, our objectives were to determine: 1) the viability of using attributes of forest structure to predict the presence of vertebrate species; 2) the validity of model predictions using spatially and temporally independent data; and, 3) if statistical artefacts (e.g., sample prevalence, detection uncertainty) or biological traits of vertebrate species (e.g., mobility, territory size) consistently influence the prediction accuracy of these models.

Methods

Study area

Our study took place near the northern extent of the dry-warm subzone of the Interior Douglas-Fir (IDF) Biogeoclimatic zone (Meidinger and Pojar, 1991) approximately 30 km south of Williams Lake, British Columbia, Canada (Williams Lake Study Area; Figure 3.1). Data were collected from May 2001 through January 2004 for original model development (development sites). For spatial validation data, the study area was extended in the summer of 2004 within the IDF to the south-east extent of the moist-cool subzone of the Sub-Boreal Pine Spruce (SBPS) Biogeoclimatic zone (Figure 3.1).

The IDF was characterised by stands of closed- and open-canopy Douglas-fir (*Pseudotsuga menziesii*). At higher elevations within the IDF (>1000 m above sea level) or where crown fires had occurred in the past, Lodgepole Pine (*Pinus contorta*) was common. At lower elevations (~850 m above sea level) grassland communities and wetland communities were dispersed throughout the forested landscape. There were localised stands of hybrid White Spruce (*Picea engelmannii* x *glauca*) and Trembling Aspen (*Populus tremuloides*) throughout the IDF. Even-aged lodgepole pine stands dominated the SBPS landscape, as large-scale fires historically occurred frequently. Moist sites were dominated by White Spruce (*Picea glauca*). Wetlands were also common throughout this zone. Livestock grazing, primarily in the IDF, but also the SBPS, and forest harvesting were predominant anthropogenic disturbances and insect outbreaks continued to influence stand dynamics of both biogeoclimatic zones. The mean annual temperature is 4.2°C (range = -1.3 to 9.6 °C; Environment Canada, 2002).

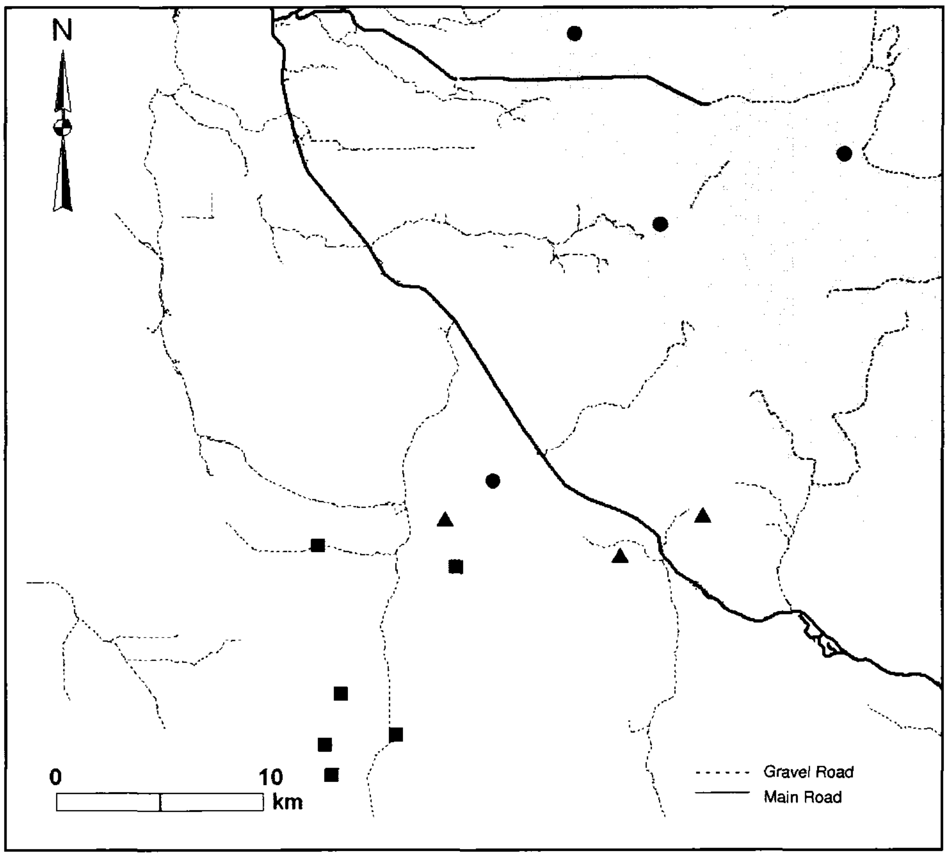


Figure 3.1. The distribution of sites within the Williams Lake Study Area in central British Columbia, Canada (approximately 30km south of Williams Lake). Multiple plots were located within each site. Development sites (▲ and ■) included 243 plots used for 2001-2004 model construction. In the summer of 2004, we established an additional 123 plots at spatial validation sites (●) and continued to monitor 91 plots at temporal validation sites (▲) to assess the prediction accuracy of these models with independent data. The shaded area of the map indicates the Sub-Boreal Pine-Spruce (SBPS) biogeoclimatic zone, the unshaded area is Interior Douglas-fir (IDF).

Initial plot layout and stratification were accomplished using a Geographic Information System (GIS) with forest cover and orthophoto layers. We established 243 plots within 107 stands across a range of structural variation within the IDF in 2001-2002 (Figure 3.2). We excluded plots from our final analysis if industrial activity resulted in alteration of forest structure (e.g., complete removal of trees or thinning; $n = 15$). Therefore, the final sample included 228 plots within 97 stands. Stands were defined based on forest inventory polygons of homogeneous vegetation characteristics as delineated on forest inventory maps (Tolko Ltd., Vernon, BC).

In 2004, we established an additional 123 plots within the IDF ($n = 32$) and SBPS ($n = 91$) for collection of spatial validation data. Twenty-three of the plots in the SBPS were very close to the IDF boundary and had a large component of Douglas-fir; therefore, the new plots were distributed along a gradient of Douglas-fir dominance through the transition between IDF into SBPS zones. In 2004, we also continued visiting a subset of the plots established in 2001-2002 for temporal validation of models ($n = 90$). All plots were spaced at least 150 m apart, but occasionally 300 m separated plots where roads, landings, or water interrupted the transect.

Habitat measurements

We measured local habitat variables using a combination of methods. Shrub species and cover, canopy gaps, and coarse-woody debris were measured along the intercept of 2, 48-m transects laid perpendicular through plot centre (Figure 3.3). For coarse-woody debris, we recorded the diameter of the piece perpendicular to where it crossed the axis, the tree species (if possible), decay class (Maser et al., 1979), and any signs of use by wildlife. At 5, 2-m radius plots located at 11.28 m away from plot centre on each axis and at plot centre,

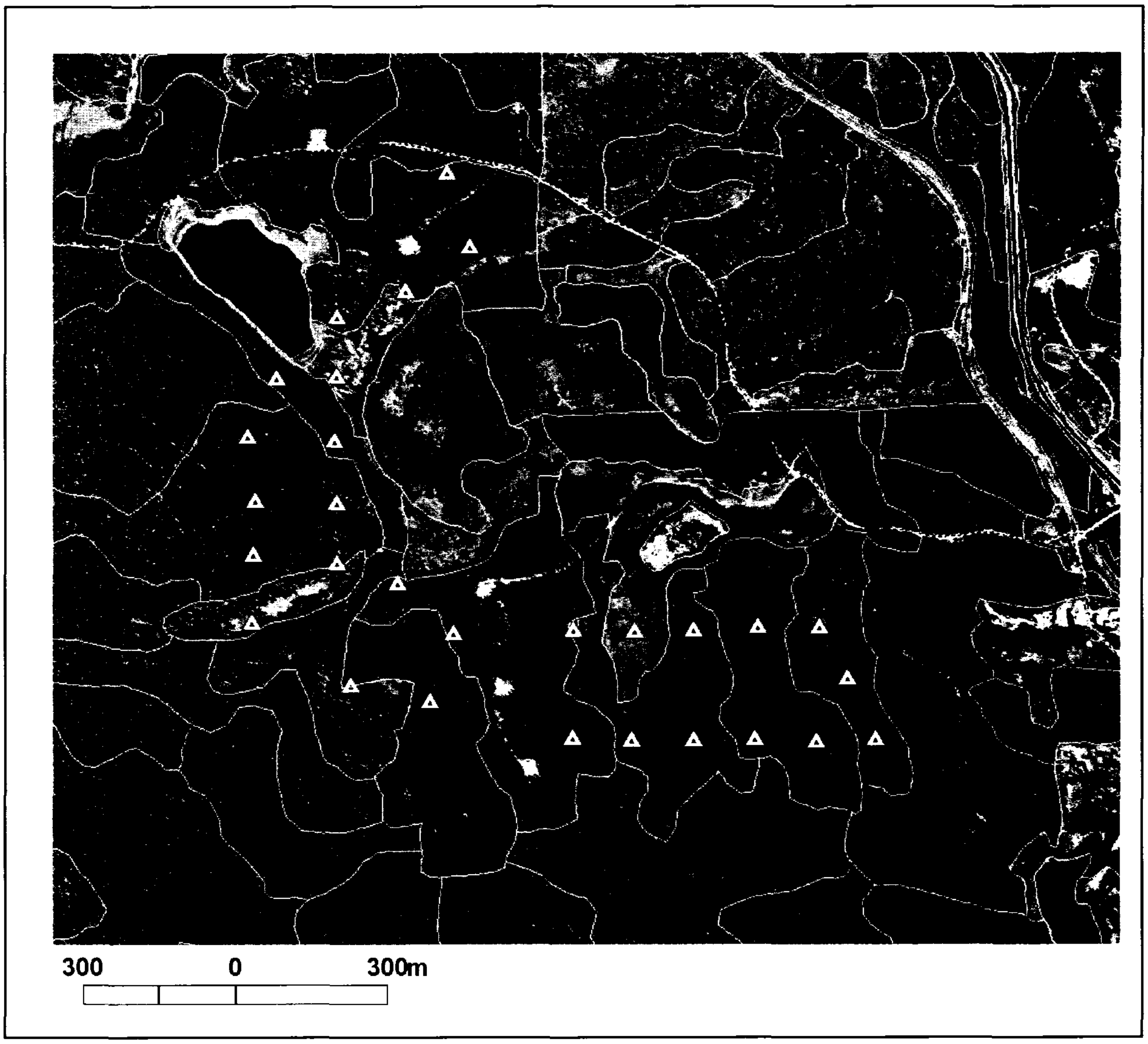
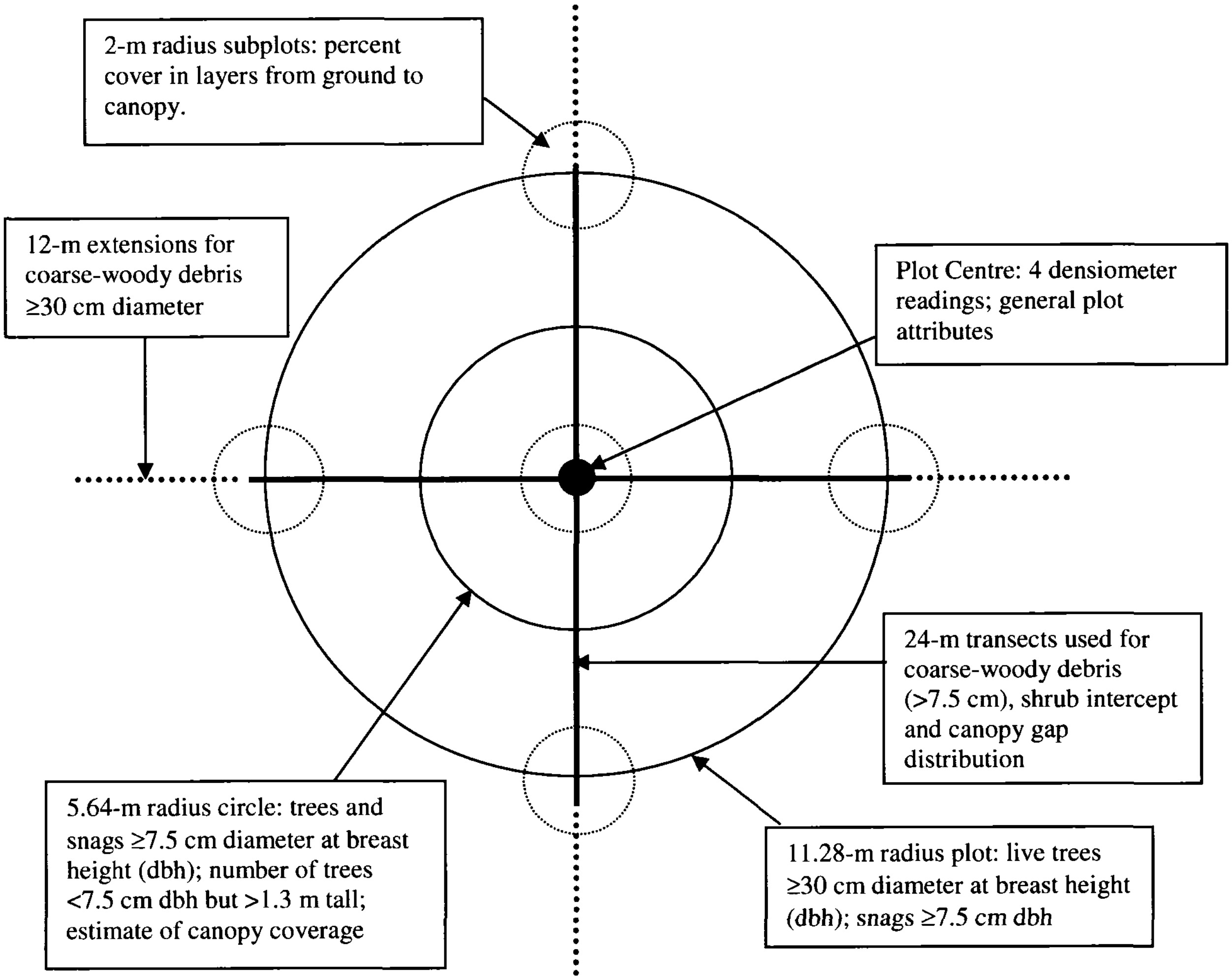


Figure 3.2. Example of plot (Δ) layout within the Williams Lake Study Area. Most plots were connected with a 150-m transect, although some were connected with a 300-m transect. The boundary for Vegetation Resource Inventory (VRI) polygons that were used to define forest stands are highlighted with white.



2-m radius subplots: percent cover in layers from ground to canopy.

12-m extensions for coarse-woody debris ≥30 cm diameter

Plot Centre: 4 densiometer readings; general plot attributes

24-m transects used for coarse-woody debris (>7.5 cm), shrub intercept and canopy gap distribution

5.64-m radius circle: trees and snags ≥7.5 cm diameter at breast height (dbh); number of trees <7.5 cm dbh but >1.3 m tall; estimate of canopy coverage

11.28-m radius plot: live trees ≥30 cm diameter at breast height (dbh); snags ≥7.5 cm dbh

Figure 3.3. Schematic of the vegetation sampling scheme used to assess the vegetation and other structures present in each of the sampling plots.

we measured the percent coverage for litter, coarse-woody debris, herb species, moss and lichens, shrub species, sapling species, bare ground, and rock. Within a 5.64-m radius plot around plot centre, we tallied all trees and stumps ≥7 cm diameter at breast height (dbh) and recorded tree species, dbh, and height. We tallied all trees ≥30-cm dbh and snags within an 11.28-m radius. We recorded general information for each plot including canopy closure around plot centre, as an average of 4 measurements taken on each axis (Robert E. Lemmon model C densiometer; Bartlesville, Oklahoma), aspect, slope, canopy stratification and complexity, disturbance history (evidence of fire, grazing, logging), and the elevation (in m) above sea level. We averaged vegetation data collected at multiple plots measured within stands, as defined by forest inventory polygons, to create stand-level variables.

Because the study area is currently undergoing a major mountain pine beetle (*Dendroctous ponderosae*) outbreak, we also included beetle presence as a potential predictor variable for woodpecker species, Black-capped Chickadee (*Poecile atricapillus*), and Townsend's Warbler (*Dendroica townsendi*). These data were derived from our plot surveys as well as provincial aerial forest health surveys (Province of British Columbia, 2000). Using the ArcView GIS (version 3.2a; ESRI, 2000) extension Patch Analyst 3.1 (Rempel and Carr, 2003), we created a 75-m buffer around plot centres and intersected this layer with the provincial data layer that contained the insect pest distribution data. In cases where provincial maps and our plot data disagreed, we reviewed transect data and helicopter survey data provided to us by the forest company tenured in the study area (Tolko, Ltd., Vernon, BC) to resolve this discrepancy.

To obtain landscape-level attributes, we subsetted a Landsat 7 (30-m resolution) image of the study area (July 2002) and used PCI Works GIS software (version 7.0; PCI

Geomatics Corp., 2001) to complete a supervised maximum-likelihood classification. Six habitat classes were identified: water, nonforest, early seral, shrub and Aspen, moderate retention conifer, and conifer. We used colour airphotos, orthophotos, and the vegetation data collected at plots to seed areas for training and to assess the accuracy of the classification. We assessed accuracy of the classification by determining the number of correctly classified pixels from a randomly selected subset. Water, nonforest, and conifer classes had the highest accuracy (97%, 94%, and 88%, respectively). Early seral, shrub and Aspen, and moderate retention conifer were less often classified correctly (67%, 78%, 67%, respectively). Overall classification accuracy was 81%.

We calculated landscape metrics using the Patch Analyst 3.1 (Grid) extension (Rempel and Carr, 2003) for ArcView GIS (version 3.2a; ESRI, 2000) to interface to the PC raster version of FRAGSTATS 2 (McGarigal and Marks, 1995). We intersected the classification layer with a buffer created around plot centres at 3 scales: 2 ha, 50 ha, and 300 ha. We selected these extents based on available information of species home-range size (Gillingham, 2003). We determined centroids for each stand polygon and repeated this process with 50- and 300-ha buffers around each centroid. Distance from plot centres and polygon centroids to water, high-contrast edge (e.g., meadow – forest), and roads were estimated using the GIS.

Vertebrate sampling

For each vertebrate observation, we used a handheld Global Positioning System (GPS; Garmin eTrex GPS, Olathe, Kansas) to obtain coordinates or used known plot coordinates to import detections into a GIS (ESRI, 2000). If necessary, detections were corrected with an estimated bearing and distance to the individual. To ensure that observations were associated with the correct plot- and stand-structural characteristics, we calculated distance to nearest plot and associated each detection to the nearest plot (<75 m) and to the stand polygon. We used a variety of techniques to determine the presence of vertebrate species.

Point counts

We conducted variable-radius point counts at each of the plots (Reynolds et al., 1980; Ralph et al., 1995) 3 times throughout the breeding season (mid-May – early July) in each year. Point counts began no earlier than 30 min before sunrise and were ceased no later than 4 h after sunrise when there was little or no wind or rain and temperature was at least 3°C (Robbins, 1981; Province of British Columbia, 1999b). A minimum of 10 days passed between each successive visit. Observers were rotated between plots (1 visit per observer per plot per year) and direction of travel along the transect was changed between surveys to reduce bias associated with the observer and time of day. We recorded all birds detected during a 6-min recording period that began after a 1-min settling period. Distance and direction to bird from plot centre was estimated and recorded as either within 50 m, 50-75 m, or outside 75 m. Training was conducted prior to the onset of surveys and opportunistically throughout the field season to calibrate distance estimates among observers.

Woodpecker surveys

We conducted woodpecker playback surveys from mid-May until mid-June at plots a minimum of 300 m apart (usually every other plot), 3 times per year. We began surveys no earlier than 30 min before sunrise and ended no later than 1100 h, in appropriate weather conditions as for point counts. A pre-recorded cassette tape of the calls and drumming of the 7 species expected to occur in the study area was broadcasted starting from the smallest species and ending with the largest species (Downy Woodpecker, *Picoides pubescens*; Red-naped Sapsucker, *Sphyrapicus nuchalis*; Hairy Woodpecker, *Picoides villosus*; Three-toed Woodpecker, *Picoides tridactylus*; Black-backed Woodpecker, *Picoides arcticus*; Northern Flicker, *Colaptes auratus*; Pileated Woodpecker, *Dryocopus pileatus*) in an attempt to invoke woodpecker responses (Johnson et al., 1981). Passive sampling was also conducted at each plot in conjunction with point-count surveys. When point counts were conducted in conjunction with playbacks, playbacks were always conducted after the passive listening period of the point count was finished.

Encounter transects and time-constrained searches

We conducted encounter-transect surveys with unlimited width along transects between plots throughout each field season and in 2 winters (see below). If a species was detected along the transect, a GPS waypoint was recorded with species ID, distance and bearing from waypoint, as well as a sign code (singing, call, visual, den/nest, track, remains, browse, or feces).

In 2001, we conducted time-constrained searches for amphibians and reptiles at both plots and along transects. These searches involved lifting cover and replacing cover objects with a restriction on the amount of time spent searching (Scott, 1994). We also searched ponds and riparian areas for presence of amphibians (all life stages). These searches produced relatively few detections for the effort spent; therefore, in 2002 - 2004 we incorporated search methods (e.g., lifting cover objects) into encounter-transect surveys. Auditory detections for vocal amphibian species were also recorded opportunistically during owl playback and surveys near marshes at dusk.

Owl surveys

We established several roadside-calling stations for owl-playback surveys at locations that maximised the coverage of stands where we had established our plots. Calls for each owl species expected to occur in the study area were broadcasted 3 times, progressing from smallest species to the largest species (Northern Pygmy Owl, *Glaucidium gnoma*; Northern Saw-whet Owl, *Aegolius acadicus*; Boreal Owl, *Aegolius funereus*; Short-eared Owl, *Asio flammeus*; Long-eared Owl, *Asio otus* ; Barred Owl, *Strix varia*; Great-horned Owl, *Bubo virginianus*; and Great Grey Owl, *Strix nebulosa*), using a prerecorded CD and megaphone. As with woodpecker playbacks, the broadcasted call is intended to invoke a vocal response or attract an individual (Fuller and Mosher, 1981). Surveys were conducted from late April until late May, as well as on visits during winter-tracking surveys (see below). Passive owl detections were recorded throughout the season. These data were entered into the species database as were coordinates obtained during encounter-transect surveys.

Remote cameras

We used 7 TrailMaster TM1000 (Goodson & Associates, Inc. Lenexa, KS) active-infrared monitoring systems and 3 TrailMaster TM550 passive-infrared systems to record the presence of medium and large vertebrates in our plots. The 2-piece active-infrared trail monitor used an infrared beam across the trail between the transmitter and receiver (30-m range). When the beam was broken for the specified length of time (0.25 s), a camera was triggered to photograph the area. All events were logged on the receiver and photographs were indexed to specific times. The passive-infrared trail monitor was a single unit that detected the combination of heat-and-motion in the area it was monitoring. The area of sensitivity formed a wedge radiating outward in front of the monitor. We constrained the wedge, which was 20-m deep and spread 150° wide, with electrical tape so that it was restricted to the field of view of the camera. Endotherms, generally squirrel-sized or larger, that moved within this wedge registered as an event and a photograph was triggered.

Cameras were placed along game trails and at game-trail intersections, latrine sites, across logs, and other positions where evidence of species presence existed, but specific species was not determined (e.g., mustelid or canid scat). At or near previously documented scat of these types, cameras were placed in locations for a minimum of 12 days, which is the recommended minimum based on the travel behaviour of weasels through their home ranges (Zielinski and Kucera, 1995).

Small-mammal trapping

We conducted live trapping for small terrestrial mammals in all years. Collapsible-live traps (H. B. Sherman Traps, Inc. Tallahassee, FL) were placed at 25-m intervals along the primary and secondary axes of all plots (4 traps; Figure 3.3) in each year. In 2002, an additional 4 traps were placed 25 m from the plot centre in 45° increments between axes. Each trap location was pre-baited for a minimum of 24 h prior to deploying live traps. Traps contained a small piece of carrot to provide moisture, oats and sunflower seed for energy, and a small wad of cotton bedding for warmth (Jones et al., 1996; Province of British Columbia, 1998).

We trapped over 3 nights, opening the traps at dusk and checking them beginning at dawn. In 2002, we marked all animals captured with ear tags; in other years we clipped hair on individuals to identify recaptures. In 2002, we also conducted day trapping at approximately 50% of the plots following the same routine, but traps were checked between 4 and 7.5 h after opening. Traps were not opened in unseasonable cool overnight weather.

Bat detections

In 2002-2004, we surveyed for bats at plot centres using Anabat™ broadband bat detectors coupled with Zcaim recording units (Titley Electronics, Ballina NSW, Australia), which record echolocation calls directly to a flash disk. We placed Anabat™ detectors 1.3 m off the ground, at an angle of 45° and directed north. At sites where transects between plots could be safely navigated at night, plots were surveyed for bat activity in a transect method. Bat activity was recorded for a minimum of 30 min at each plot before moving the detector to a new plot along the transect. Sampling was conducted between 2000 and 0200 h on 3 consecutive nights, unless weather conditions precluded sampling (rain or strong wind). On each successive night we switched the direction traveled along the transect so that plots were visited at different times. During the 3-night period, 1 plot was sampled throughout the night for the entire survey period to obtain a reference of overall nightly bat activity and variation among nights (Hayes, 1997). Where terrain or vegetation made it difficult and dangerous to travel at night, detectors were placed at plot centres and programmed to record data from 2000 to 0600 h for 4 consecutive nights.

We mist-netted bats to obtain reference calls for the identification of echolocation calls recorded using discriminant function analyses (DFA; Statistica 6.0, StatSoft, Inc. 2003; O'Farrell and Gannon, 1999). Because of similarity in echolocation calls for species belonging to the genus *Myotis* (Thomas et al., 1987; Corben and O'Farrell, 1999) and the variability by calls of big brown (*Eptesicus fuscus*) and silver-haired bats (*Lasionycteris noctivigans*; Fenton and Bell, 1981; Thomas et al., 1987), we grouped detections into 1 of 3 groups (long-eared myotis, little brown or long-legged myotis, or big brown/silver-haired; Table 3.1).

Table 3.1. Echolocation frequency and species groupings for bats expected to occur in the Williams Lake Study Area. Identification of the recorded echolocation calls of bats was based primarily on the minimum frequency and slope characteristics. For some species we also used maximum frequency. Species were confirmed present in the study area if we captured them in mist-nets. Because we could not record reference calls for species not captured, we could not confirm presence and, therefore, did not assign that species to an echolocation group (NA), although characteristics of calls for some species are distinctive.

Minimum frequency	Species membership	Slope characteristic	Confirmed presence in Study area by capture	Group
≤30-35 Khz	Western Long-eared Myotis (*Myotis evotis*)	Steep slope with little or no curve	Yes	1
≥35-40 Khz	Little Brown Myotis (*M. lucifugus*)	Steep slope, usually less time between calls	Yes	2
	Long-legged Myotis (*M. volans*)		Yes	2
≥50 Khz	Yuma Myotis (*M. yumansis*)	Steep slope, Maximum frequency >90 Khz	No	NA
	California Myotis (*M. californicus*)		No	NA
20-30 Khz	Big Brown Bat (*Eptesicus fuscus*)	Varies from sweeping to steep	Yes	3
	Silver-haired Bat (*Lasionycteris noctivagans*)		Yes	3
17-20 Khz	Hoary Bat (*Lasiurus cinereus*)	Shallow sweep, little change in frequency	No	NA
5-8 Khz	Spotted Bat (*Euderma maculatum*)	Maximum frequency 12 Khz	No	NA

Winter tracking

We conducted snow-tracking surveys along all transect routes connecting plot centres twice in January and March of 2002 and once through January and February 2004 at 4 areas accessible by vehicle (plot $n = 93$). We considered conditions suitable for tracking after a significant snowfall (accumulation of >5 cm), with stable temperatures, and low winds (Beauvais and Buskirk, 1999). Poor snow conditions in 2002-2003 and 2003-2004 winters precluded additional surveys. We began our surveys no earlier than 24 h after snowfall and made our best attempts to cover as much of the transects in as short a time as possible. Each track observed was identified to species and its location on the transect was recorded and georeferenced as for detections from encounter-transects surveys. We also recorded all species detected visually or vocally.

Intensive plot surveys and miscellaneous detections

Each plot was intensively searched to a radius of 50 m for all animal sign (visuals, calls/songs, nests, denning, feeding, feces, prey remains); cover objects were lifted and replaced where appropriate (Crump and Scott, 1994). We searched plots once each year during the collection of vegetation data, which occurred primarily in the month August. As part of a concurrent study, we conducted encounter-transect surveys and intensive-searches around marshes and were provided with a number of detections from helicopter surveys conducted by Ducks Unlimited Ltd.

Analysis

We converted our data detections to presence and absence, given the use of several different methods to detect species presence (Magurran, 2003). We then used logistic regression (Hosmer and Lemshow, 2000) to examine the relationship of species occurrence to vegetation structure and composition. We only considered species that were detected at a minimum of 10% of the plots or stands surveyed, but not more than 90% because of the effect sample prevalence can have on model assessment and prediction accuracy (Manel et al., 2001; Liu et al., 2005; Seoane et al., 2005). For each species, we selected a subset of structural variables based on habitat associations as determined by a review of the literature (Gillingham, 2003) and examined correlations among the variable subset and species occurrence. If variables existed that were measures of the same characteristic (e.g., percent Aspen cover and deciduous stems ha^{-1}), the variable with the highest correlation coefficient with species presence was included in the candidate model. We constructed a set of candidate models using the final subset of structural variables for both plot presence and stand presence. We carefully considered variable combinations to minimize data mining (Guthery et al., 2005); one model included all the uncorrelated candidate variables (i.e., global model).

We tested *a priori* candidate models for multicollinearity among independent variables by calculated variance inflation factor scores after linear regression (Neter et al., 1985; StataCorp, 2003). We adopted a variance inflation factor of 5 or above, which corresponds with a tolerance score of 0.2 as a cut-off for variable inclusion (Menard, 2002). If multicollinearity was indicated, we reran our model using only one of the indicated problem variables and compared outcomes using a log-ratio test (Menard, 2002; StataCorp, 2003). We performed Box-Tidwell transformation of the variables to determine the relationship between the logit of predictor and response variables (Box and Tidwell, 1962; Menard, 2002). If a non-linear relationship was identified, we considered transforming the variable (arcsine or natural log) or removing the variable(s) from the candidate list. Variables were removed if there was little contribution to the model or if no interpretable transformation rectified the problem. Therefore, for each of the 55 species for which we had sufficient data, we had a set of several candidate models including different combinations of relevant structural variables that were not correlated at both stand and plot scales (Table 3.2)[1].

We ranked competing *a priori* models using Akaike's Information Criteria (AIC) with a correction to account for small sample sizes (AIC_c; Akaike, 1973; Burnham and Anderson, 2002). AIC-model selection estimates the information loss when the probability distribution with the true model is approximated by the probability distribution associated with the model that is to be evaluated. Choosing the model with the lowest expected information loss between the true model and the approximating model is asymptotically equivalent to choosing a model that has the lowest AIC value (Burnham and Anderson, 2002). We determined the Akaike weight (w_i), the likelihood of the model given the data (Burnham and Anderson, 2002), for all models within a competing set. Models were eliminated if the variables were complete subsets of the highest ranked model and there was little change in the maximized log-likelihood (Burnham and Anderson, 2002) or the area under the receiver-operating characteristic curve (ROC) value was <0.70 (i.e., poor; Manel et al., 2001; see below). We examined the model set with ΔAIC <2.0, as models within this range are considered to be equally plausible (Burnham and Anderson, 2002), to determine the best model for validation. Given our restricted criteria for use of variables in model development, we used this cut-off as a minimum limit because the AIC method ranks all models in the candidate list and will identify a "best model" even if all proposed models are

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[1] The literature review used to derive candidate models, variable lists, and full model results can be found in Appendix I (electronic).

Table 3.2. Example of the candidate model set to describe the occurrence of Red-naped Sapsucker (*Sphyrapicus nuchali*) within the Williams Lake Study Area at the plot level. Full lists of the candidate variables used for 55 vertebrate species are included in Appendix I (electronic).

Model ID	Model
1	Percent Gap, Distance to edge, Proportion shrub and Aspen (50 ha), Stumps ha^{-1}
2	Percent Gap, Distance to edge, Percent Aspen, Stumps ha^{-1}
3	Percent Gap, Distance to edge, Proportion shrub and Aspen (50 ha)
4	Distance to edge, Proportion shrub and Aspen (50 ha)
5	Distance to edge, Proportion shrub and Aspen (50 ha), Stumps ha^{-1}
6	Percent Gap, Percent Aspen, Distance to edge
7	Percent Gap, Percent Aspen, Distance to edge, Stumps ha^{-1}
8	Percent Aspen, Distance to edge, Stumps ha^{-1}
9	Distance to edge, Stumps ha^{-1}
10	Percent Gap, Distance to edge
11	Percent Gap, Distance to edge, Stumps ha^{-1}
12	Percent Aspen, Distance to edge
13	Percent Gap, Proportion shrub and Aspen (50 ha)
14	Percent Gap, Proportion shrub and Aspen (50 ha), Stumps ha^{-1}
15	Proportion shrub and Aspen (50 ha), Stumps ha^{-1}
16	Proportion shrub and Aspen (50 ha)
17	Percent Gap, Percent Aspen, Stumps ha^{-1}
18	Percent Gap, Percent Aspen
19	Percent Aspen, Stumps ha^{-1}
20	Percent Gap, Stumps ha^{-1}
21	Percent Aspen

"bad" (Guthery et al., 2005). If multiple models remained in the final model set, we considered them to be competing best models and validated each model. After the final model(s) were selected, we reviewed cases for high leverage and studentised residual values to determine if any cases were disproportionately driving the model relationship (Menard, 2002).

Model assessment

We examined two aspects of prediction accuracy, discrimination and reliability, for spatial and temporal validation. Discrimination refers to a model's capacity to correctly classify occupied and unoccupied sites, whereas reliability measures the agreement between predicted probabilities of occurrence and observed sites occupied (Pearce and Ferrier, 2000). When presence and absence data are available, calculating the area under the receiver-operating characteristic curve (ROC) is a favoured measure used to assess the discrimination ability of a logistic model (Fielding and Bell, 1997; Pearce and Ferrier, 2000). The ROC value is calculated by plotting the number of sites where presence is correctly predicted divided by the total number of positive sites (sensitivity), against the fraction of incorrect cases where presence is predicted (1 – specificity) across available thresholds (Deleo, 1993). The area under the resulting curve is an estimate of predictive accuracy not based on threshold probabilities (i.e., $p > 0.5$ designated as presence; Deleo, 1993; Fielding and Bell, 1997) or species prevalence (i.e., one outcome greatly outnumbers the other; Manel et al., 2001). A ROC value is interpreted as the percentage of time that a random selection from the positive class will have a higher predictive score than a randomly drawn case from the negative class (Deleo, 1993). ROC values of 0.5 indicate the explanatory variables do not improve discrimination beyond random assignment and 1.0 indicates perfect discrimination.

A value below 0.5 indicates the model performs more poorly with the explanatory variables than without them. We classified ROC values between 0.5 – 0.7 as low, 0.7 – 0.9 as good and >0.9 as high model prediction accuracy (Manel et al., 2001).

To determine model reliability (i.e., the agreement between predicted probabilities of occurrence and observed occurrence), we examined calibration plots (Cox, 1958; Miller et al., 1991; Pearce and Ferrier, 2000). Calibration plots are calculated by plotting the median probability for predictions, divided into 10 equal classes (x-axis), against the proportion of occupied sites within each class (y-axis; Pearce and Ferrier, 2000). The expected distribution is equivalent to a slope of 1 through the origin, where the proportion of occurrences equals the median for each class. In a reliable model, observed proportion of occupied sites equals the median predicted value and thus regression of the points results in a slope of 1 (Pearce and Ferrier, 2000) in the calibration plot. We considered models reliable, therefore, if regression slopes were not significantly different from 1.

Prediction accuracy bias

To determine whether sample prevalence, species traits, or detection uncertainty systematically affected prediction accuracy, we examined correlations between sample prevalence (%) and ROC values for all models and used ANOVA and *t*-tests to test for differences in ROC values among groups. We tested ROC values within groups for normality, as well as for homogeneity of variance. If a significant difference was indicated by ANOVA, we conducted post-hoc analysis using Tukey's HSD test (Zar, 1999).

We classified migration strategies as resident, short-distance migrants, and neotropical migrants; territory size as small (<10 ha), medium (10 – 50 ha), and large (>50 ha); and mobility as limited (terrestrial, small-bodied), moderate (terrestrial, medium- or large-bodied), and high (volant). Spatial uncertainty was classed as either <10 m from plot centre, between 10 m and 75 m, or >75 m from plot centre. This coincides with error associated with obtaining a GPS waypoint (approximately 10 m), our general vegetation measures at the plot level and stand level, as well as the largest distance category for point counts (>75 m). Species that typically call while in flight or have calls that travel long distances (e.g., Sandhill Crane, *Grus canadensis*) were given a rank of 3 (i.e., >75 m) and species primarily detected by visual detections or sign were assigned 1 (<10 m; e.g., southern Red-backed Vole, *Clethrionomys gapperi*). We classified most songbirds as a 2 because these species are primarily detected by song or calls, but do not have great audio range. Temporal uncertainty was classified as none (i.e., visual or vocal detections that are in real time) or possible (e.g., tracks or scat that can persist for extended periods). Likewise, identification uncertainty was classified as low, for species very unlikely to be misidentified, or possible, for species with tracks, calls, or appearances close to that of other species. We did not include detections of species where observers noted unconfirmed identification; therefore, identification uncertainty is a substitute for potential observer error. We used the program STATA (version 8.2; StataCorp, 2003) for all statistical analyses.

Results

Species detection

We recorded 38,389 observations for 191 species (Table 3.3) from May 2001 to the beginning of January 2004. During the summer of 2004, we recorded 9,419 observations for 148 species at temporal and spatial validation plots. Two-hundred species were observed in all years (Appendix II; annual detections by species are located in the electronic Appendix I).

Table 3.3. Number of vertebrate species, summarized by order, detected by different monitoring methods during model development phase (2001-2004) in the Williams Lake Study Area. The total number of detections are presented in brackets below the number of species. Detections by species and by year are included in Appendix I (electronic).

	Reptilia	**Amphibia**	**Aves**	**Mammalia**	**Total Species**
Species Included in Literature Review	6	6	204	64	280
Total Species Detected	2	3	155	39	200
Point Count	0	0	112 (21,424)	7 (492)	119
Remote Camera	0	0	3 (5)	10 (171)	13
Helicopter	0	0	21 (268)	2 (3)	23
Marsh Survey	1 (1)	3 (66)	89 (1,231)	13 (95)	106
Plot Survey	0	2 (27)	87 (1,974)	17 (828)	106
Mist-netting	0	0	0	5 (37)	5
Owl Playback	0	0	4 (29)	0	4

Table 3.3. Detections by taxa and method (continued).

	Reptilia	Amphibia	Aves	Mammalia	Total Species
Woodpecker Playback	0	0	31 (516)	1 (5)	32
Anabat	0	0	0	3[1] (563)	3
Track Plate	0	1 (4)	0	3[2] (324)	3
Encounter Transect	2 (4)	4 (103)	91 (1,134)	24 (5,824)	121
Small-mammal Trap	0	1 (1)	0	12 (2,668)	13

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[1] Confirmed species identification; other detections placed into echolocation frequency groups.

[2] Confirmed species identification; others grouped into *Sorex* spp. or *Microtus* spp.

Point counts yielded the highest number of individual detections and encounter transects resulted in the highest number of species detected from a variety of taxa (Table 3.3). Intensive-plot surveys and marsh surveys also resulted in detections for a large number of species from a variety of taxa. In 2002, the capture rate at each trap for Southern Red-backed Vole was much greater than any other year (2001 = 53.4%, 2002 = 87.2%, 2003 = 44.7%), possibly indicating a population high (Cheveau et al., 2004). Further, this was the only year that we trapped in plots using 8 traps per plot and conducted a second round of day-time trapping. During population peaks, dispersal to lower quality habitats is more likely because of density-dependent processes such as competition (Holt, 1987). Because our use of presence and absence data could obscure relationships with preferred structures, we did not include capture data from 2002 to model the probability of Southern Red-back Vole occurrence.

We had sufficient data to construct species-habitat models for 55 species at the plot and/or stand level, 27.5% of the species detected (Table 3.4). Ten species were not modelled because of high abundance (i.e., detected at greater than 90% of the plots; Table 3.5). Because some species could not be modelled at both the plot and stand level because of low (<10%) or high (>90%) prevalence (Liu et al., 2005; Vaughan and Ormerod, 2005), we examined 101 model sets in total. We detected 7 of 32 (21.9%) species listed as management concern (e.g., threatened status); only the Sandhill Crane was detected often enough to model.

We present an example of how we interpreted model results and then provide a summary of all models. The Red-naped Sapsucker (*Sphyrapicus nuchalis*) is associated with deciduous forests, frequently adjacent to water and other edges. We were able to validate

Table 3.4. The 55 species detected in the Williams Lake Study Area that met sample prevalence criteria (>10% and <90%) from 2001-2004, with the exception of Southern Red-backed Vole (see text for details, page 62). Prevalence is reported as a percentage of all plots (n = 228) and stands (n = 97), which were not altered by harvesting through the course of data collection, where presence was detected. Latin names are available in Appendix II.

Class	Species	Plot Prevalence %	Stand Prevalence %
Amphibia	Western Toad	13.2	37.1
Aves	Alder Flycatcher	20.6	35.1
	American Crow	9.7	24.7
	American Redstart	12.7	17.5
	American Robin	82.9	95.9
	Barred Owl	3.1	18.6
	Black-backed Woodpecker	8.8	21.7
	Black-capped Chickadee	78.5	89.7
	Brown Creeper	49.6	67.0
	Brown-headed Cowbird	32.5	47.4
	Cassin's Vireo	84.2	85.1
	Clay-colored Sparrow	7.9	17.5
	Cedar Waxwing	5.3	11.3
	Common Raven	28.1	75.3
	Common Yellowthroat	15.8	29.9
	Downy Woodpecker	10.1	26.8
	Dusky Flycatcher	27.6	51.6
	Golden-crowned Kinglet	77.6	89.7
	Gray Jay	48.3	75.3
	Hammond's Flycatcher	34.2	53.6
	Hairy Woodpecker	34.2	58.8
	Hermit Thrush	63.2	77.3
	Least Flycatcher	21.9	36.1
	Mountain Chickadee	88.6	93.4
	Northern Flicker	50.9	81.4
	Northern Waterthrush	16.7	24.7
	Northern Saw-whet Owl	0.9	13.4
	Olive-sided Flycatcher	42.5	69.1
	Orange-crowned Warbler	63.2	79.3
	Pileated Woodpecker	43.4	79.4
	Red Crossbill	33.8	57.7
	Red-naped Sapsucker	39.5	62.9
	Ruffed Grouse	32.9	66.0
	Sandhill Crane	16.2	57.7
	Song Sparrow	12.7	25.8
	Spruce Grouse	7.5	17.5
	Townsend's Solitaire	40.8	56.7
	Townsend's Warbler	18.9	29.9

Table 3.4. Species modelled and sample prevalence (continued).

Class	Species	Plot Prevalence %	Stand Prevalence %
	Tree Swallow	14.0	29.9
	Three-toed Woodpecker	9.7	22.7
	Warbling Vireo	52.6	70.1
	Wilson's Warbler	31.1	57.7
	Winter Wren	14.5	26.8
	Western Wood-Pewee	35.1	53.6
	Yellow Warbler	26.3	48.5
Mammalia	Deer Mouse	50.9	70.1
	Southern Red-backed Vole	70.2	83.3
	Yellow-pine Chipmunk	32.0	43.3
	Snowshoe Hare	68.0	77.3
	Ermine	9.7	19.6
	Long-tailed Weasel	13.6	23.7
	Moose	76.8	85.6
	Black Bear	55.3	78.3
	Coyote	22.4	49.5
	Lynx	10.1	20.6

Table 3.5. Ten species detected in the Williams Lake Study Area, from 2001-2004, that were not modelled to predict occurrence because of high prevalence at the plot and stand scale (i.e., presence was detected at >90% of plots). Latin names can be found in Appendix II.

Taxa	**Species**	**Total detections all years**
Aves	Chipping Sparrow	1650
	Dark-eyed Junco	2403
	Evening Grosbeak	1209
	Pine Siskin	863
	Red-breasted Nuthatch	1868
	Ruby-crowned Kinglet	2021
	Swainson's Thrush	1959
	Yellow-rumped Warbler	1863
Mammalia	Mule Deer	2255
	Red Squirrel	2449

models to predict presence and absence of Red-naped Sapsucker for both plot and stand data. At the plot level, percent canopy gap ($\beta = 1.251$; Table 3.6), distance to forest edge ($\beta = -0.007$; Table 3.6), and proportion shrub and Aspen landscape class in the surrounding 50 ha ($\beta = 3.413$; Table 3.6) were included in the best model. The relationship of all variables was consistent across years with the exception of percent canopy gap in 2004 ($\beta = -1.236$; Table 3.6). Predictive accuracy varied, but was good in 2002 and 2004 (ROC = 0.692 - 0.773; Table 3.6). Likewise, the predictive accuracy of this model with spatially independent data was good (ROC = 0.737; Table 3.6). The stand model for Red-naped Sapsuckers included percent Aspen ($\beta = 0.041$; Table 3.6) and edge density in the surrounding 50-ha area ($\beta = 0.012$; Table 3.6). The relationship with edge density was consistently positive, but relationship with percent Aspen varied among years. Predictive accuracy was good for the spatial validation model (ROC = 0.752; Table 3.6) and in all years except 2001 (2001 ROC = 0.659; Table 3.6). Calibration plots indicated 2001-2004 models were well calibrated, but the spatial validation models overestimated the predicted probability of occurrence (Figure 3.4).

Fifty-seven of the 101 models (56.4%) had good or excellent predictive accuracy. Stand models performed best, with 60.4% having good or better predictive accuracy (i.e., ROC ≥ 0.70) compared to 52.1% of plot models (Table 3.7). Of the 38 variables used in all plot models, the most often included were: percent canopy gap ($n = 19$), distance to edge ($n = 19$), distance to water ($n = 14$), edge density in the surrounding 50 ha ($n = 10$), deciduous stems ha^{-1} ($n = 7$), large tree basal area ($n = 6$), dead tree basal area ($n = 5$), and percent Douglas-fir ($n = 5$). Common variables within stand models included percent canopy gap ($n = 25$), distance to edge ($n = 16$), edge density in the surrounding 50 ha ($n = 12$), percent Aspen ($n = 12$), percent Douglas-fir ($n = 11$), and main canopy height ($n = 10$; Table 3.8).

Table 3.6. Example of model results to predict the occurrence of Red-naped Sapsucker (*Sphyrapicus nuchalis*) in the Williams Lake Study Area. Variables, coefficients, and receiver-operating characteristic curve (ROC) values are presented for the best plot and stand models and their temporal and spatial validation counterparts. All model results for 55 vertebrate species can be found in the electronic Appendix I.

		β-coefficient					Spatial ROC	
Model	Variable	2001-2004	2001	2002	2003	2004	2001-2004	2004
Plot	Percent canopy gap	1.251	2.096	0.456	0.558	-1.236	0.753	0.737
	Distance to forest edge	-0.007	-0.005	-0.013	-0.007	-0.011		
	Proportion Aspen and shrub (50 ha)	3.413	1.195	2.995	2.058	5.501		
	Constant	-1.398	-3.441	-1.713	-1.325	-1.232		
	ROC	0.753	0.692	0.748	0.692	0.773		
Stand	Percent Aspen	0.041	-0.037	0.080	-0.006	-0.072	0.716	0.752
	Edge density (50 ha)	0.012	0.007	0.014	0.014	0.006		
	Constant	-2.371	-2.731	-4.421	-3.188	-1.574		
	ROC	0.716	0.659	0.761	0.726	0.702		

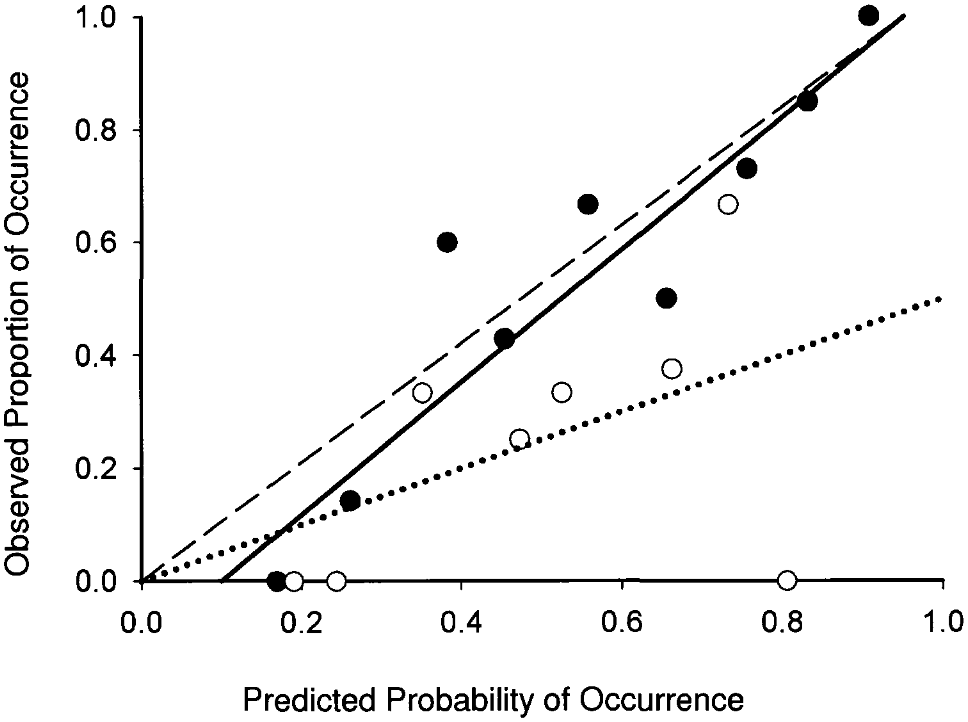

Figure 3.4. Example of a calibration plot for the Red-naped Sapsucker (*Sphyrapicus nuchalis*) plot-level model. The expected distribution of a well-calibrated model has a slope (β) of 1(---) to describe the relationship between observed proportion of occurrence and predicted probability of occurrence. The slope of the 2001-04 model was close to 1 (closed circles, —, β = 0.915, p = 0.004). The 2004 spatial validation data had a slope of less than 1 (open circles, ······, β = 0.889, p = 0.146) indicating that the model is misspecified for the spatially independent data.

Table 3.7. Summary of area under the receiver-operating characteristic curve (ROC) values for each of the 55 species detected in the Williams Lake Study Area. Each species modelled met our detection prevalence criteria from 2001-2004 at the plot and / or stand scale. ROCs are only reported for the top model with the lowest AIC_c.Not all species could be modelled at both the plot and stand scale (-).

Class	Species	Plot ROC	Stand ROC
Amphibia	Western Toad	0.749	0.733
Aves	Alder Flycatcher	0.629	0.683
	American Crow	0.589	0.611
	American Redstart	0.629	0.680
	American Robin	0.710	-
	Barred Owl	-	0.780
	Black-backed Woodpecker	-	0.542
	Black-capped Chickadee	0.850	0.681
	Brown Creeper	0.752	0.757
	Brown-headed Cowbird	0.749	0.704
	Cassin's Vireo	0.681	0.867
	Clay-colored Sparrow	-	0.637
	Cedar Waxwing	-	0.589
	Common Raven	0.617	0.550
	Common Yellowthroat	0.769	0.721
	Downy Woodpecker	0.706	0.723
	Dusky Flycatcher	0.637	0.574
	Golden-crowned Kinglet	0.776	0.792
	Gray Jay	0.674	0.804
	Hammond's Flycatcher	0.597	0.671
	Hairy Woodpecker	0.671	0.703
	Hermit Thrush	0.712	0.758
	Least Flycatcher	0.782	0.719
	Mountain Chickadee	0.712	-
	Northern Flicker	0.660	0.755
	Northern Waterthrush	0.797	0.803
	Northern Saw-whet Owl	-	0.629
	Olive-sided Flycatcher	0.734	0.863
	Orange-crowned Warbler	0.697	0.796
	Pileated Woodpecker	0.624	0.707
	Red Crossbill	0.573	0.633
	Red-naped Sapsucker	0.753	0.716
	Ruffed Grouse	0.619	0.627
	Sandhill Crane	0.673	0.714
	Song Sparrow	0.848	0.851
	Spruce Grouse	-	0.810
	Townsend's Solitaire	0.595	0.718
	Townsend's Warbler	0.786	0.759
	Tree Swallow	0.619	0.682
	Three-toed Woodpecker	-	0.733

Table 3.7. Area under the receiver-operating characteristic curve (ROC) values for species modelled (continued).

Class	Species	Plot ROC	Stand ROC
	Warbling Vireo	0.753	0.698
	Wilson's Warbler	0.648	0.610
	Winter Wren	0.714	0.787
	Western Wood-Pewee	0.791	0.683
	Yellow Warbler	0.587	0.656
Mammalia	Deer Mouse	0.660	0.686
	Southern Red-backed Vole	0.635	0.789
	Yellow-pine Chipmunk	0.733	0.701
	Snowshoe Hare	0.884	0.839
	Ermine	-	0.780
	Long-tailed Weasel	0.689	0.629
	Moose	0.675	0.738
	Black Bear	0.709	0.719
	Coyote	0.769	0.668
	Lynx	0.821	0.743

Table 3.8. Most common variables found in the top models used to predict occurrence of vertebrate species in the Williams Lake Study Area. The direction of the species' association with the variable (selection with positive coefficient or avoidance with negative coefficient) is also reported. Structure data were derived from measures taken at each plot, as determined from a GIS, or as calculated using a classified landscape image and FRAGSTATS (McGarigal and Marks, 1995).

Model level	Variable	Data Source	# Selection associations	# Avoidance associations
Plot	Percent canopy gap	Plot measures	10	9
	Distance to edge	GIS	4	15
	Distance to water	GIS	2	12
	Edge density 50 ha	Landscape	5	5
	Deciduous stems ha^{-1}	Plot measures	6	1
	Large tree basal area	Plot measures	5	1
	Dead tree basal area	Plot measures	3	2
	Percent Douglas-fir	Plot measures	5	0
Stand	Percent canopy gap	Plot measures	14	11
	Distance to edge	GIS	5	11
	Edge density 50 ha	Landscape	10	2
	Percent Aspen	Plot measures	10	2
	Percent Douglas-fir	Plot measures	11	0
	Main canopy height	Plot measures	7	3

Model validation and accuracy

We collected sufficient independent-presence data from spatial validation plots to validate 43 of the 101 models. Of these spatially validated models, predictive accuracy was good or excellent for 12 plot and 12 stand models (55.8% in total). We temporally validated 44 models with independent data; predictive accuracy was good or excellent for 12 plot and 13 stand models (56.8%). On average, predictive accuracy declined in temporally and spatially validated models compared to the accuracy of predictions for the years from which data were collected (Table 3.9). Generally, predictive accuracy was slightly better for temporal data.

Our assessment of model reliability with data used to construct the model, indicated that 60% of plot and 84.6% of stand models were well calibrated (i.e., plotting the predicted probabilities and proportion of occurrence resulted in a slope close to 1). Model reliability was poor, however, when assessed with spatially and temporally independent data. Only 21.1% of plot level and 3.4% of stand level models had slopes of 1 with spatial validation data (Table 3.10; e.g., Figure 3.4). Results were slightly better for temporal validation models where 21.1% of plot and 32.1% of stand models had slopes of 1 (Table 3.10).

Detection uncertainty and species traits

Prevalence in 2001-2004 was not related to ROC values at the plot ($n = 48$, $r = 0.088$, $p = 0.553$) or stand ($n = 53$, $r = 0.131$, $p = 0.117$) level; however, there was a weak negative correlation between sample prevalence and spatial ($n = 43$, $r = -0.319$ $p = 0.007$) and temporal ($n = 44$, $r = -0.385$, $p = 0.018$) ROC values in 2004 models.

Table 3.9. Summary of prediction accuracy (ROC values) for plot and stand models, and their spatial and temporal validation results. Models were constructed to predict the occurrence of vertebrate species in the Williams Lake Study Area. Not all models could be spatially and / or temporally validated because of insufficient detections in the new plots or for a particular year. The mean difference in prediction accuracy between 2001-2004 models and the 2004 spatial and temporal validation model was negative for each model set.

	2001-2004				Spatial Validation			Temporal Validation		
			ROC ≥ 0.70		ROC		Difference	ROC		Difference
Model level	*n*	Mean (SE)	*n*	Mean (SE)	*n*	Mean (SE)	Mean (SE)	*n*	Mean (SE)	Mean (SE)
Plot	48	0.704 (0.011)	25	0.764 (0.010)	19	0.730 (0.022)	-0.0006 (0.026)	19	0.748 (0.028)	-0.006 (0.024)
Stand	53	0.712 (0.010)	32	0.758 (0.008)	23	0.698 (0.024)	-0.051 (0.025)	25	0.726 (0.024)	-0.023 (0.026)

Table 3.10. Summary of the calibration plot regression slopes for stand and plot models (e.g., Fig. 3.4) constructed to predict species occurrences in the Williams Lake Study Area, and their spatially and temporally validated counterparts. Regression slopes describe the observed proportion of occupied sites versus predicted probability of occurrence for vertebrate species. Percentage of slopes that were non-significant, near 1 (significant), and significantly different from 1 are reported. Those models with slopes near 1 can be deemed well calibrated and, therefore, reliable.

	Plot Models			**Stand Models**		
Slope	2001-2004	Spatial Validation	Temporal Validation	2001-2004	Spatial Validation	Temporal Validation
	$n = 48$	$n = 19$	$n = 19$	$n = 53$	$n = 23$	$n = 25$
No Slope	31.6	68.4	68.4	28.1	93.2	64.3
Slope = 1	57.9	21.1	21.1	34.4	3.4	32.1
Slope ≠ 1	10.5	10.5	10.5	37.5	3.4	3.6

Prediction accuracy was not related to identification or temporal uncertainty for any model level; however, the spatial uncertainty of detections did significantly affect ROC values of plot models ($F_{(2,45)} = 3.75$, $p = 0.031$), but not stand models ($F_{(2,50)} = 2.58$, $p = 0.086$). Post-hoc analysis using Tukey's HSD test of significance indicated that the difference was between detections >75 m from plot centre ($\bar{x} = 0.655$, $SE = 0.017$) and those between 10 and <75 m ($\bar{x} = 0.717$, $SE = 0.014$, $p = 0.043$). There was no relationship between prediction accuracy of 2001-2004 models and migration strategy, territory size, or mobility (Table 3.11).

Discussion

Structure as a surrogate measure

Use of habitat measures, such as forest structure, to model species occurrence, abundance, or population dynamics is a fundamental aspect of both theoretical and applied ecological science. It is well accepted that habitat heterogeneity (e.g., MacArthur and MacArthur, 1961) and certain forest elements (e.g., coarse-woody debris, snags, large trees) are associated with species diversity (Mazurek and Zielinski, 2004; Loehle et al., 2005). Measuring aspects of environmental diversity, such as structural complexity, has become preferred as a surrogate measure of diversity over species-based surrogates (Margules et al., 2002; Faith et al., 2004), and is particularly appealing to forest-land managers because of the ease of incorporating measures into forest inventory databases (McElhinny et al., 2005) relative to separate monitoring programs for species. Structural diversity has been shown to correlate with diversity of several taxa (e.g., mammals, Mac Nally et al., 2001; amphibians and reptiles, Loehle et al., 2005; spiders, Oxbrough et al., 2005). To be effective as a

Table 3.11. Summary of ANOVA results to test if species' traits affected the accuracy of predictions (ROC values) for the occurrence of vertebrate species. ROC values were used from models constructed with data collected in the Williams Lake Study Area from 2001-2004.

	Plot				**Stand**			
Grouping	*n*	Mean (*SE*)	*F*	*p*	*n*	Mean (*SE*)	*F*	*p*
Migration Strategy								
Resident	23	0.708 (0.016)	0.14	0.874	27	0.708 (0.015)	0.20	0.819
Short-distance migrant	13	0.694 (0.019)			13	0.724 (0.020)		
Neotropical migrant	12	0.705 (0.026)			13	0.711 (0.019)		
Territory size								
Small (<10 ha)	30	0.711 (0.014)	0.46	0.633	13	0.720 (0.012)	0.39	0.679
Medium (10 – 50 ha)	12	0.686 (0.024)			16	0.703 (0.021)		
Large (>50 ha)	6	0.703 (0.033)			7	0.701 (0.028)		
Mobility								
Limited mobility	6	0.698 (0.040)	0.49	0.613	6	0.707 (0.012)	0.38	0.685
Moderately mobile	5	0.733 (0.027)			7	0.727 (0.024)		
Highly mobile	37	0.713 (0.012)			40	0.729 (0.031)		

surrogate measure of species occurrence, however, models that use forest structural characteristics must have a strong relationship with the probability of species occurrence across the range of the model's intended use (Rykiel, 1996; Lindenmayer, 1999). The discrimination accuracy and reliability of most of the models we developed were not satisfactory and, therefore, we conclude that forest structural characteristics, by themselves, are not effective as surrogate measures for predicting the occurrence of a broad range of vertebrate species or to guide management targets for structural retention or recruitment at the scales we tested.

Of those species modelled ($n = 55$) only 52% of plot and 60% of stand models had acceptable prediction accuracy (i.e., ROC $\geq$0.70; Table 3.9). Because we were specifically looking for relationships with structural elements, misspecification of the models (Burnham and Anderson, 2002) may explain the overall poor performance. Because the goal of our study was to examine the possible use of structure as a surrogate measure, the selection of habitat variables was narrow by necessity. Most of the species we modelled, however, are found across broad ranges (e.g., continental) and thus likely have broad niche breadths indicating flexibility in habitat selection and less dependence on specific habitat elements. For several of the species that we modelled, however, discrimination (Table 3.4) and reliability were relatively high. For those species, structure may act as a useful surrogate, but as a part of a complementary program to ensure monitoring of a broad range of taxa (Lindenmayer and Franklin, 2002).

Variables, scale and spatial context

The complexity among species associations with structure, the scale and spatial relationship with structure, and the landscape context make generalisations of models and structural variables difficult. The variables most often included in plot models (i.e., distance to water, large tree basal area, and dead tree basal area; Table 3.8) were included less often in stand models suggesting that the influence of these structures on species presence is localized. Forested areas near riparian zones offer a unique set of characteristics and these habitats are often diverse (Naiman and Décamps, 1997). Likewise, the influence of single large trees and dead trees can influence diversity at a relatively small scale (Mazurek and Zielinski, 2004). For example, nesting habitat for weak cavity excavators that require trees in specific stages of decay to excavate their nest site (e.g., Red-breasted Nuthatch, *Sitta canadensis*), or secondary cavity users that inhabit abandoned cavities may be quite flexible in the selection of foraging habitats. The availability of a single nest tree represents a requirement that is on a much smaller spatial scale than foraging; therefore, the availability of a single nest site may influence species presence at the plot level, but not the larger spatial scale of the stand where foraging may take place.

As was the case in the example for the Red-naped Sapsucker, many of the plot and stand models included variables related to the spatial relationship of the plot or stand (e.g., distance to edge or water) or aspects of the surrounding landscape (e.g., edge density and percentage forest composition; Table 3.8) indicating that landscape structure and composition influenced species presence (e.g., Saab, 1999; Hagen and Meehan, 2002). Distance to edge and edge density, although related, are not exactly the same variable. Distance to edge was measured to the closest forest / non-forest boundary. Non-forest may have been a road, clearcut, meadow, or water body. Edge density was a measure of all contrasting landscape class boundaries within a defined area (usually 50 ha), and thus includes less distinct edges such as the contrast between unharvested-conifer forest and partially-harvested forest. Because different species likely perceive edges and edge contrasts differently, it is difficult to make a generalized statement of how to treat these 2 variables; however, because harvesting practices contribute to fragmentation of habitats, species that avoid edges are most likely detected in areas with low edge density (i.e., continuous landscape classes). Therefore, species that are sensitive to (avoid) edge or edge density may require specific management planning to ensure continuous areas of forest. If structure is to be used as a surrogate, spatial context and scale should be included in forest-inventory databases, which is not typically done at present.

We found that canopy closure and some measure of deciduous forest cover were commonly included in both plot and stand models (Table 3.8). There was a fairly even split among species associated with open-canopy forests and closed-canopy forests. Canopy closure is an easily obtained structural variable, from ground surveys and photo interpretation. Because harvesting activities consistently open canopies, identifying species with negative association with open canopies, and determining if there are thresholds to occupancy, could provide forest managers with a useful target for stands across the landscape. In landscapes dominated by coniferous-forest cover, deciduous stands and mixed-woods can be areas of high diversity (Stelfox, 1995). Other research has documented the importance of deciduous species to cavity nesting birds (Martin and Eadie, 1999) in the region and this research reinforces the importance of deciduous stands, specifically Aspen, to a host of species.

Validation

More problematic than the difficulty in drawing general recommendations linking specific structural characteristics to a broad array of species was that prediction accuracy remained good or better for only 58% of the models when temporally and spatially validated

(Table 3.9). If models that predicted species presence well (i.e., ROC ≥ 0.70) are used to meet diversity-monitoring objectives, the relationships to structure must be robust with good or better prediction accuracy across spatial and temporal scales (Rykiel, 1996). Stand-level models performed slightly better than plot models with the data used to develop models; however, for models that were externally validated, plot models were more likely to retain higher predictive accuracy. Overall, stand-level modelling is probably more appropriate for a broader range of species because of the confounding effects of small-scale variation in structure and spatial uncertainty for detections at the plot level.

When model reliability was assessed with calibration plots, temporal validation models performed better than the spatial validation plots, emphasizing that caution is required if models are to be applied outside the geographic area in which they were developed. Declines in prediction accuracy for temporal validation may be a result of year-to-year variance in prevalence and a higher probability of false negative detection during one year of data collection (Manel et al., 2001; Tyre et al., 2003; Gu and Swihart, 2004; McPherson et al., 2004). Further, a species' relationship to habitat can fluctuate through time because of various aspects of population dynamics and density (Wiens, 1989; Haila et al., 1996; Green and Stamps, 2001).

Prediction errors may also arise from data collection error and other statistical artefacts, species interactions, regional variability in habitat, and intraspecific variability (Fielding and Haworth, 1995; Fielding and Bell, 1997; McPherson et al., 2004). Because we used the same sampling methodologies throughout the course of the study and assessed accuracy using area under the ROC curve, statistical artefacts were likely minimized (McPherson et al. 2004). Further, there was no correlation between ROC values and prevalence within the set minimum (>10%) and maximum (<90%), with the exception of 2004 ROC values, suggesting that this criteria was sufficient. The negative correlation between species prevalence and ROC values in 2004 was unexpected, because prevalence usually has a positive relationship with predictive accuracy (Manel et al., 2001; Seoane et al., 2005). Species that were less common in the SBPS biogeoclimatic zone, however, may have been more selective for habitats similar to those sampled in the IDF (i.e., narrower habitat breadth) resulting in better ROC values. Conversely, species that were common in the SBPS may have broader niche breadths and thus did not respond to basic differences in structure between the 2 zones, reducing predictive accuracy. This result was also supported by the reduced reliability of spatially validated models (i.e., slope <1.0). Slope departed from the expected 45° pattern for most calibration plots when applied to independent data; therefore, it is likely that the species we modelled respond to different structural elements in the IDF and SBPS, or that structural characteristics of forests alone are not the best predictors of species presence across this range of conditions. Presence for some species may, therefore, be related more to other factors such as population legacies, stand history, or species interactions and not characteristics of the habitat structure (Fielding and Haworth, 1995; Tyre et al., 2001).

Species traits, such as environmental specialization, regional distribution, detectability, and body size have been linked to prediction errors in other studies (Karl et al., 2000; Scott et al., 2002; McPherson et al., 2004; Seoane et al., 2005); however, we did not find any differences among migratory strategy, territory size, or mobility and predictive accuracy. Our results may contradict other studies because of the spatial extent of our study area and the general characteristics of species modelled (Karl et al., 2000). Although we established our plots and sampled across a range of variation in structural features, on a regional scale we sampled a narrow range of environmental conditions. The species that were modelled were those that met our prevalence criteria (>10% or <90%) and, therefore, inherently may not be representative of the full range of biological traits, especially those associated with rarity (Kunin and Gaston, 1993; Gaston and Blackburn, 1996; Davis et al., 2000). Only spatial uncertainty at the plot level systematically affected ROC values, which likely reflects error associated with the measures of structural characteristics and the actual location of the individual.

Van Horne (2002) argued against validation of species-habitat models because specific models can only make predictions for specific populations at specific times and, therefore, species presence cannot be tested with new data. Although results support Van Horne's supposition, as most models had reduced discrimination and reliability when validated, this premise is also potentially dangerous. Non-validated species-structure models may be tenuously implemented at best, although structure performed poorly at predicting the occurrence of species, even with data used to develop models. Likewise, others have cautioned strongly against the dependence on species-habitat models in general because they can only be considered correlative and do not indicate causal mechanisms or processes (Morrison, 2001; Mitchell, 2005). Species-habitat models are implemented effectively as management tools, however, in a variety of ways including habitat suitability models and resource selection functions. The weakness of such approaches is that it is simply not possible to measure the life-history aspects or conduct intensive studies for all species. Forest structure may be a suitable surrogate if used only to make general guideline recommendations and not species-specific targets, more in line with a coarse-filter approach

(Simberloff, 1999; Lindenmayer and Franklin, 2002) and not as a monitoring tool of species occurrence.

Multi-species inventory

Conducting a multi-taxa inventory contributes to baseline occurrence data for future monitoring inventories, identifies species for which methodologies are not sufficient to detect presence, identifies species that may be of management concern and helps to form specific management goals as they relate to biodiversity objectives (Manley et al., 2004). By compiling detections for species from a variety of methods, species that may be under-represented in samples of a single approach because of methodological biases may be reduced. Point counts, encounter transects, and intensive-plot searches all achieved high numbers of species detections. As expected, the greatest diversity of vertebrate species in our study area was represented by birds, and point counts resulted in a high proportion of species and observations. Encounter-transect surveys were effective in that we detected a breadth of species from a variety of taxa. Overall, the multi-taxa inventory was successful in that we detected a high proportion of the species expected to occur (71.4%).

Amphibians and reptiles had very low rates of detection (Table 3.3). We targeted amphibians and reptiles by lifting potential cover objects during time-constrained searches, encounter-transects surveys, and intensive-plot searches (Heyer et al., 1994). We opted not to place artificial cover boards or arrays of drift fences and pitfall traps because we did not want to alter the interpretation of structural aspects of stands artificially or potentially influence non-target species (e.g., attraction or avoidance). Given that our encounter rates were so low, however, we do not recommend our methods for successful monitoring of species from these taxa. Because most amphibians and reptiles have reasonably limited mobility, however, if the objective was purely for monitoring purposes, using artificial structure would not affect interpretations regarding species presence of amphibians specifically.

Our method of measuring bat activity was also not satisfactory because calls could only be categorized into species groups (Table 3.1) and, therefore, we could not construct single-species models. Bats are difficult species to monitor because they are volant, nocturnal, and echolocate (Kunz, 1988), but often represent a large portion of mammalian-species richness (up to 22% in our study area) and thus are an important component of vertebrate diversity. Activity levels and echolocation groups, however, could be monitored and modelled and whether or not that was sufficient would depend on the objectives of the study (e.g., Baxter et al. *in press*). Further research is needed to identify the habitat requirements for individual bat species using different methods (e.g., telemetry study) until methods to identify species by call are refined.

Other than black bear (*Ursus americanus*), an omnivore, we detected few mammalian or avian predators. Although predatory species tend to have large home ranges with naturally lower densities and, therefore, are expected to be detected less frequently (Tyre et al., 2003; MacKenzie, 2005), there is growing evidence of the role that predators play in increasing diversity (Soulé and Terborgh, 1999; Shurin and Allen, 2001; Hebblewhite et al., 2005; Sergio et al., 2005). Our study area was a heavily managed, multi-use landscape (i.e., industrial forestry, cattle grazing, hunting and recreation uses) and has high road density, which affects the distribution of several predators that may have been more abundant historically (e.g., Grizzly Bear, *Ursus arctos*; Grey Wolf, *Canis lupus*). Overall, the species community present in the Williams Lake Study Area may not be representative of the full range of goals for a program with the objective of conserving biodiversity, and therefore, restoration activities may need to be considered as part of a comprehensive biodiversity program.

Species of management concern, either because of sensitivity to disturbance, limited distribution, or rarity, were not well represented in our sample. This result was not unexpected (Margules and Pressey, 2000; Noon et al., 2003), but it does highlight a weakness of the general approach of targeting a breadth of species (Manley et al., 2004). More intensive survey methodologies are required to determine the presence and absence of rare or cryptic species to assess predictive accuracy of structural models. Many of the rare species and species of concern should be included in fine-filter management approaches (Hansen et al., 1999; Hunter, 2001). Therefore, not detecting them in a broad survey should not necessarily be a criticism, but the approach cannot be assumed to encompass these species.

Conclusion

In an industrial forest landscape, where structural aspects are changing frequently, land managers require an understanding of how species will respond and persist within the dynamics of the changing forest environment so that strategies can be implemented to retain and recruit structural aspects necessary for the persistence of populations. Some of the models that we tested had good predictive accuracy that was retained when validated and thus have application in terms of implementation as management tools (e.g., Red-naped Sapsucker). However, because structure did not predict the presence of the majority of vertebrate species, there was not a single set of forest structure measures that predicted several species. Because we did not find robust relationships that are necessary to guide management targets for retention and recruitment of specific structures, using these models as surrogates for species occurrence is limited. Models based on stand structural requirements meant to meet specific targets will need further examination and testing (e.g., volume, coarse-woody debris, snag density, etc.). Given the variability in species' responses, it may be most efficient to study the response of species that appear most closely linked to structure and sensitive to the loss of specific attributes.

In our results, modelling success varied depending on whether plot or stand data were used and many models included variables related to spatial relationships of structures suggesting that relationships with structure are complex across species and scales. Other surrogate approaches have had varying success, but are generally poor predictors of diversity at stand scales (McElhinny et al., 2005). We did not examine the relationship between vertebrate richness and structure, but given the complexity of relationships with scale and the different scales that species use across landscapes, this will be an important research question to pursue before surrogate measures are adopted with confidence. In the interim, because the preservation of structures known to be negatively affected by harvesting (e.g., dead wood, large trees, closed canopies, continuous forests) contributes to local and landscape heterogeneity and has been shown to affect species presence in this study and others (Lindenmayer et al., 2000; Mazurek and Zielinski, 2004; Hunter, 2005), insuring that these structures are present on the landscape should still be a part of programs that have goals of maintaining biodiversity.

There is an abundance of literature on recommendations for the validation of ecological models (e.g., Rykiel, 1996; Pearce and Ferrier, 2000; Boyce et al., 2002; Vaughan and Ormerod, 2005), and a pervasiveness of the use of predictive models to describe the relationships of species to their environments (see review Guisan and Zimmerman, 2000); however, models are frequently accepted without full validation of the predictive performance (Guthery et al., 2005). Few models in our study were reliable when applied to the independent data; therefore, our results indicate that models cannot be assumed to be applicable in different years or applied outside the area where the model was developed, even when the spatial and temporal context is relatively close. Until models provide confident predictions of multiple-species occurrence, as well as response to habitat alteration, land managers may find that monitoring species directly is a more beneficial contribution to biodiversity monitoring (e.g., Manley et al., 2004).

Chapter 4. Using forest structure to predict the occurrence of vertebrate assemblages[1]

Abstract

Land-use practices can have significant impacts on biodiversity. In industrial forests, efficiently measuring, monitoring, and mitigating impacts on biodiversity are major challenges for forest managers. Several studies have reported on the relationship between characteristics of forest structure and the occurrence of single species or taxonomic groups such as birds. Few studies, however, have examined the relationship between forest structure and species occurrence across taxonomic groups. If linkages between forest structure and multiple species can be made, forest structure may be used as a surrogate measure to monitor the potential effects of management on species occurrence. In this paper, we examined whether or not species, from different taxonomic groups, could reliably be grouped together based on their co-occurrence in space and time using non-metric multidimensional scaling and cluster analysis. We determined species presence and absence at 225 plots over a 3-year period (2001-2004). We used presence and absence records and structural characteristics of forests to group similar plots. Using groupings based on species co-occurrence, we used classification and regression tree analysis to determine if structural characteristics of forests could be used to predict occurrence of group members. Plots could be statistically defined using both characteristics of forest structure and species co-occurrence. There was high variation within groups, however, suggesting the ecological significance of groupings was weak. Although there were correlations among species groups and forest structure, prediction of group membership using structural characteristics was poor (45.8%). The structure

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[1] This chapter is written in the first person plural to recognize the contribution of others to the work. The manuscript will be submitted with the authorship Psyllakis, J.M. and M.P. Gillingham.

variables identified with correlation analyses were also included in models used to predict group memberships. These variables included distance to water and edges and characteristics of larger scale surroundings (e.g., edge density). Overall, our results suggest that forest structure by itself is a poor surrogate of species co-occurrence and that the spatial aspects of structure were important determinants of species occurrence.

Introduction

Scientists find it difficult to quantify and monitor the effects of various activities that alter habitat on biodiversity largely because of difficulties in measuring biodiversity (Purvis and Hector, 2000; Sarkar and Margules, 2002). Because it is not feasible to measure all aspects of biodiversity, or even some aspects (e.g., species richness), surrogate measures are often used as alternatives to describe and monitor biodiversity (Noss, 1990; Sarkar and Margules, 2002). The use of surrogate approaches is critical to biodiversity planning and conservation across spatial and temporal scales, because information for complete species inventories over all areas is not available (Margules and Pressey, 2000; Faith, 2003). For example, the occurrence of certain indicator species (e.g., Mac Nally and Fleishman, 2004) and areas with high environmental heterogeneity (e.g., Faith et al., 2004) are correlated with increased species richness. Using environmental heterogeneity is often less expensive to measure, monitor, and forecast change for than measuring species or a subset of species directly. Further, information regarding habitat types can be obtained over large areas with the aid of remote-sensing technology. Therefore, as a substitute for measuring species richness, using indicator species or environmental heterogeneity as a surrogate for species richness has frequently been applied to various management purposes, such as the designation of reserves (Myers et al., 2000; Fleishman et al., 2005).

Species-based surrogates have been criticised because robust relationships have not been identified consistently (Caro and O'Doherty, 1999; Margules et al., 2002). Surrogates of environmental heterogeneity have been criticised because of unclear relationships among species and habitat, as well as a lack of representation for species interactions (e.g., competition or prey availability). Testing of both species-based and habitat-based approaches remains to be done to confirm that relationships are stable through time (Lindenmayer and Franklin, 2002). The lack of reliable approaches, however, does not absolve land managers from minimising impacts to diversity and many levels of government have pledged to implement programs specifically to mitigate the effects of human activities on biodiversity loss (e.g., United Nations Environment Programme, 1992; Province of British Columbia, 1995; Montreal Process Working Group, 1999; Canadian Council of Forest Ministers, 2003).

Habitat-based approaches are appealing in an industrial forests context, where many stand-structure characteristics are already measured, monitored, and managed. There is considerable interest from forest managers to link structural characteristics to species occurrence and / or richness (Lindenmayer and Franklin, 2002; Kavanagh and Stanton, 2005; McElhinny et al., 2005). Because forest-management activities directly alter structural characteristics of forests, there are several advantages to developing surrogate monitoring programs around forest structure. Structure is an aspect of habitat that managers have some control over and various forms of vegetation databases are maintained for harvest forecasting, standardized techniques exist for the measurement of structural characteristics, and characteristics are described at the same spatial and temporal scales as management. Therefore, using forest structure as a surrogate for species richness or species occurrence may be a cost-effective and efficient alternative to species-monitoring programs (Lahde et al.

1999; Lindenmayer and Franklin, 2002; McElhinny et al., 2005). Overall, a successful monitoring program could contribute to sustainable management of forest resources by ensuring the conservation of species diversity through time. To accomplish this goal, however, requires strong relationships among structure and species occurrence and the testing of these relationships across spatial and temporal scales (Lindenmayer and Franklin, 2002; Fleishman et al., 2005).

Using forest-structure variables to predict species richness has shown promise in different forest types (e.g., Eastern US, Loehle et al. 2005; South America, Diaz et al., 2005). Other studies report that models using a combination of forest management and physical properties of stands (e.g., elevation, aspect) and scale variables are better predictors of species richness than structure type measurements alone (e.g., du Bus de Warnaffe and Dufrêne, 2004). Regardless, species richness alone does not provide detailed information for species representation across taxa or different taxonomic groups (Magurran, 2003; Schulze et al., 2004), therefore grouping species based on some defined aspects may provide better inference to the effects of management activities. Species may be grouped based on: functional groups (e.g., Cummins, 1974); environmental responses or trophic criteria (Gaines et al., 1989); the shared use of specific resources (e.g., guilds, Root, 1967); or co-occurrence in space and time (e.g., species assemblages, Kavanagh and Stanton, 2005). These terminologies are often used interchangeably, although there are distinct differences and several authors have attempted to clearly define the terms (e.g., Fauth et al., 1996; Blondel, 2003). Groups based on species assemblages may be a preferred approach because no assumptions are made regarding the role a species plays in the ecosystem or specific types of interactions with other species, which are often unknown.

Multiple-species approaches require multivariate techniques to first determine the relationship among species co-occurrence and then predictive models can be used to determine if there are variables that accurately predict the occurrence of groups or group members. Applying multivariate statistical techniques to relate species groups based on their co-occurrence have been widely used in community ecology (Jongman et al., 1995; McCune and Grace, 2002). There are several challenges to defining meaningful groups, including a lack of statistically objective ways to define group boundaries. There remains debate whether or not it is ecologically feasible to distinguish distinct groups versus continuums of occurrence with overlap (Blondel, 2003). Therefore, it is advisable to use complementary techniques to define groups and follow up with separate techniques to test the statistical significance of groupings (McCune and Grace, 2002). This approach still requires that ecological interpretations are made cautiously as statistical and biological significance are not always one and the same (McCune and Mefford, 1999).

Linking variables directly affected by forest-management activities, specifically measures of forest structure, to the occurrence of species assemblages may provide forest managers with a useful tool to monitor, manage, and mitigate the effects of industrial harvest on species diversity. Determining relationships among species may account for some unexplained variation when examining structural variables and, therefore, account for biological influences on species distributions. In this paper, we used presence and absence data collected during intensive species inventories (Chapter 3) to determine if: 1) forest plots could be reliably grouped based on vertebrate-species assemblages (i.e., based on co-occurrence in space and time) as well as on structural characteristics of the vegetation; 2) species-based and structure-based groupings were correlated with one another; and 3) forest-structure characteristics could be used to predict group membership based on vertebrate-species assemblages. We specifically tested the hypothesis that forest structure can reliably predict the occurrence of vertebrate-species assemblages and, therefore, has the potential to be used as a surrogate measure to implement forest management targets and to monitor species distributions within an operational forest landscape.

Methods

Study area

We collected data from May 2001 through January 2004. Our study area, in central British Columbia, Canada was located approximately 30 km south of the community of Williams Lake, hereafter the Williams Lake Study Area (Figure 4.1). Land uses included industrial forestry, free-range cattle ranching, and a broad diversity of all-season recreation (e.g., hunting, snowmobile touring). The Williams Lake Study Area, at the northern extent of the Interior Douglas-Fir (IDF) Biogeoclimatic zone (Meidinger and Pojar, 1991), was characterised by stands of closed- and open-canopy Douglas-fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*) at higher elevations (e.g., >1000 m above sea level). At lower elevations (~ 850 m – 1000 m above sea level) forests were intermixed with grassland and wetland communities. There were localised stands of hybrid White Spruce (*Picea engelmannii* x *glauca*) and Trembling Aspen (*Populus tremuloides*) throughout the study area. Harvesting activities in stands dominated by Douglas-fir were characterized by multiple-pass selective harvests; where other species were dominant, clear-cuts were more frequent. A major insect outbreak (mountain pine beetle; *Dendroctonus ponderosae*) influenced stands across the study area. Mean annual temperature is 4.2°C (range = -1.3 to 9.6 °C; Environment Canada, 2002).

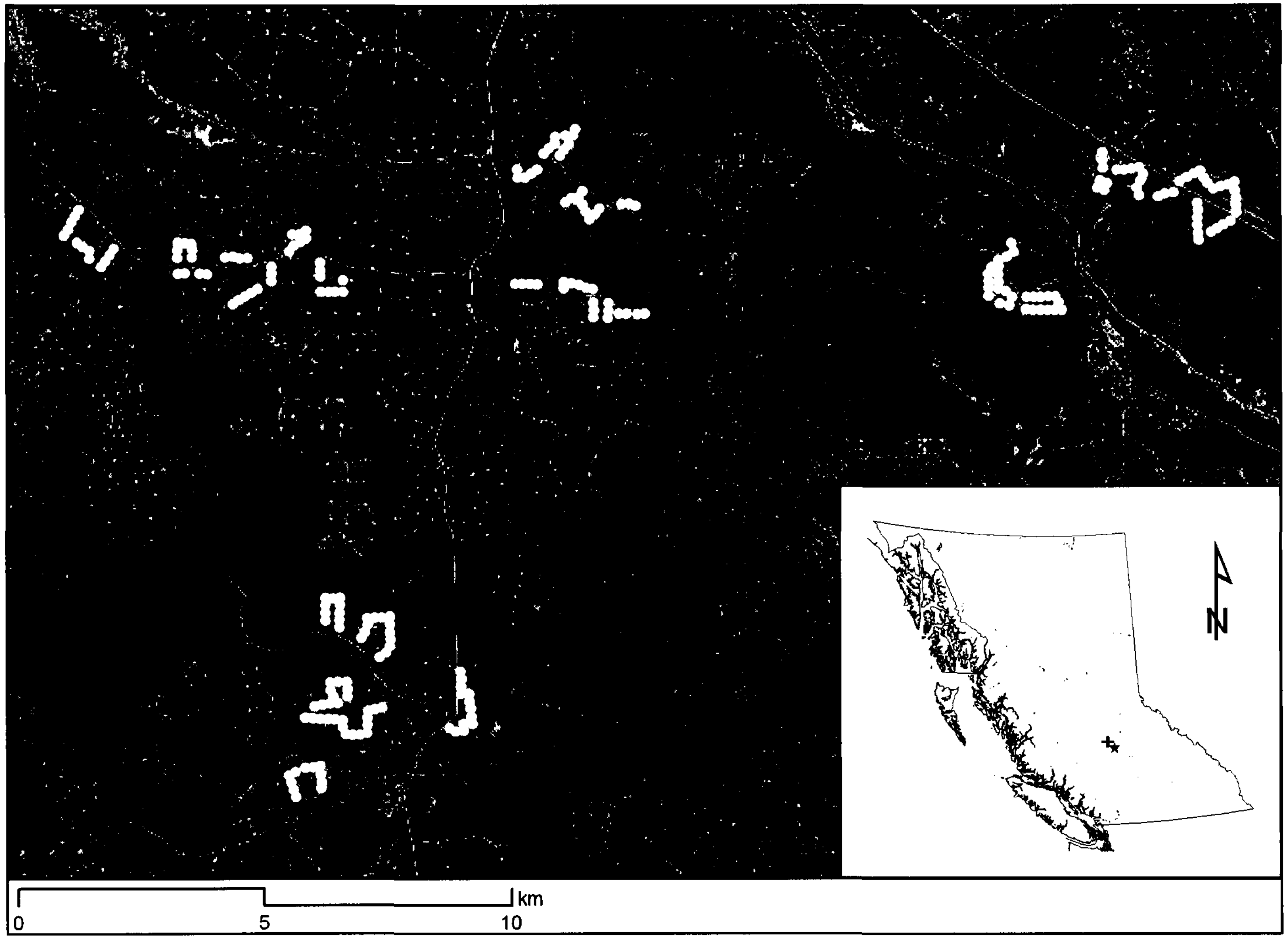

Figure 4.1. Plot (○) layout in the Williams Lake Study Area (★; inset) approximately 30 km south of Williams Lake, British Columbia (+; inset). Each plot was connected by a 150- or 300-m transect.

Habitat measurements

We established 243 plots spaced systematically 150 m or 300 m apart along transects and measured local habitat variables using a combination of methods. Shrub species and cover, canopy gaps, and coarse-woody debris were measured along the intercept of 2, 48-m transects laid perpendicular through plot centre. For coarse-woody debris, we recorded the diameter of the piece perpendicular to where it crossed the axis, the tree species (if possible), and decay class (Maser et al., 1979). At 5, 2-m radius plots located at 11.28 m away from plot centre on each axis and at plot centre, we measured the percent coverage for litter, coarse-woody debris, herb species, moss and lichens, shrub species, sapling species, bare ground, and rock. Within a 5.64-m radius around plot centre we tallied all trees and stumps ≥7.5 cm diameter at breast height (dbh) and recorded tree species, dbh, and height; we recorded trees <7.5 cm dbh as live or dead saplings. We extended the radius to 11.28 m and tallied any additional trees ≥30 cm dbh and snags. We recorded general information for each plot including aspect, slope, canopy stratification and complexity, disturbance history (evidence of fire, grazing, logging), and the elevation (in m) above sea level. We averaged vegetation data collected at multiple plots measured within stands, as defined by forest inventory polygons, to create stand level variables.

To obtain spatial measures (e.g., distance to water), proportion of cover, and landscape metrics, we subsetted a Landsat 7 (30-m resolution) image of the study area (July 2002) and used PCI Works GIS software (version 7.0; PCI Geomatics Corp., 2001) to complete a supervised maximum-likelihood classification. Six habitat classes were identified: water, nonforest, early seral, shrub and Aspen, moderate retention conifer, and conifer. We used colour airphotos, orthophotos, and the vegetation data collected at plots to seed areas for training and to assess the accuracy of the classification. We assessed accuracy of the classification by determining the number of correctly classified pixels from a randomly selected subset. Water, nonforest, and conifer classes had the highest accuracy (97%, 94%, and 88%, respectively). Early seral, shrub and Aspen, and moderate retention conifer were less often classified correctly (67%, 78%, 67%, respectively). Overall classification accuracy was 81%.

We calculated landscape metrics using the Patch Analyst 3.1 (Grid) extension (Rempel and Carr, 2003) for ArcView GIS (version 3.2a; ESRI, 2000) to interface to the PC raster version of FRAGSTATS 2 (McGarigal and Marks, 1995). We intersected the classification layer with a buffer created around plot and stand centres and measured characteristics in the surrounding 50 ha and 300 ha. Distance from plot centres to water and high-contrast edge (e.g., meadow-forest), and roads were estimated using the GIS. For a full description of methods and plot layout, see Chapter 3.

Vertebrate sampling

We used a variety of techniques to determine the presence of vertebrate species (Table 4.1; see Chapter 3 for a full description of vertebrate sampling methods). We georeferenced all vertebrate observations and imported them into a GIS (ESRI, 2000). Observations >75 m from a plot centre were excluded to reduce possible effects of spatial uncertainty on structure association (see Chapter 3).

Because of the variety of methods used to collect species-occurrence data, we converted species detections to presence and absence for each plot (Magurran, 2003). We deleted species detected at fewer than 5% of the plots, to maximize the detection of patterns of structure, if present (McCune and Grace, 2002). Species that had high spatial uncertainty

Table 4.1. Methods used to detect species presence in the Williams Lake Study Area and the time of year surveys were conducted from 2001-2004.

Target species	Method	Timing	References
Song Birds	Variable-radius point counts	3 surveys at each plot (mid-May – early July)	Reynolds et al., 1980; Ralph et al., 1995; Robbins, 1981
Woodpeckers	Call playback	3 surveys at each plot (mid-May – mid-June)	Johnson et al., 1981
Owls	Call playback	Late April – early May; Winter opportunistically	Fuller and Mosher, 1981
Small Mammals	Live trapping; Track plates	July - August	Jones et al., 1996; Province of British Columbia, 1998
Bats	Bat detectors	July August	Hayes, 1997; O'Farrell and Gannon, 1999
Birds and mammals	Winter tracking	November - February	Beauvais and Buskirk, 1999
Medium - large vertebrates	Remote cameras	May – August	Zielinski and Kucera, 1995
All vertebrate taxa	Intensive searches	July - August	Crump and Scott, 1994; Wilson et al., 1996
All vertebrate taxa	Encounter transects and Time-constrained searches	May – August	Scott, 1994; Wilson et al., 1996

associated with their detection were also deleted ($n = 5$), either because of their frequent detection while in flight (e.g., Evening Grosbeak; *Coccothraustes vespertinus*; Red Crossbill, *Loxia curvirostra*; Tree Swallow, *Tachycineta bicolor*) or because their calls may have travelled long distances (e.g., Barred Owl, *Strix varia*; Sandhill Crane, *Grus canadensis*; Chapter 3). Therefore, we used 66 species in all subsequent analyses (Appendix III). Because of the high number of zeros in the resulting matrix of species occurrence by plot, we transformed the data using Beals smoothing (Beals, 1984). Beals smoothing replaces the matrix cells with a probability of occurrence for that species at that location based on its joint occurrence with the other species present at that plot. Likewise, for our structure-data matrix, we transformed data using general relativization by row and column totals (McCune and Grace, 2002). Relativization transforms matrix elements by a row or column standard (e.g., maximum, sum, mean, etc.) and is useful when different units of measure (e.g., basal area and percent cover) need to be standardized for comparison (McCune and Grace, 2002). We removed plots that had substantial change in structure because of industrial harvesting ($n = 15$) and examined the species composition at other plots for outliers (defined as >3.0 standard deviations; Tabachnik and Fidell, 2001) and considered them for removal. We concluded that 3 plots were notable anomalies because of increased numbers of non-forest vertebrate species. Two of these plots occurred in open, marshy meadows, and the third at the edge of a recent harvest. Thus, our final analysis consisted of 225 plots and 66 vertebrate species.

Data analysis

Community-level data often violate assumptions of parametric approaches, although some multivariate approaches are robust to violation of some assumptions (Jongman et al., 1995). Because inference must be drawn from sets of correlative predictors, confidence in the interpretation increases when results are consistent using different methods and data are compared to randomisations of the data (Jongman et al., 1995; McCune and Grace, 2002). To describe species assemblages and determine their relationship to structural variables, we used non-metric multidimensional scaling ordination (NMS; Shepard 1962a, b; Kruskal, 1964a, b), cluster analysis (Lance and Williams, 1967), multiple response permutation procedures (MRPP; Zimmerman et al., 1985) and classification and regression trees (CART; Breiman et al., 1984). We used the Sørenson distance measure in all analyses where a distance measure was necessary as it has repeatedly been shown to be an effective measure regardless of approach and consistency is recommended when using multiple approaches (Faith et al., 1987; McCune and Grace, 2002). We completed most analyses with the software PC-Ord (version 4.37; McCune and Mefford, 1999); we used Statistica (version 6.1; StatSoft, Inc., 2003) for CART analysis and correlation analyses of environmental and species ordination coordinates.

Ordination techniques arrange entities along single or multiple axes summarizing the continuous trend within data; sites with similar species composition or environmental characteristics are depicted closer together in this ordination space. NMS differs from other ordination techniques in that it does not carry assumptions of linearity among variables, it preserves similarity distances in ranked order (i.e., nonparametric) and tends to linearise distances in species and environmental space, and is not constrained to any specific distance measure or relativization method (Clarke, 1993; McGune and Grace, 2002). NMS is, therefore, often a preferred method to use with community data (Clarke, 1993; McCune and Grace, 2002).

The final solution for NMS ordination is accepted after comparing several runs with real data to randomizations of data through Monte-Carlo simulations (McCune and Grace, 2002). Two measures are used to evaluate the structure of the ordination results: stress and instability. Stress, analogous to a goodness-of-fit measure, is the deviation from monotonicity when distance is compared between the original species space and distance in the reduced ordination space (McCune and Grace, 2002). Stress is typically in the range of 10 - 20 for community data (McCune and Grace, 2002), but at the upper end of this scale cautious interpretation should be made as plots are relatively easy to misinterpret (Kruskal, 1964a; Clarke, 1993). Instability is a measure of change in stress at each iteration. Stable, low stress solutions indicate strong data structure.

To derive ordination results, we conducted 40 runs with real data and 50 runs with presence and absence data randomized among plots. We repeated each run with 1 to 6 axes (i.e., dimensions in ordination space). Stress was compared for each ordination result with different number of axes. The starting configuration coordinates for the final run, used to determine stress and instability values for the final solution, were derived from the solution with the number of axes where stress did not decrease substantially when fewer axes were used. We repeated this procedure for ordinations of species detected at plots and structure measures at each plot to determine if plot structure driven by species assemblage was comparable to pattern derived from structural characteristics. To evaluate the effectiveness of the ordination, we calculated the coefficient of determination (R^2) between the distances of plots in ordination space relative to the distances in the original, unreduced space (McCune and Grace, 2002).

To elucidate discrete groupings of the plot sample units we used cluster analysis. There are several approaches for clustering and results vary with the approach (e.g., agglomerative or divisive; McCune and Grace, 2002), distance measure, and group linkage method used (McCune and Grace, 2002). We used an agglomerative-hierarchical approach (Breiman et al., 1984) where all sample units are grouped from the bottom up with Sørenson distance, as in the ordination, and a flexible beta linkage of -0.25. A flexible beta linkage of -0.25 has been shown to minimize increases in errors in the sum of squares of distances from each individual to the centroid of its group (Lance and Williams, 1967) and is recommended for ordinations that use Sørenson distance (McCune and Grace, 2002). We selected the number of groups based on a compromise between total information remaining (analogous to R^2 in multiple regression approaches) and ecological interpretation. We tested statistical difference among groups with MRPP. MRPP tests the hypothesis that there is no difference among groups and is also a non-parametric approach. It provides a statistic of how different groups are, analogous to effect size, given as the chance-corrected, within-group agreement (A) and a p-value. A is equal to 1 when all items are identical within groups and 0 when heterogeneity within groups equals expectation by chance.

To infer relationships of vertebrate assemblage to structural variables measured at plots, we first examined the correlation of environmental variables with the plot coordinates on each ordination axis for species-based and structure-based ordinations (Pearson's r). Second, we assessed correlations between the coordinates for the species-based and structure-based ordinations. To compare the visualization of the continuous plot structure derived from NMS ordination and the discrete groupings defined with cluster analysis, we overlaid cluster groupings on the ordination diagram, thus providing a hybrid explanation of patterns observed within the data structure. We repeated the group definition for both species-based and structure-based clusters.

To describe the structural characteristics that distinguished groups, we used classification and regression trees (CART) analysis (Breiman et al., 1984). CART analysis is similar to discriminant analysis, but is more flexible partially because it is a nonparametric approach and thus is not influenced by deviations from normal distributions, data transformations, or outliers (Breiman et al., 1984, De'ath and Fabricius, 2000). Comparative studies have concluded that it performs as well or better with predictive classifications as logistic regression, discriminant analysis, and artificial neural networks (Selker et al., 1995; Vayssières et al., 2000; Karels et al., 2004) and given the ease of interpretability of the results, CART analysis may be preferential in many instances (Olden and Jackson, 2002; Worth and Cronin, 2003). Other advantages result because CART analysis makes several individual selections of where to split the data. Therefore, the amount of available information is maximised because collinear variables can all be included and used as surrogates when data are missing and variables can be included at multiple locations in the tree elucidating complex relationships (Breiman et al., 1984, De'ath and Fabricius, 2000; Vayssières et al., 2000). CART analysis, however, can overfit data (McCune and Grace, 2002). Therefore, it is important to carefully consider variables to be included in the analysis, and determine the method of determining the split decisions of the tree and as well as when to stop splitting (Breiman et al., 1984). We were specifically interested in the ability of forest-structure variables to predict species group membership; therefore, our variable list was selective (Table 4.2). Because we reduced our variable set to structural variables at the outset, we used an exhaustive search for all possible univariate splits. With this method, all possible splits for

Table 4.2. Variables used in the classification and regression tree (CART) analysis to predict group membership for plots in the Williams Lake Study Area. Plots were grouped based on the co-occurrence of vertebrate species detected from 2001-2004.

Variable Name	Abbreviation	Units	Measurement Technique
Total coarse-woody debris volume	total_cw	m^3	Plot transects
Canopy gap	P_gap	%	Plot transects
Shrub cover	P_shrub_	%	Plot transects
Shrub height	P_sh	m	Plot transects
Forb cover	P_2_forb	%	Average of 5 * 2 m cover plots
Saplings ha^{-1}	P_sap_ha	Count	5.64-m radius plot
Deciduous stems	P_dec_st	Count	5.64-m radius plot
Conifer stems	P_con_st	Count	5.64-m radius plot
Total basal area	M_ba_ha	ha^{-1}	5.64-m radius plot
Dead wood basal area	dead_ba_	ha^{-1}	11.28-m radius plot
Large tree basal area	large_ba	ha^{-1}	11.28-m radius plot
Douglas-fir basal area	Fd	ha^{-1}	5.64-m radius plot
Pine basal area	pl	ha^{-1}	5.64-m radius plot
Spruce basal area	sx	ha^{-1}	5.64-m radius plot
Distance to edge	d_edge	m	GIS
Distance to water	d_water	m	GIS
Edge density	ed_50ha	m ha^{-1}	GIS
Canopy stratification	p_diffa	m	5.64-m radius plot

each predictor variable at each node are examined and the split producing the largest improvement in goodness-of-fit is used, for which we used the Gini goodness-of-fit measure (Breiman et al., 1984). To reduce the possibility of overfitting with large classification trees (i.e., several splits), we used the smallest tree (i.e., fewest splits) with classification errors nearest to the lowest number of classification errors for the largest tree (Breiman et al., 1984; De'ath and Fabricius, 2000). We used similar criteria for CART analysis as in our cluster analysis in that we compromised between variation explained and ecological interpretability. We set prior probabilities for group membership equally (n = 11; p = 0.91) because we did not assume higher risks for misclassifying plots belonging to different groups (Breiman et al., 1984). Therefore, to determine the potential of using forest structure as a surrogate measure for the occurrence of species groups, our analyses were a complementary approach of several techniques.

Results

Plot groupings

We accepted a 3-dimentional solution for NMS ordinations based on both species occurrence and structural characteristics. For the species-based ordination, correlation analysis with the structural variables and ordination axes indicated the most influential variables for species occurrence were edge density, distance to edge, and distance to water (Table 4.3; stress = 11.61; instability = 0.0001, iterations = 116; p = 0.020). Total variance explained by all axes was 92.6% indicating that the ordination represented similarity among plots well. Proportion of variance represented by each axis based on R^2 between distance in the ordination space and distance in the original space indicated that the first axis captured

Table 4.3. Pearson correlation coefficients for ordination axes resulting from non-metric multidimensional scaling. Ordination was based on species co-occurrence at plots in the Williams Lake Study Area from 2001-2004.

Variable	Axis 1	Axis 2	Axis 3
Distance to edge	-0.501**	0.290**	0.449**
Distance to water	-0.313**	0.587**	0.216*
Edge density	0.484**	-0.215*	-0.555**

* $p < 0.05$
** $p < 0.001$

most of the variance (49.3%); the second and third dimension contained 16.5% and 26.8%, respectively.

For the structure-based ordination, tree-species composition dominated correlations with the 3 axes, either by basal area by species or counts of conifer or deciduous stems (Table 4.4; stress =13.47; instability = 0.0001; iterations = 96; $p = 0.020$). Variance captured by the first, second and third axis was 30.1%, 14.4%, and 42.1%, respectively, for a cumulative total of 86.6% variance captured. Plot coordinates in ordination space were highly correlated for all axes between the species-based and structure-based ordinations (Table 4.5), indicating that both ordinations resulted in plots within similar positions in ordination space. Based on the presence or absence of species within plots when overlaid in continuous ordination space, several species showed no relationship to any of the variables most strongly correlated with the ordination axis ($n = 37$). Some species, however, showed avoidance or selection for characteristics on one or more axes ($n = 29$; Table 4.6). For example, presence of Brown-headed Cowbird (*Molothrus ater*) was positively associated with edge density on both axis 1 and axis 3 and negatively associated with distance to water on axis 1 (i.e., found closer to water).

Cluster analysis of plots based on species composition and structural characteristics resulted in the identification of 11 groups. Groups based on species composition had 27% unexplained variance (Figure 4.2; Appendix IV)[1]. Plots within the same groups had species occurrences more similar to one another than to plots in other groups. The cluster analysis based on structural characteristics had 30% unexplained variance (Figure 4.3; Appendix IV). MRPP analysis indicated that both groupings, species and structure, were statistically significant. The species grouping, however, had less within-group variance than structure-

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[1] Species most associated with each group are presented in Appendix V.

Table 4.4. Pearson correlation coefficients for ordination axes resulting from non-metric multidimensional scaling. Ordination was based on structural characteristics measured at plots in the Williams Lake Study Area.

Variable	Axis 1	Axis 2	Axis 3
Percent gap	0.494**	-0.500**	-0.259**
Percent shrub cover	0.051	0.108	-0.600**
Saplings ha^{-1}	-0.495**	-0.009	0.297**
Deciduous stems ha^{-1}	-0.247**	0.478**	-0.314**
Coniferous stems ha^{-1}	-0.624**	0.226**	0.397**
Basal area Douglas-fir	-0.204*	0.325**	0.668**
Basal area Pine	-0.505**	-0.111	-0.143*
Basal area Spruce	-0.321**	0.342**	-0.463**
Distance to edge	-0.443**	-0.151*	0.479**
Distance to water	-0.027	-0.509**	0.390**
Edge density	0.472**	0.095	-0.369**

* $p < 0.05$
** $p < 0.001$

Table 4.5. Pearson correlation coefficients for plot coordinates based on species and structure using non-metric multidimensional scaling ordinations. Species occurrence was determined from 2001-2004 in the Williams Lake Study Area.

	Species-based		
Structure-based	Axis 1	Axis 2	Axis 3
Axis 1	-0.335**	0.101	-0.331**
Axis 2	-0.299**	0.163*	0.300**
Axis 3	0.503**	0.024	-0.030

* $p < 0.05$
** $p < 0.001$

Table 4.6. Relationship between vertebrate species presence and absence with ordination axes as determined by non-metric multidimensional scaling. Axis one is defined by distance to edge (-) and edge density (+), axis 2 by distance to water (+), and axis 3 by distance to edge (+) and edge density (-). Variables are described in Table 4.2. Species with no clear relationship to any of the variables defining ordination space are not listed (*n* = 37). If species were not located in a particular quadrant of the 2-dimensional space, then the relationship was interpreted as avoidance. Latin names for all species are listed in Appendix II.

Species	Axis 1	Axis 2	Axis 3
Moose	-	-	ed_50ha (-)
Alder Flycatcher	d_water (+)		ed_50ha (+)
Black-blacked Woodpecker	-	d_edge (+)	d_edge (+)
Brown-headed Cowbird	ed_50ha (+)	d_water (-)	ed_50ha (+)
Brown Creeper	ed_50ha (-)	-	ed_50ha (-)
Coyote	ed_50ha (+)	-	ed_50ha (+)
Clay-colored Sparrow	ed_50ha (+)	d_water (-)	-
Common Yellowthroat	ed_50ha (+)	d_water (-)	-
Downy Woodpecker	ed_50ha (+)	-	-
Dusky Flycatcher	-	d_water (-)	-
Gray Jay	ed_50ha (-)	-	-
Hairy Woodpecker	ed_50ha (+)	d_edge (-) d_water (-)	-
Snowshoe Hare	ed_50ha (-)	d_edge (+) d_water (+)	
Least Flycatcher	-	d_edge (-) d_water (-)	-
Lynx	ed_50ha (-)	d_edge (+)	-
McGillivary's Warbler	ed_50ha (-)	-	-
Meadow Vole	ed_50ha (+)	-	-
Ermine	ed_50ha (-)	-	-
Long-tailed Weasel	ed_50ha (+)	d_edge (-) d_water (-)	-
Northern Flicker	ed_50ha (+)	-	-
Northern Waterthrush	ed_50ha (+)	d_water (+)	-
Olive-sided Flycatcher	ed_50ha (+)	d_edge (-)	-
Song Sparrow	ed_50ha (+)	d_water (-)	-
Yellow-pine Chipmunk	ed_50ha (-)	-	ed_50ha (-)
Townsend's Warbler	-	d_edge (+)	-
Three-toed Woodpecker	ed_50ha (-)	d_edge (+)	
Red Fox	ed_50ha (-)	d_edge (-) d_water (-)	-
Winter Wren	-	d_edge (+) d_water (-)	-
Western Wood-peewee	ed_50ha (+)	d_edge (-) d_water (-)	-

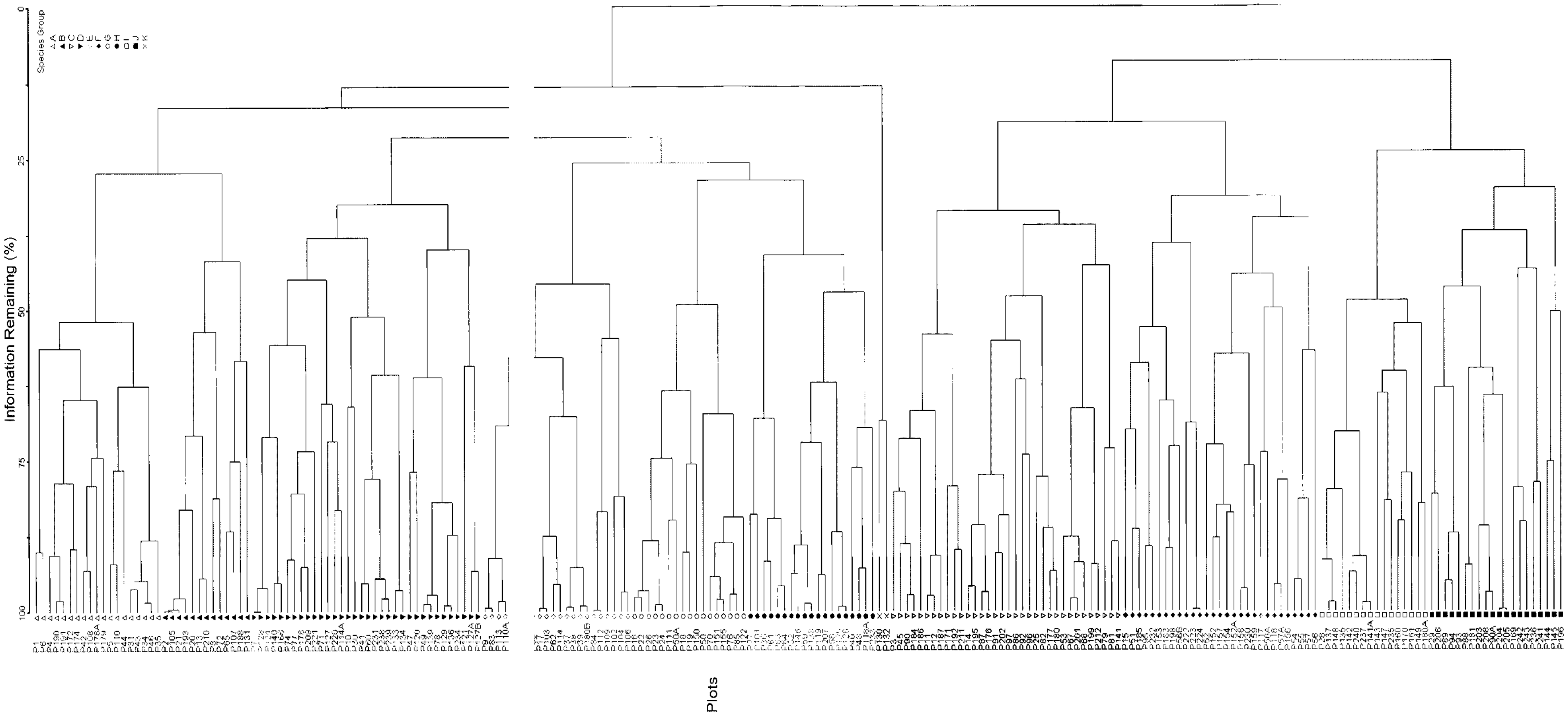

Figure 4.2. Dendrogram from hierarchical cluster analysis of plots in the Williams Lake Study Area by species co-occurrence detections from 2001-2004. Symbols indicate groups of associated plots. Plots in the same groups have species composition more similar to one another than to plots in other groups.

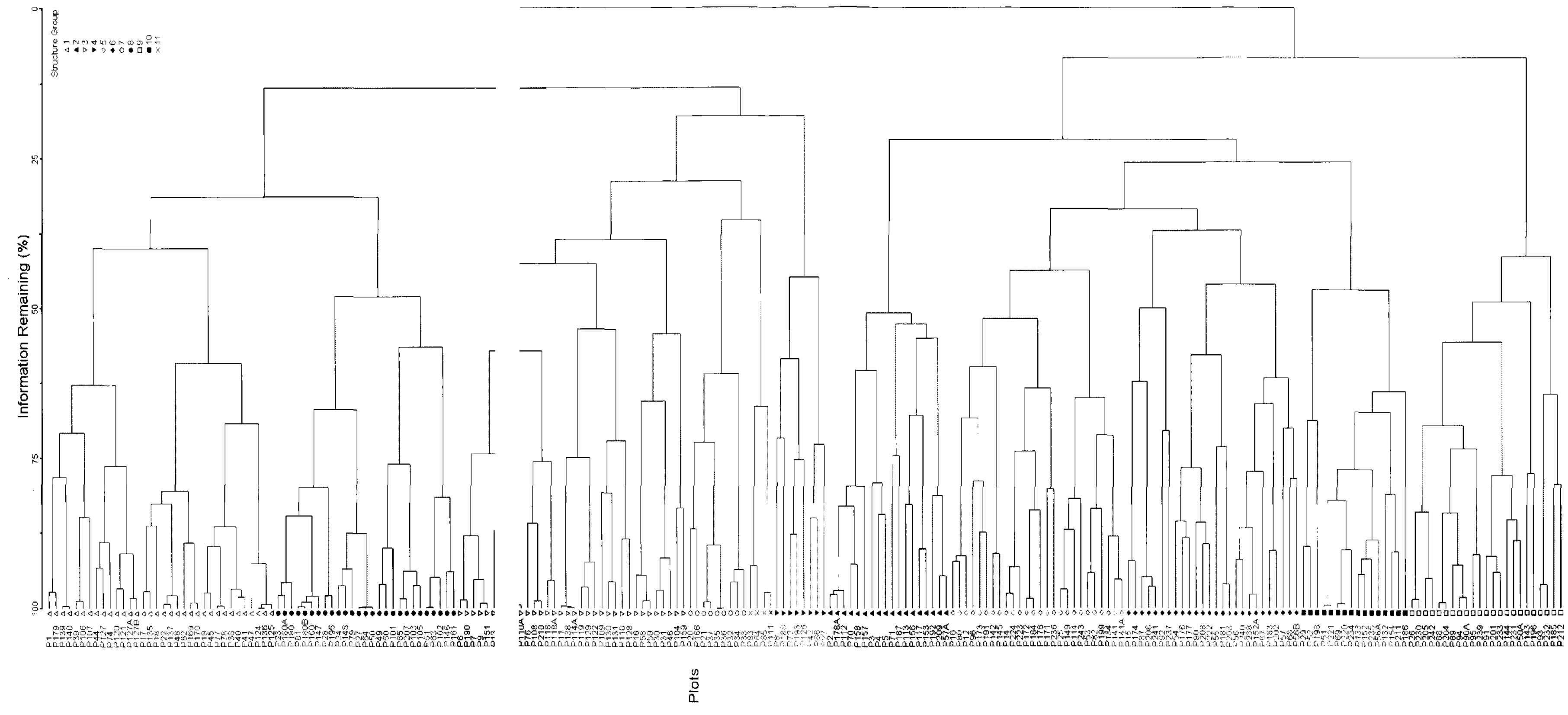

Figure 4.3. Dendrogram from hierarchical cluster analysis of plots by characteristics of forest structure at plots located in the Williams Lake Study Area. Symbols indicate groups of associated plots. Plots in the same groups have structural characteristics more similar to one another than to plots in other groups.

based groups (species groups: $A = 0.292, p < 0.01$; structure groups: $A = 0.090, p < 0.01$). Species groups were distinct when overlaid on the ordination plot (Figure 4.4A, B, C); groups defined by similarity in structural variables were not distinct on any of the ordination planes (Figure 4.5A, B, C). These results indicate that cluster analysis and ordinations based on species occurrence support each other, but the same can not be said of the structure cluster and ordination analyses. Overall, overlap between species-based and structure-based groups ranged from 16.7-50.0% (Appendix IV).

Predictions using structure

Using the groups defined by species co-occurrence, predicting group membership with CART analysis resulted in low classification success (45.8%) and ranged widely among groups (0% - 100%; Table 4.7). Seven structural variables were used to discriminate among plots; edge density and distance to edge were ranked as most important (i.e., explained more of the variation, appeared at the top of the tree, and occurred multiple times; Table 4.8). The CART dendrogram depicts which variable defines the split at each branch, the number of cases in the group, and classification success (Figure 4.6). Edge density defined the first split among groups, indicating it was the most important variable discriminating among groupings. Moving to the left branch of the tree, edge density and saplings ha^{-1} led to 2 terminal nodes that correctly predicted 8.5% of group 5 members and group 11 perfectly (Table 4.8); although there were misclassifications included within these splits. The dendrogram thus illustrates the variable splits that define the groups and how impure the groups are on each branch.

Distance to water and edge density led to one terminal node and the correct prediction of 50% of group 8 plots, to the right outer branch of the dendrogram. Adding edge density

A

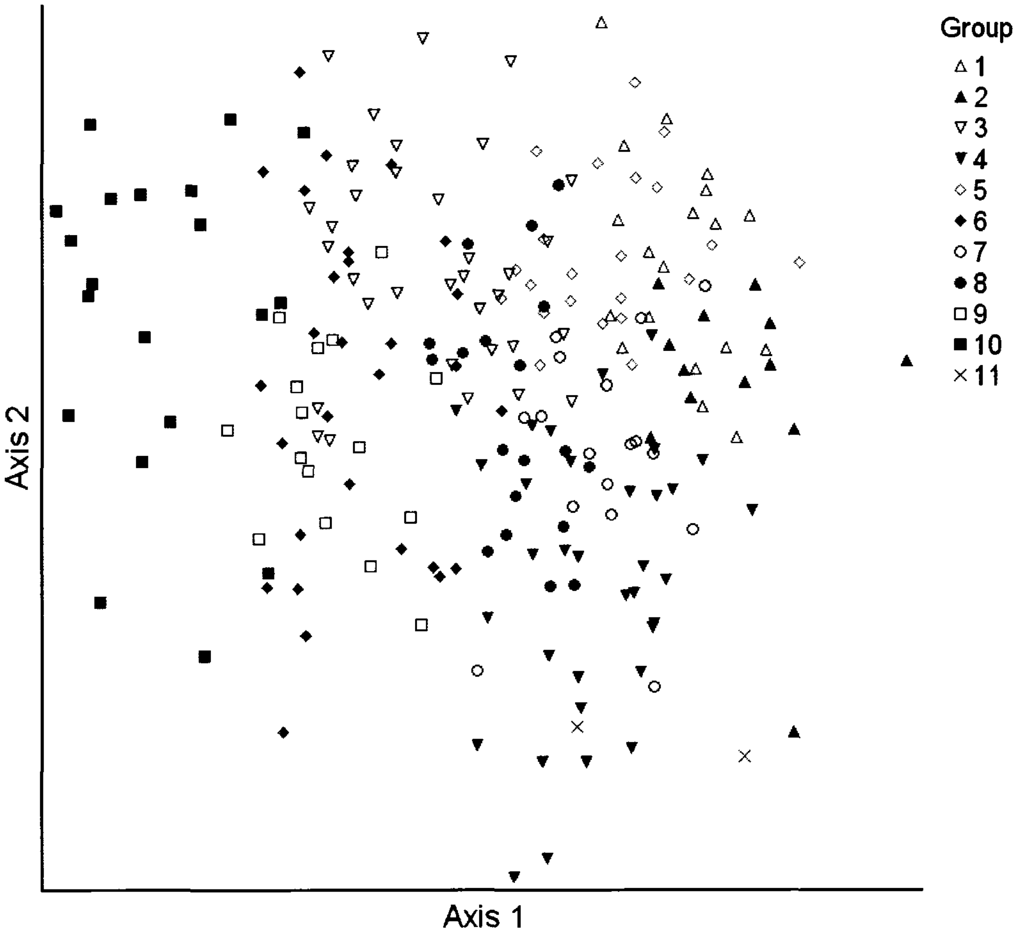

Figure 4.4. Non-metric multidimensional scaling ordination (NMS) of plots based on presence and absence data for vertebrate species detected at plots in the Williams Lake Study Area from 2001-2004. Separate figures are presented for each pair of ordination axes (A, B, C). Cluster analysis groups are depicted by different symbols. Plots shown closer to one another are more similar in species composition.

B

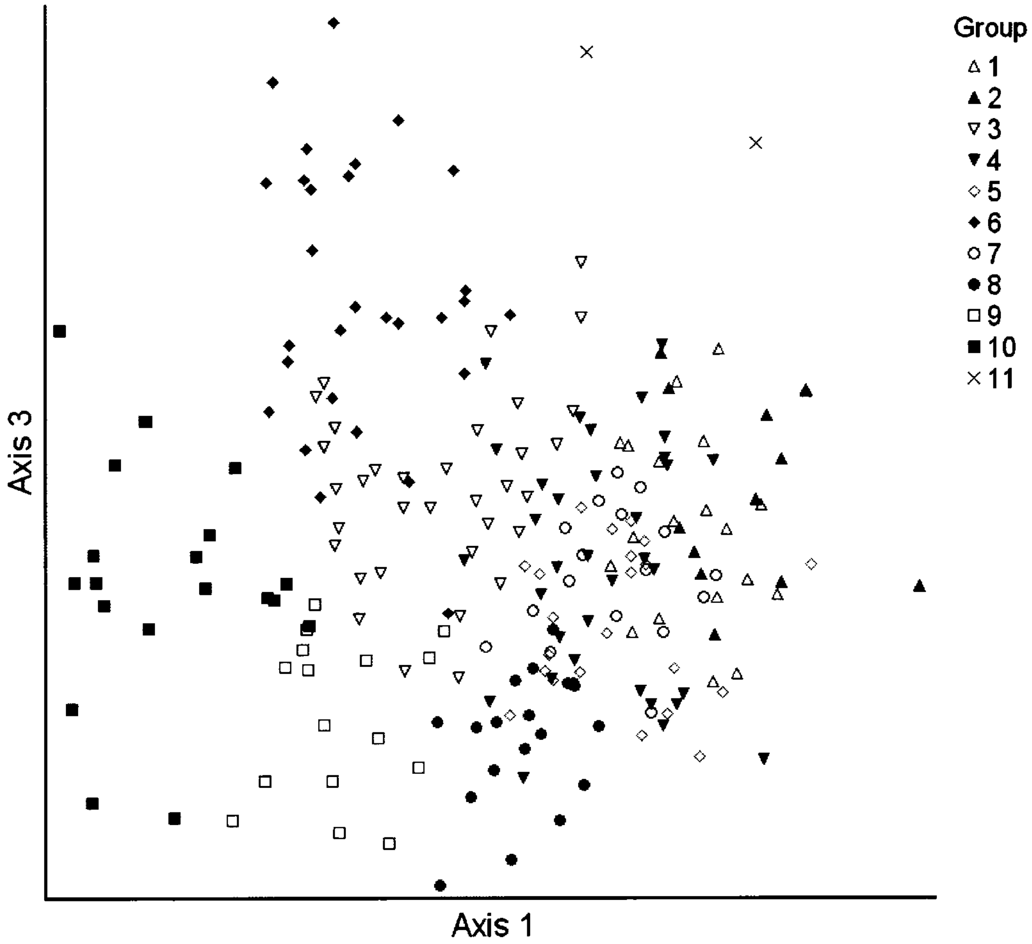

Figure 4.4. NMS ordination plots for plots based on presence and absence data of species assemblages (continued).

C

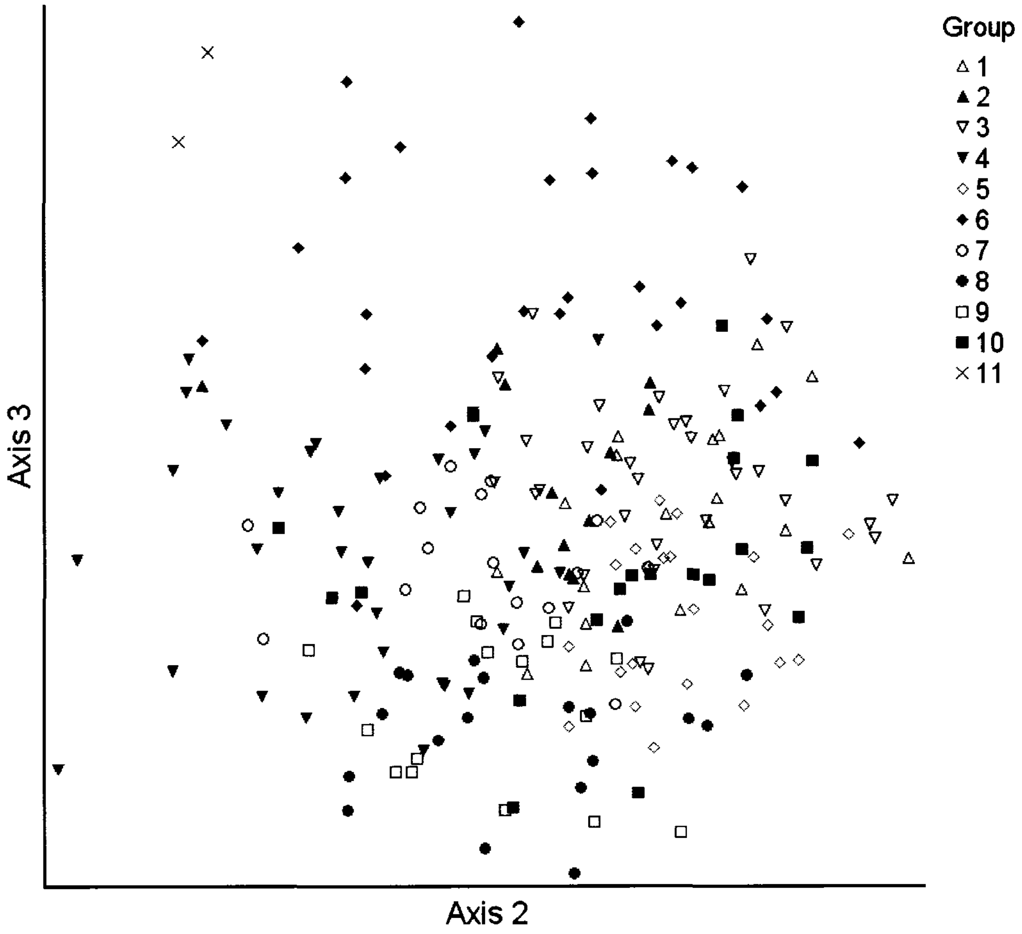

Figure 4.4. NMS ordination plots for plots based on presence and absence data of species assemblages (continued).

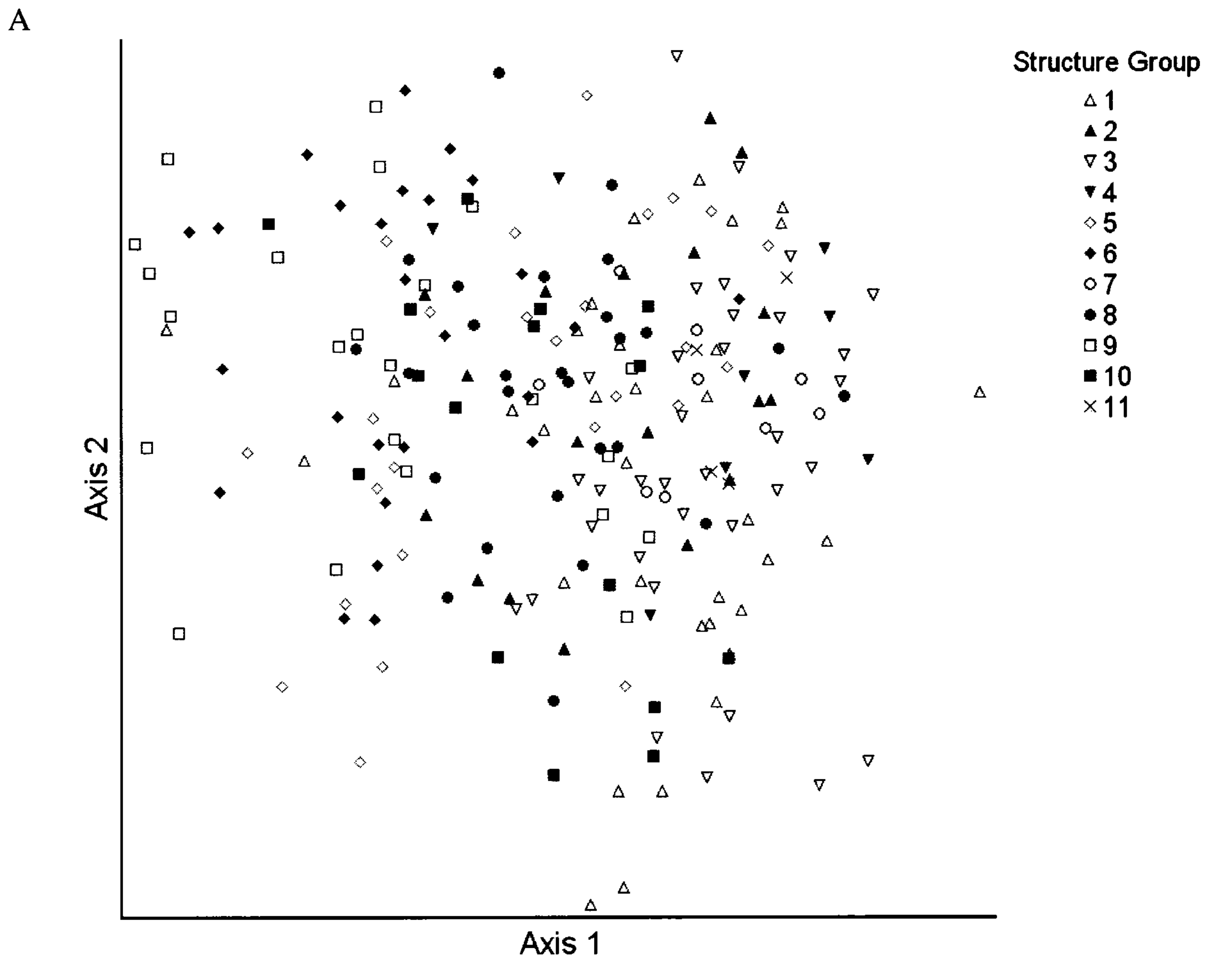

Figure 4.5. Non-metric multidimensional scaling ordination (NMS) of plots based on characteristics of forest structure at plots in the Williams Lake Study Area. Separate figures are presented for each pair of ordination axes (A, B, C). Cluster analysis groups are depicted by different symbols. Plots shown closer to one another are more similar in forest-structural characteristics.

B

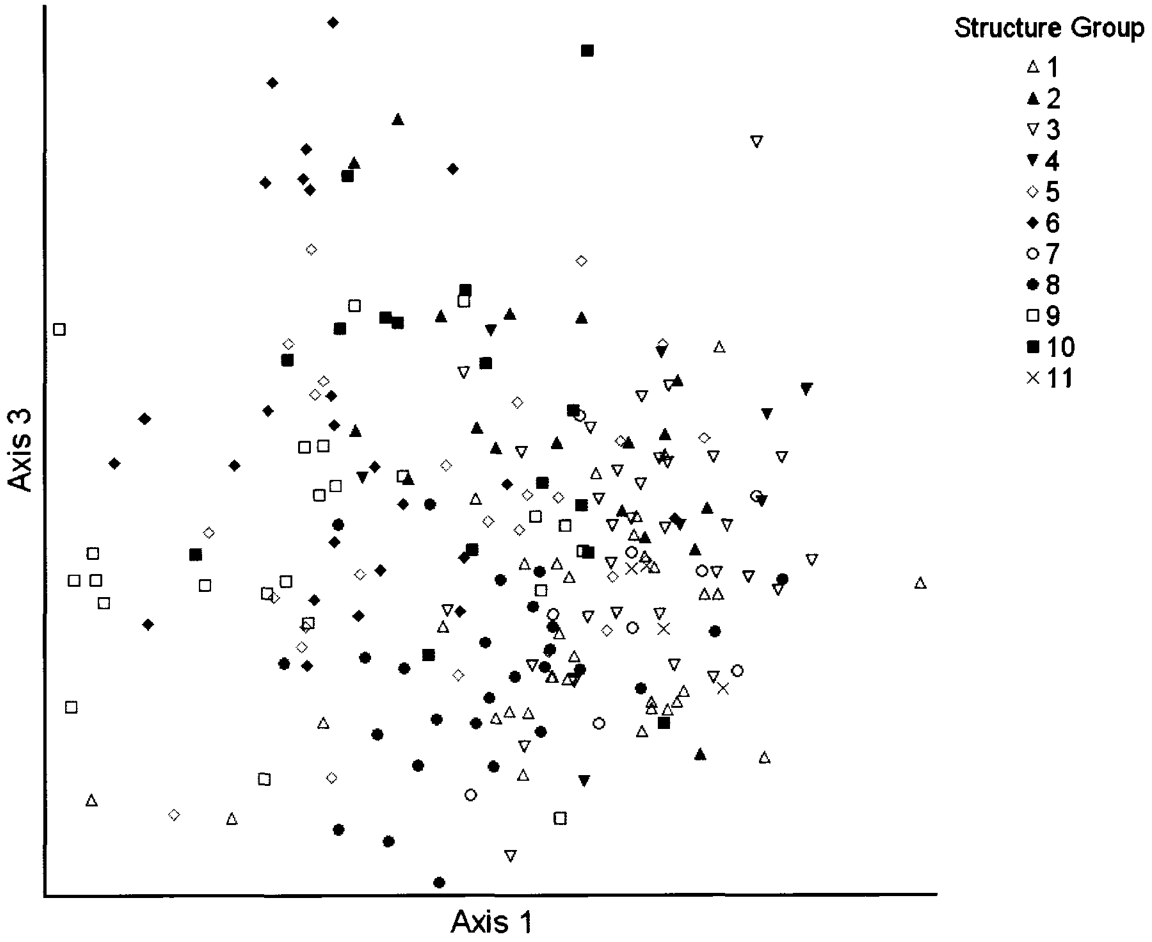

Figure 4.5. NMS ordination for plots based on characteristics of forest structure (continued).

C

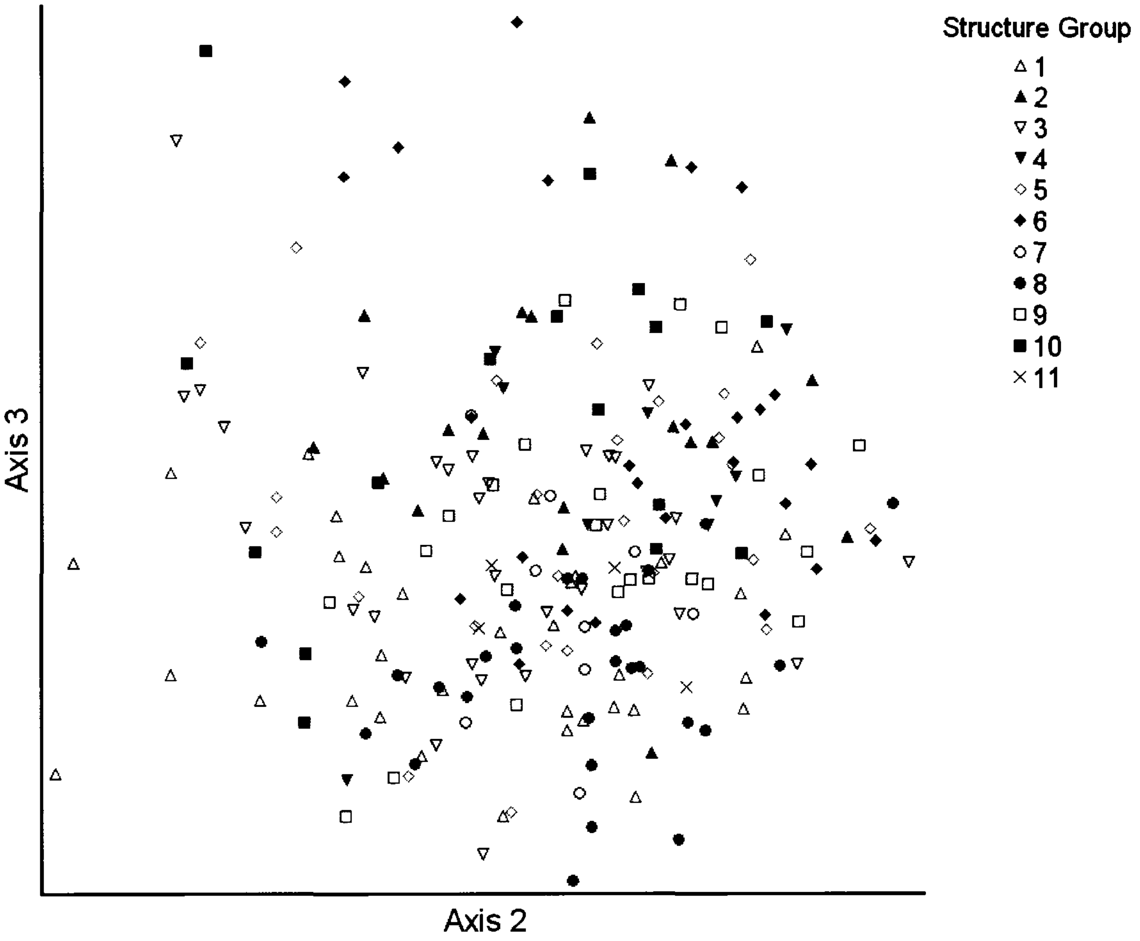

Figure 4.5. NMS ordination for plots based on characteristics of forest structure (continued).

Table 4.7. Correct classification matrix of observed class against predicted class for CART analysis. Structural characteristics of plots were used to predict group membership and groups were defined based on similarities in species co-occurrence from 2001-2004 at plots in the Williams Lake Study Area. The 11 classes were defined using cluster analysis. Overall classification accuracy was 45.8%. Number of correct classifications are in bold for each class.

	Observed Class											
Predicted Class	Class 1	Class 2	Class 3	Class 4	Class 5	Class 6	Class 7	Class 8	Class 9	Class 10	Class 11	Percent Correct
1	**0**	0	0	0	0	0	0	0	0	0	0	0.0
2	4	**7**	7	2	2	0	0	0	0	2	0	43.8
3	0	0	**0**	0	0	0	0	0	0	0	0	0.0
4	21	1	16	**9**	23	1	0	2	1	1	0	56.3
5	0	0	0	0	**5**	0	0	0	0	0	0	8.5
6	0	0	0	0	4	**7**	0	1	0	3	0	63.6
7	1	1	0	0	5	1	**12**	5	5	0	0	92.3
8	1	1	3	0	16	0	0	**10**	1	0	0	50.0
9	0	1	1	0	0	0	1	0	**5**	0	0	35.7
10	1	5	3	0	8	2	0	2	2	**7**	0	53.8
11	1	0	1	0	1	0	0	0	0	0	**3**	100

Table 4.8. Ranking of importance for structural variables used in CART analysis to predict membership of plots grouped based on species co-occurrence from 2001-2004 in the Williams Lake Study Area; 100 = most important, 0 = least important.

Variable	Ranking
Distance to edge	100
Edge density	93
Distance to water	76
Saplings ha^{-1}	59
Percent gap	56
Shrub cover Percent	45
Forb cover percent	42

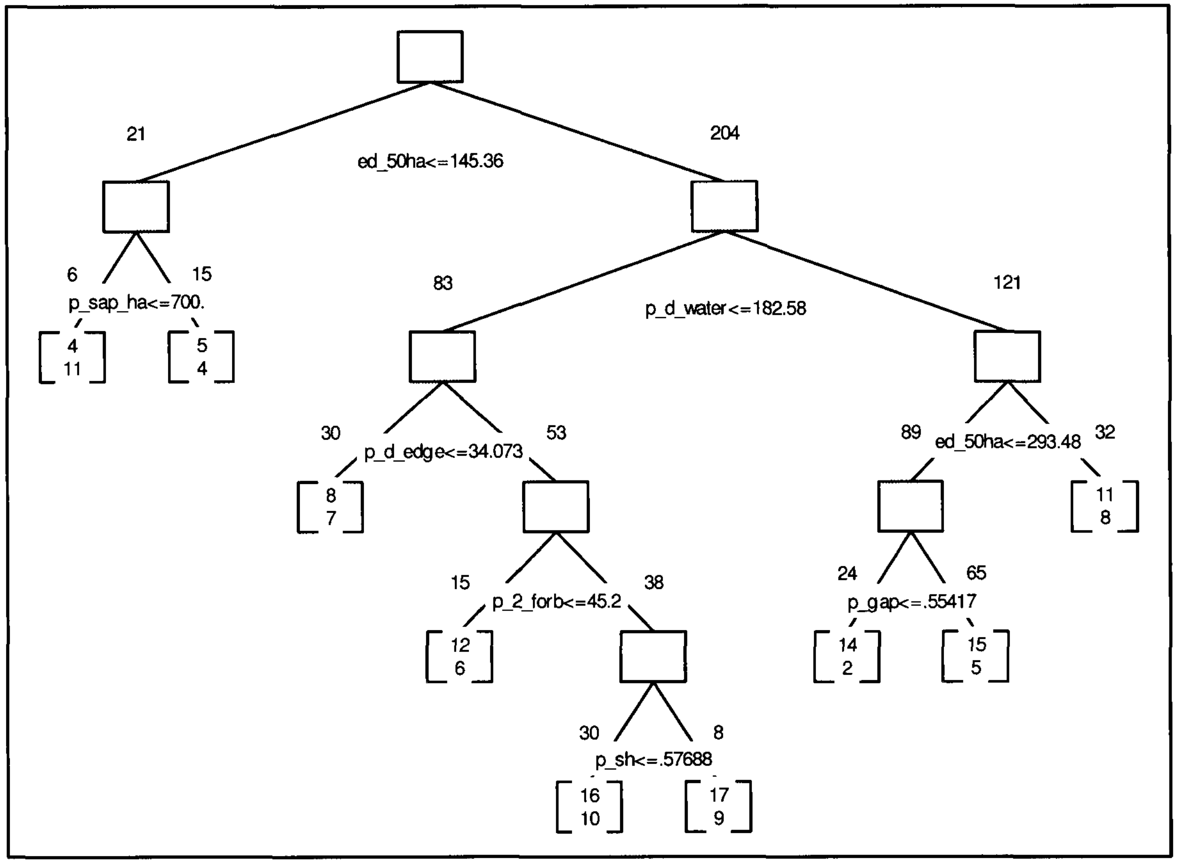

Figure 4.6. Dendrogram for the classification and regression tree analysis. Plots were grouped based on species co-occurrence from 2001-2004 in the Williams Lake Study Area. Group membership was predicted using forest structural variables. Nodes to the left of each decision criteria meet the stated condition, whereas nodes to the right do not meet the stated criteria. The numbers along each decision branch indicates the number of cases that did or did not meet the decision criteria. The upper number within terminal nodes (red) is the number of cases assigned to the predicted class, the lower number within terminal nodes is the group name. Not all cases are correctly classified. Overall classification success is presented in Table 4.7.

and percent canopy gap led to the correct prediction of 43.8% of group 2 and 56.3% of group 4. In the centre branch, the addition of distance to edge led to the correct prediction of 92.3% of group 7; the addition of forb cover predicted 63.6% of group 6; and finally, shrub height distinguished 53.8% of group 10 and 35.7% of group 9. The presence of only 9 terminal nodes, instead of the 11 groups identified with cluster analysis, reflected the lack of successful predictions for any members of groups 1 and 3. The right and centre branch are distinctive from the left branch in that they each contained a spatial measure near the top of the branches (i.e., high variable importance). Overall, the results from the CART analysis indicate that although there was a correlative relationship between groups classified with species co-occurrence and structural characteristics, the relationships were not strong enough to accurately predict the groups.

Given the results of the ordination and correlation analyses, plots could reliably be grouped based on both structure and the occurrence of species. Plot groupings from both approaches had similarities indicated by significant correlation among coordinates in ordination space. Three variables (edge density, distance to water, and distance to edge) consistently appeared in each analysis suggesting that both spatial context and larger scale aspects of structure were the best correlates of species occurrence. Overall, however, these relationships were not strong enough to reliably predict the membership of plots to groups based on species co-occurrence. Therefore, although species groups were distinctive, indicating that species co-occur with some degree of pattern, the structural characteristics we measured were not sufficient to describe the relationships.

Discussion

Plots could be grouped into significant assemblage types as well as structural types. Both approaches resulted in groups that had considerable variation, more so for the structurally defined groups. Consequently, the biological significance of the groupings is suspect (McCune and Mefford, 1999). Further, poor predictive ability of forest structure and the overall weak relationships between species-based groupings of plots and structure-based groupings of plots suggest that these patterns are driven by factors other than those we measured (e.g., biological factors such as competition, prey availability, other environmental variables). Therefore, reliance on structure as a surrogate for predicting the occurrence of species cannot be recommended.

To facilitate comparison among groupings, we selected the same number of groups for each set of groups based on explained variation and simplicity. Improved grouping for structure groups may have been achieved if fewer classes had been selected. Other researchers have used clustering techniques to define structure groups in our study area by cumulative distribution plots of basal area ha^{-1} and tree stems ha^{-1} (Moss, 2002). The clustering techniques were used to distinguish differences between narrow- and wide-ranging diameter distributions and were implemented for management purposes, although the classification had considerable variation within and among groupings (Farnden et al., 2003). The use of such groupings may carry lower risks when used to characterize structure alone, especially with supporting vegetation inventories, but not if being used as a surrogate approach to monitoring species presence.

It has been debated whether or not it makes ecological sense to define community units or species assemblages into discrete entities because the groups may be too simplistic and do not take into account ecological factors such as competition and stand history (Allen and Hoekstra, 1992; McIntosh, 1995; Heino et al., 2003). For vertebrate species, as opposed to vegetation structure composition differences, alternative techniques using individualist concepts relating species along continuums may be more ecologically meaningful. Data needed to develop predictive models for several species are lacking, however, and models are often limited by low predictive ability (Chapter 3). These data are also difficult and expensive to obtain. For example, in our study area, where extensive inventories were conducted for species presence, several vertebrate species were not detected often enough to model and few species were modelled with good predictive accuracy (Chapter 3). Grouping species by co-occurrence should account for species interactions that play a significant role in species presence (Caswell, 1976; Gotelli and Graves, 1996) and if structure predicted groups well, management and monitoring objectives could be more efficiently implemented (Angermeirer and Schlosser, 1995). Because the single-species models had few overlapping variables, generalisations about structural characteristics for several species were not practical (Chapter 3). Further, taking an assemblage-level approach would be advantageous only if species were reliably grouped and structure measures predicted groupings well, which was not the case.

We limited our selection of variables to these that would normally be measured in forest inventories and are affected by forest-management activities. Other variables may help to improve the unexplained variation in groups. Other studies have reported that non-structural variables (e.g., aspect, moisture, elevation; du Bus de Warnaffe and Dufrêne, 2004; stand history, Tyre et al., 2001), ecological interactions, and scale influenced the variation explained in predictive models (Heino et al., 2003; du Bus de Warnaffe and Dufrêne, 2004;

Oxbrough et al., 2005). Our study area is heavily managed by multiple users (e.g., harvesting, ranching, recreation). Therefore, disturbance history, types of disturbance, and disturbance intervals may help predict the occurrence of species. Although non-structural variables and stand-history variables may be relatively easy to obtain, the lack of overall relationships between species co-occurrence and structural variables alone suggest that forest structure is limited in terms of a surrogate approach for monitoring and that the biological influences override those of structure.

Small-scale variation in plot structure may have further confounded group definition. Most species that we included in our analysis are highly mobile (i.e., capable of flight) or have large home ranges. Species groupings are thus less likely to be influenced by small-scale variation. Further, species may not have grouped well because of a wide range of environmental tolerances and geographic distributions. Many of the species that were included in the assemblages are found across provincial or continental scales; therefore, we may not have sampled over a broad enough environmental range. Overall in our analyses, we found groups were statistically distinct, but ecological significance was difficult to interpret and without strong relationships to predictive variables, assemblage-level approaches are not feasible or more efficient than single-species approaches (Chapter 3).

There was significant correlation among plot coordinates in ordination space for species-based and structure-based groupings. The variables most strongly correlated to each ordination axis, however, differed (Table 4.3; Table 4.4). The variables most highly correlated with the species ordination were related to spatial aspects of plot location (i.e., distance to water, distance to edge) and aspects of the surrounding habitat (i.e., edge density). In contrast, the structure-based ordination variables related to tree species composition were highly correlated to axes. Further, when we overlaid the cluster-analysis groups onto the plots in ordination space, the species ordination had much more distinct groupings than structure ordination (Figures 4.3, 4.4, respectively). This suggests that although the processes driving the correlations may be related, characteristics of forest structure are not good surrogates for those processes. Again, scale of measurement and landscape interactions confound the interpretation of results. It was important, however, to determine the relationship at the scales we measured because this scale is representative of management practices. Further, we needed to standardize our measures of species co-occurrence. Overall, these results suggest that species more likely responded to the co-occurrence of other species or conspecifics and spatial aspects of plots than to structural characteristics alone. Settling near conspecifics may provide benefits. For example, it may provide assessment of habitat suitability (Desrochers and Magrath, 1993; Doligez et al., 2002), reduced risk of predation (Stephens and Sutherland, 1999), and reduced territorial defence costs (Meadows, 1995). Increasing the geographic scope and management regimes may improve groupings and predictive models relative to structural characteristics, but it is not likely to improve aspects of monitoring diversity at the operational scale of forest harvesting.

Defining species assemblages and predicting their occurrence for a single taxonomic group, particularly birds (e.g., Diaz et al., 2005) and invertebrates (e.g., Oxbrough et al., 2005), have proven successful in other studies. Conservation assessment and diversity monitoring, however, should not be based on a single taxonomic group. In fact, even all vertebrate groups comprise a relatively small proportion of biodiversity. Spanning taxonomic groups may have confounded structural relationships because of differences in the scale that species use to respond to structure. For example, Coyote (*Canis latrans*) and Meadow Vole

(*Microtus pennsylvanicus*) were both positively associated with edge density (Table 4.6; Appendix 1), but perceive their habitat at very different spatial scales. Although many researchers advocate multiple taxonomic approaches as desirable for diversity monitoring programs (Fleishman et al., 2005; Heino et al., 2003), and the approaches have shown correspondence between indicator species of birds and invertebrate richness (Fleishman et al., 2005), modelling for individual taxa may be required for the development of effective programs. Other approaches that use species richness as the response variable in predictive models (e.g., Loehle et al., 2005) require caution because it is difficult to distinguish loss of sensitive species and ensure the full representation of regional or local species when richness is used (Lindenmayer, 1999; Magurran, 2003).

Habitat-based surrogates are appealing because they do not require the direct measurement of species occurrence and can usually be described cost effectively. Predicting the occurrence of species rapidly and cost effectively for landscapes that are changing frequently because of management practices, however, is a challenging issue. Successful approaches have been proposed and tested for some species, but these studies tend to more intensely measure habitat use or use abundance as a response variable (e.g., Florida Scrub Jay, *Aphelocoma coerulescens*; Carter et al., 2006). The cost of obtaining these data is often prohibitive. If similarities in structural association could be identified for groups of species, predicting occurrence and response to management practices could be made even more efficient. Although we found statistically distinct groups, we did not find that they were predicted well by structure.

Other studies have analyzed prediction errors and questioned the underlying habitat-relationship models used to predict occurrence (Boone and Krohn, 1999), or more broadly the use of environmental diversity as a surrogate for species diversity (Araújo et al., 2001). In our study there were significant correlations among structure and species groups, but the relationships were weak. Given the lack of predictive success and variance within groups, using structure alone to monitor species assemblages is not a feasible management option in our study area. With the results of our study we agree with Kavanagh and Stanton (2005) and Manley et al. (2004) that it is better to monitor species directly than to rely on habitat surrogates that are not proven reliable.

Ensuring that surrogate measures are thoroughly tested and robust through time in the dynamic environments of forests will also require long-term monitoring data. Continued species monitoring and research on the development of surrogate approaches in forested environments would benefit from adaptive management (i.e., experiments with controls and replicates; *sensu* Walters, 1986). Although recording presence and absence of different species does not necessarily provide insight as to how to improve management because causal mechanisms are not identified (Stone and Porter, 1998), these data collected over the long term through monitoring could potentially identify the responses of species to modification of structure and, therefore, go beyond correlative inference.

Chapter 5. General Conclusions

Accurately predicting species occurrence is an important aspect in the studies of ecology and conservation management. Economic and social values often conflict with ecologic values on forested landscapes. With efficient biodiversity monitoring programs, forest managers may be able to better incorporate a balance of competing goals. Linking variables directly affected by forest management activities, specifically measures of forest structure, to the occurrence of species and assemblages may provide forest managers with a useful tool to monitor, manage, and help mitigate the effects of industrial harvest on species diversity. Through my research, I investigated using forest structure to predict the occurrence of single species and species groups, as well as how methods of detection may influence model outcomes. Unique aspects of the research I conducted include simultaneous collection of distribution data for multiple species, the use of external data to validate single-species models, and the extremely detailed structure data collected over multiple scales. Overall, the success of forest structure as a surrogate measure of vertebrate presence was poor. Therefore, the hypothesis that structure can be used in place of direct species monitoring can not be accepted.

Structure as a surrogate measure

I was able to model a small portion of the species detected ($n = 55$). Although this was a low percentage (<30%) of the overall species detected in the study area, it can be considered successful in that modelling this number of species by taking a species-by-species approach would have taken considerably more time, effort, and other resources. By conducting concurrent inventories, significant amounts of data were collected relatively efficiently. Further, the presence and absence data provide baseline distribution and habitat association information that can be used to improve future modelling efforts. Research designed for a single species, however, often has much better results in terms of model outcomes, likely because of more intensive measurement of habitat use, either through direct observation or radio-telemetry.

In my research, I found that different types of detection (e.g., sign, audio, visual) led to inclusion of different habitat variables in models and different levels of model discrimination (i.e., ROC values; Chapter 2). I believe this result is a consequence of species being more selective of habitat for certain activities that may result in different types of detection. For example, the Pileated Woodpecker may be highly selective in using a tree for foraging or nesting, which results in sign detections, but not very selective in choosing habitat to commute through, which may result in visual or audio detections. Future inventory efforts may consider modifying methodologies to increase the detection of species use of specific forest structures deemed critical habitat elements and should always include the detection type for the potential of separate analysis.

Relating species presence to habitat characteristics is not without its critics because of the correlative nature of relationships, interactions with others species, and various aspects of behaviour (see review Mitchell, 2005). Regardless, describing species-habitat relationships remains an extremely important research and management goal. Other researchers have found significant relationships between species richness and physical characteristics of the environments and forest structure in particular (e.g., birds; Diaz et al., 2005; herptofauna; Loehle et al., 2005; spiders; Oxbrough, et al., 2005). Using species richness as a response variable, however, may not reveal losses or population declines of specific species. For example, areas subjected to intermediate disturbance (Connell, 1978) and ecotones (e.g., riparian areas; Naiman and Décamps, 1997) often have high diversity, but the species represented may not include species that are sensitive to disturbance or require large areas of contiguous forests. Using species richness, therefore, may miss sensitive species that are important components of the suite of species that occur in an area (Magurran, 2003). Ensuring that all species are represented across the landscape and that viable populations are maintained remains the overall goal of most management programs aimed at conserving biodiversity. More sensitive species could be included in a fine-filter approach and, therefore, complementary approaches should continue to be recommended (Lindenmayer and Franklin, 2002).

Neither single-species (Chapter 3) nor multiple-species (Chapter 4) models resulted in clear relationships with forest structure. There were several variables, however, that were repeatedly used, independent of the approach or statistical methodology. Specifically, distance to edge, distance to water, and edge density were common predictors of species or species-group occurrence. Further, several single-species models combined variables that described forest structure at multiple scales and the variables most often included in plot models (i.e., distance to water, large tree basal area, and dead tree basal area) were not as frequently included in stand models, suggesting that the influence of these structures on species presence was localized (Chapter 3). Overall, because the scale at which different species use habitat varies so widely, generalisations among presence and forest structure across species are difficult to infer (Chapter 3 and Chapter 4). The results of my research, and that of others, highlight the importance of spatial context and scale of habitat as factors related to habitat use (e.g., Scott et al., 2002). Spatial context, however, is not a routinely described component of structure when used for forest management purposes. Further research on the influence of spatial configuration of elements of forest structure (e.g., large trees, dead trees) and the spatial context of habitats (i.e., distance to specific habitat features) should be a priority to improve the potential of management recommendations regarding harvest patterns, retention, and recruitment of important elements as the current emphasis on structure without context appears misguided.

Uncertainty

Examining potential sources of error is frequently overlooked, but is an important aspect of model validation (Barry and Elith, *in press*). My examination of potential sources of error indicated that spatial uncertainty was the most problematic. Models derived from detections that were spatially certain (e.g., sign) resulted in models with better discrimination (i.e., higher ROC values; Chapter 2) and models for species that were associated with high spatial uncertainty at the plot level (e.g., Sandhill Crane) had poorer discrimination (i.e., lower ROC values; Chapter 3). Because variation in forest structure was high within plots, accurately determining the location of a species seems particularly crucial to model performance. For species that are rarely detected with high levels of spatial certainty, plot-level monitoring is not likely appropriate without high confidence in occurrence data. Methods that illicit responses from individuals that are highly mobile (e.g., owls and woodpeckers) may further confound determination of the relationship with habitat elements as individuals may move before they are detected (these occurrence points could be modelled at larger landscape scales). I did not find a relationship between temporal uncertainty and model discrimination, which is probably because of the short lifespan of most measures of presence through sign (e.g., tracks and scat) relative to changes in forest characteristics from disturbance (e.g., harvest, fire, or windthrow).

Validation

With the presence and absence data collected, species-structure models were developed for 55 species, some at multiple scales. Discrimination and reliability of several of these models, however, were weak (Chapter 3). Further, when the models were validated with spatially and temporally independent data, most models failed to meet the criteria of a "good" model (i.e., had poor discrimination and / or reliability). Discrimination and reliability tended to be less when spatially validated compared to temporal validation, suggesting that site history may be an important factor influencing species presence (e.g., Tyre et al., 2001) and that models cannot be applied across an environmental gradient in my study area (Van Horne, 2002). This also reinforces the association of spatial uncertainty and poor model performance. Habitat models have often been used for management purposes without adequate validation (Rykiel, 1996), and this research casts further doubt on that practice. Given the dynamic nature of forests and species populations, continued assessment of models through time should be a required aspect of any program that uses species-habitat models as a surrogate measure of presence.

Summary

The extensive presence and absence data across taxa, vegetation data collection at multiple scales, examination of relationships between structure and single species and species assemblages, and the comparative analysis among techniques allowed for a thorough examination of the potential of structure as a surrogate measure of species occurrence. One outcome of this approach was the demonstration that multiple-species monitoring can be achieved efficiently and cost-effectively. The external validation of models allowed for confident conclusions to be drawn regarding the ability of the model to accurately predict the occurrence of species. Finally, using individual species presence and absence, as opposed to species richness, explicitly tested the potential of forest structure as a surrogate measure to monitor occurrence for a broad range of species. Few studies have examined such a breadth of species concurrently and several of the species modelled are not frequently studied. The model results highlight the complex relationship among species presence and spatial aspects of forest structure and overall, they provide a strong starting point for the continued development of biodiversity monitoring objectives.

Species that show strong avoidance of edge and selection for continuous stands are likely to be negatively impacted by the current management practices in the study area and may be species of concern. Species with strong relationships with certain structural elements could be tested for their potential as indicator species. Within broader biodiversity management objectives, such as ecosystem management and representation and single-species management, the models developed in my research can complement a comprehensive approach to biodiversity monitoring.

As much as the above aspects are strengths of my research, they also identify important weaknesses of the approach. Presence and absence data are often criticised because they do not provide information on important demographic parameters such as fecundity and mortality (Magurran, 2003); however, these data are much more costly and time consuming to collect. Using several different methodologies to collect data made it difficult to quantify effort across methods for different taxa, and therefore, the potential of using another measure, such as relative density was limited. Variables that described spatial context and models that included variables measured at multiple scales were frequently identified as best models for several species and groups of species (Chapter 3 and 4). This was not unexpected, but because of characteristics of species, such as mobility and territory size that result in the perception of landscapes at different scales (e.g., Vos et al., 2001), generalisations were difficult across single-species models (Chapter 3) and limit the utility of the surrogate approach. Finally, my focus on vertebrate species may be criticized because, overall, vertebrates represent a small portion of species diversity. Indeed, future studies may benefit from the examination of taxa that are more diverse, use structure at smaller scales, and are not as flexible in their habitat selection (e.g., Redak, 2000). However, the availability of standardized methodology, relatively easy identification, and potential "buy-in" of stakeholders are benefits of using vertebrates. Further, in other studies, vertebrates have been shown to be effective surrogates of species richness (e.g., Grelle, 2002).

Future research should examine presence-only modelling methodologies (e.g., ecological-niche factor analysis; Hirzel et al., 2002) that may account for differences in methodologies and uncertainty in detections. An extension of the study area to include areas that are not impacted by management activities may also help to elucidate important relationships between species occurrence and structure, although in my study area this option is limited because of extensive impacts of multiple users. Finally, an analysis of single taxon or subset of a taxon (e.g., birds or neotropical migrants) may provide further insights into management recommendations as birds, in particular, are often associated with specific elements of forest structure (e.g., MacArthur and MacArthur, 1961; Hagen and Meehan, 2002; Diaz et al., 2005).

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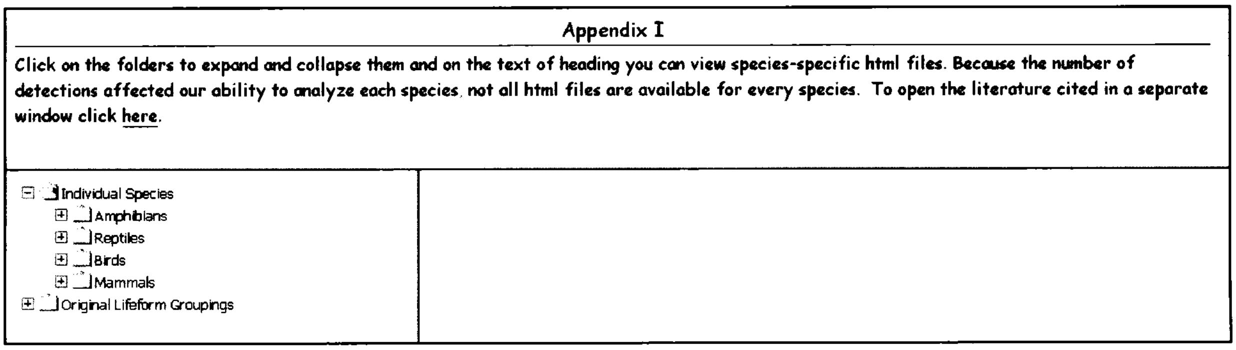
Appendix I. Explanation for electronic files and data CD.

This electronic appendix includes a menu structure that accesses a literature review for all vertebrate species expected to occur in the Williams Lake Study Area, detection summaries for each species by year and, for each species that had sufficient detections to model, candidate variables used in models to predict presence and absence, model results, and validation results. The literature review (Gillingham, 2003) was mostly complete at the outset of this study, although I added and contributed to several species. The goal of this literature review was to identify key structural and non-structural (biological) requirements of species expected to occur in the study area. The literature review was used in the development of *a priori* groupings of species based on structural associations, as part of a parallel study (Gillingham and Psyllakis, 2004; see original lifeform groupings file; Figure I.1). I used this literature review extensively to determine candidate models and ran all subsequent analyses. It is included here for completeness.

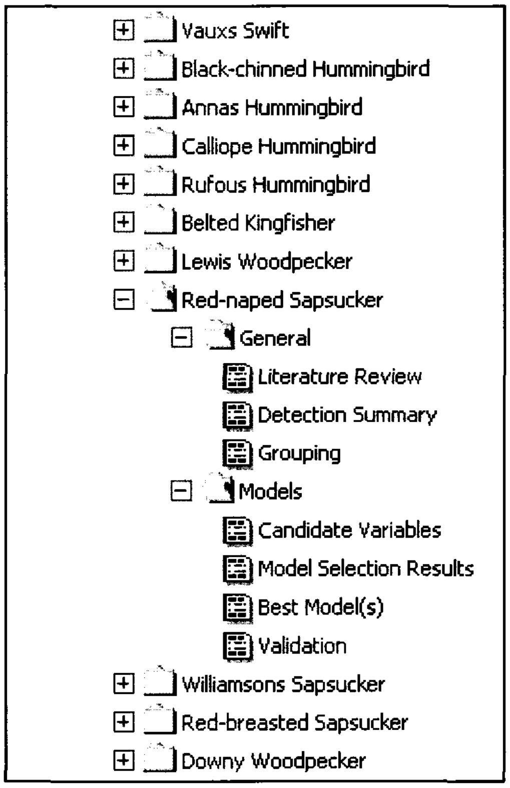
To access the files, select the "index.html" file to load the menu structure. It may take a minute to completely load in your browser. Once loaded, an expandable menu structure will appear (Figure I.1) that lists each species, in taxonomic order. The literature cited is also available at any time by clicking the appropriate location in the header. Selecting the folder for the species of interest expands the text of the heading and displays the available files (Figure I.2). Using the Red-naped Sapsucker (*Sphyrapicus nuchalis*) as an example, several additional tables are presented that explain each available file for species that were modelled in the order displayed in Figure I.2: Files included in the "General" folder are: Literature Review (Table I.1), Detection Summary (Table I.2), and Grouping (Table I.3). Files included in the "Models" folder include: Candidate Variables (Table I.4), Model Selection Results (Table I.5), Best Model(s) (Table I.6), and Validation (Table I.7).



Appendix I

Click on the folders to expand and collapse them and on the text of heading you can view species-specific html files. Because the number of detections affected our ability to analyze each species, not all html files are available for every species. To open the literature cited in a separate window click here.

Figure I.1. Screen capture of the menu structure included in Appendix I accessed by selecting the index file on the attached data CD. Literature cited can be accessed from this location at any time by clicking the appropriate link in the header.



- ⊞ Vauxs Swift
- ⊞ Black-chinned Hummingbird
- ⊞ Annas Hummingbird
- ⊞ Calliope Hummingbird
- ⊞ Rufous Hummingbird
- ⊞ Belted Kingfisher
- ⊞ Lewis Woodpecker
- ⊟ Red-naped Sapsucker
  - ⊟ General
    - Literature Review
    - Detection Summary
    - Grouping
  - ⊟ Models
    - Candidate Variables
    - Model Selection Results
    - Best Model(s)
    - Validation
- ⊞ Williamsons Sapsucker
- ⊞ Red-breasted Sapsucker
- ⊞ Downy Woodpecker

Figure I.2. Screen capture of a portion of the bird species expected to occur in the Williams Lake Study Area. Clicking on a species will display available files. In the "General" folder, files include the complete literature review, number of detections, and *a priori* grouping. Under the "Model" folder, files include the listing of the candidate variables used in the competing model sets, the results of model selection, the explanation of the coefficients for the top models, and the temporal and spatial validation results of those top models. Not all species will have model files as several species were not sufficiently detected to model.

Table I.1. Using Red-naped Sapsucker (*Sphyrapicus nuchalis*) as an example, information included with the literature review for each species expected to occur in the Williams Lake Study Area is included on the data CD.[1]

Red-naped Sapsucker (*Sphyrapicus nuchalis*)

	SS 3-6: 6H Primary cavity nester often adj. to water in live/dead trees (esp. deciduous). PCN.
Feeding Requirements	Tree boles in deciduous/mixed woodlands near water.
Habitats	Upland and Riparian forests.
Other Critical Requirements/Comments	NA
Provincial Status / ELP Inventory List	Breeds in B.C.
General Nonstructural Information	(1) Clutch dates 6 May-16 June. Clutch size 2. Young dates 14 May-4 Aug.
Species Migratory	(1) Arrives in the Interior in late Mar.; main spring movement occurs through Apr.; autumn migration begins late Aug. - mid Sept.; a few birds documented into Oct.
Species Resident	(1) No Interior winter records, but 3 coastal.
Breeds in Area	(1) Widespread breeder across central southern and southeastern BC north to Yoho National Park and through the Chilcotin-Cariboo basin; rarely further north.
Regional/Local/Provincial	(1) Widely distrib. across south. BC E of the Pacific and Cascade ranges, N through Chilcotin-Cariboo basin and Nechako plateau; rarely to Nulki L. in Nechako lowlands; wanders irreg. W of Pacific and Cascade ranges and has been reported from the Fraser l
Specialist or Generalist	Generalist.
Principle Predators/Parasites	(3) weasels on fledged young.
Principle Prey/Food	(5) insects
Principle Competitors	NA
Links to other species	(1) may nest in trees inhabited by Pileated woodpecker, Northern flicker, European starling.
Territorial Size (Exclusive/Overlapping)	NA
General Requirements	(1) sea- 1300m elevation; (4) trees infected with disease that have been weakened inside and out: weak excavators.
Vegetation Type	(1)(4) deciduous and mixed woodlands where poplar and birch are common (McGillivray & Semenchuck 1998 in (4)).
Vegetation Species Preferred	(1)(4) aspen groves in open P. pine forests/aspen fir parkland/logged forests where decid. groves remain/ aspen groves in open rangeland/birch groves/subalpine forest edges/residential gardens; nests in decid. trees; T. aspen/birches/poplar/B. cottonwood/
Cover Type / Level Needed	NA
Food	(5) cambium, fruit, berries, pine pitch often used instead of deciduous sap.

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[1] Literature cited included in the literature review can be found on the CD.

Table I.1. Literature review for the Red-naped Sapsucker (continued).

Tree Diameter Class (DBH)	(1) 15-64cm nesting tree dbh; (6) >/= 38 cm roosting tree.
Course Woody Debris	NA
Decay Class	NA
Stem Density	NA
Stand Age/Tree Age	NA
Basal Area	NA
Understory	NA
Deadfalls Stumps Snags etc	(6) snag dbh for both nesting and roosting >/= 38 cm.
Water (Lakes, Streams, Riparian)	NA
Habitats Avoided	NA
Type, size/depth or other characters needed	NA
Water Requirement	for breeding.
Year-round (Y/N)	NA
Nest Type	(1) cavity nester; nest heights .5-22.9m; cavity entrance hole diameters 10-17cm (3) first cavity in unexcavated trees at low height; in subsequent years new nests are excavated above the last on the same tree.
Habitat Requirements	(1) edge of woodlands adjacent to water bodies such as streams, ponds, sloughs, lakes, road edges, logging slashes, transmission line rights-of-way, mountain meadows (3) trees susceptible to heart rot (Keisker 1987 in (3)); preference for trees that show
Snags/Cavities required	NA
Forest Cover type	NA
Other Breeding Needs	NA
Winter Food	NA
Winter Cover	NA
Other Winter Requirements	NA
Management Issues	(1) In BC the geographical and biological relationships between nuchalis and ruber are complex; many areas where they meet, nest side by side, and interbreed.
References Used (Number)	(1) Campbell et al. 1990 (18); (2) Keisker 1987 (1012); (3) Daily 1993 (1034); (4) McClelland & McClelland 2000 (1035); (5) Ehrlich et al. 1998 (2037); (6) BC Ministry of Forests 2001 (3719)

Table I.2. Example of the Detection Summary file for the Red-nap Sapsucker. This file exists for all species detected in the Williams Lake Study Area from 2001-2004.

Detection summary for Red-naped Sapsucker (*Sphyrapicus nuchalis*)

Year	Total Detections	Plot/Transect Detections
2001	41	24
2002	99	45
2003	137	64
2004	84	35
All	Years	All

Table I.3. Example of the lifeform assignment table for the Red-naped Sapsucker found on the data CD. Lifeform groupings were part of a concurrent study and not discussed in this dissertation. The information is included for completeness.

Lifeform assignment for Red-naped Sapsucker (*Sphyrapicus nuchalis*)

This species was assigned to 1 Lifeform grouping(s)

Lifeform 8.0: Standing dead, dying trees and forages in trees, forest openings or edges; Requires dead or dying trees for nesting, denning, perching, or foraging' 'Includes species that excavate their own cavities as well as those that use secondary cavities and natural cavities'

A full description of each lifeform grouping and their member species can be found by clicking on the 'Original Lifeform Grouping' at the bottom of the folder list.

Table I.4. Example of Candidate Variables for the Red-naped Sapsucker included on the data CD. Candidate variables were selected and used to construct competing models for all species that were detected in the Williams Lake Study Area and met prevalence criteria (>10% and <90% occurrence).

Candidate Variables for examining presence/absence of Red-naped Sapsucker (*Sphyrapicus nuchalis*)	
Plot-Level Variables	percent gap, percent at cover, deciduous stems per ha, live basal area, dead basal area, large basal area, distance from forest edge
Vegetation Resource Inventory (VRI) Variables	aspen cover, stand structure class, crown closure, leading species height, live basal area
Stand-Level Variables	percent gap, percent at cover, deciduous tree stems per ha, dead basal area, live basal area, large tree basal area, stand distance from forest edge
Landscape-Level Variables	interspersion juxtaposition index 50 ha, mean patch size 50 ha, edge density 50 ha, mean core area 50 ha, proportion conifer 50 ha, proportion aspen shrub 50 ha

Table I. 5. Example of the Model Selection Result file included on the data CD for the Red-naped Sapsucker. Models with AIC< 2.0 are reported. Tables I.5A, I.5B, I.5C include the results for models using plot, Vegetation Resource Inventory (VRI), and stand structural data models, respectively.

Table I.5A. Results from plot models for the Red-naped Sapsucker.

Model	K	N	ROC	LL	AICc	ΔAIC	wi	Evidence Ratio
Percent canopy gap Distance to forest edge Proportion aspen and shrub (50 ha)*	4	228	0.753	-133.015	274.139	0.000	0.359	1.000
Percent canopy gap Distance to forest edge Proportion aspen and shrub (50 ha)* Natural stump / ha	5	228	0.750	-132.761	275.703	1.564	0.164	2.186
Distance to forest edge Proportion aspen and shrub (50 ha)*	3	228	0.745	-134.827	275.707	1.568	0.164	2.190
Distance to forest edge Proportion aspen and shrub (50 ha)* Natural stump / ha	4	228	0.743	-133.903	275.913	1.774	0.148	2.428

* arcsine transformation

Table I.5B. Results from Vegetation Resource Inventory (VRI) models for the Red-naped Sapsucker.

Note: stand structure classes 6, 8, 13 not used due to complete separation

Model	K	N	ROC	LL	AICc	ΔAIC	wi	Evidence Ratio
Sum of crown closure	2	83	0.603	-55.706	115.463	0.000	0.175	1.000
Aspen cover	2	83	0.599	-56.052	116.153	0.691	0.124	1.413
Aspen cover Sum of crown closure	3	83	0.687	-55.188	116.529	1.066	0.103	1.704
Aspen cover Leading species height	3	83	0.655	-55.227	116.606	1.143	0.099	1.771
Live basal area	2	83	0.538	-56.389	116.827	1.365	0.089	1.979
Sum of crown closure Leading species height	3	83	0.621	-55.521	117.195	1.732	0.074	2.378

Table I.5C. Results from stand-structure data models for the Red-naped Sapsucker.

Model	K	N	ROC	LL	AICc	ΔAIC	wi	Evidence Ratio
Percent Aspen Edge density (50 ha)	3	97	0.716	-56.393	118.914	0.000	0.313	1.000
Edge density (50 ha)	2	97	0.704	-57.487	119.017	0.102	0.297	1.052

Table I.6. Example of the Best Model file for the Red-naped Sapsucker. The β-coefficeints and odds ratios are reported for each variable included in the top model (i.e., lowest AIC_c) for plot (Table I.6A), Vegetation Resource Inventory (Table I.6B), and stand models(Table I.6C).

Table I.6A. Top logistic regression model that best discriminated between presence and not detected at the plot sceale for the Red-naped Sapsucker.

						95% C.I.	
Variable	β	S.E.	Z	p-value	Odds Ratio	Lower	Upper
Percent canopy gap	1.251	0.637	1.960	0.050	3.494	0.949	12.862
Distance to forest edge	-0.007	0.003	-2.700	0.007	0.993	0.988	0.997
Proportion aspen and shrub (50 ha)*	3.413	1.296	2.630	0.008	30.363	2.232	413.075
Constant	-1.398	0.648	-2.160	0.031			

* arcsine transformed

Table I.6B. Top logistic regression model that best discriminated between presence and not detected at the stand scale using Vegetation Resource Inventory data for the Red-naped Sapsucker.

						95% C.I.	
Variable	β	S.E.	z	p-value	Odds Ratio	Lower	Upper
Sum of crown closure	-0.019	0.015	-1.238	0.216	0.981	0.956	1.008
Constant	1.430	0.986	1.450	0.147			

Table I.6C. Top logistic regression model that best discriminated between present and not detected at the stand scale using stand level data for the Red-naped Sapsucker.

						95% C.I.	
Variable	β	S.E.	z	p-value	Odds Ratio	Lower	Upper
Percent Aspen	0.041	0.030	1.369	0.171	1.042	0.981	1.106
Edge density (50 ha)	0.012	0.003	3.571	<0.000	1.012	1.005	1.019
Constant	-2.371	0.783	-3.030	0.002			

Table I.7. Example of Validation Files included on the data CD for the Red-naped Sapsucker. Files are included for those species that had sufficient detections in 2004 at the spatial or temporal validation plots to test models at either, or both, the plot and stand scale. For spatial validation models, β -coefficients, p-value, and odds ratio are reported for each variable included in the model, as well as the ROC values for the model constructed with development data and its spatially validated counterpart. For temporal validation tables the β-coefficient for each variable is reported using a single year's data for all years, including 2004, as well as ROC values for those models.

Table I.7A. Spatial validation of the best plot-level model for the Red-naped Sapsucker.

	2001-2003				2004			
Variable	β	p-value	Odds Ratio	ROC	β	p-value	Odds Ratio	ROC
Percent canopy gap	1.251	0.050	3.494	0.753	-1.496	0.418	0.224	0.737
Distance to forest edge	-0.007	0.007	0.993		-0.011	0.014	0.989	
Proportion aspen and shrub (50 ha)*	3.413	0.008	30.363		1.131	0.482	3.100	
Constant	-1.398	0.031			-0.345	0.731		

Table I.7B. Temporal validation of the best plot-level model for the Red-naped Sapsucker.

	β				
Variable	2001-03	2001	2002	2003	2004
Percent canopy gap	1.251	2.096	0.456	0.558	-1.236
Distance to forest edge	-0.007	-0.005	-0.013	-0.007	-0.011
Proportion aspen and shrub (50 ha)*	3.413	1.195	2.995	2.058	5.501
Constant	-1.398	-3.441	-1.713	-1.325	-1.232
ROC	0.753	0.692	0.748	0.692	0.773

Table I.7C. Spatial validation of the best stand-level model for the Red-naped Sapsucker.

	2001-2003				2004			
Variable	β	p-value	Odds Ratio	ROC	β	p-value	Odds Ratio	ROC
Percent Aspen	0.041	0.171	1.042	0.716	2.203	0.542	9.052	0.752
Edge density (50 ha)	0.012	<0.000	1.012		0.011	0.072	1.011	
Constant	-2.371	0.002			-3.332	0.005		

Table I.7D. Temporal validation of the best stand-level model for the Red-naped Sapsucker.

	B				
Variable	2001-03	2001	2002	2003	2004
Percent Aspen	0.041	-0.037	0.080	-0.006	-0.072
Edge density (50 ha)	0.012	0.007	0.014	0.014	0.006
Constant	-2.371	-2.731	-4.421	-3.188	-1.574
ROC	0.716	0.659	0.761	0.726	0.702

Literature Cited

Gillingham, M.P., 2003. Lifeforms, structure and biodiversity: species literature review. March 2003. 651 pp. Available at http://web.unbc.ca/biodiversity/ *accessed* March 2006.

Gillingham, M.P., Psyllakis, J.M., 2004. Lifeforms: structure and biodiversity. 27 April 2004. 120 pp. Available at http://web.unbc.ca/biodiversity/ *accessed* March 2006.

Appendix II. List of vertebrate species (200 species), with associated number of detections, detected in the Williams Lake Study Area from 2001-2004. Species modelled are in bold text.

	Species	Scientific Name	Detections all years
Reptiles	Common Garter Snake	*Thamnophis sirtalis*	2
	Western Terrestrial Garter Snake	*Thamnophis elegans*	3
Amphibians	Columbia Spotted Frog	*Rana luteiventris*	8
	Long-toed Salamander	*Ambystoma macrodactylum*	7
	Western Toad	*Bufo boreas*	151
	Wood Frog	*Rana sylvatica*	47
Birds	**Alder Flycatcher**	*Empidonax alnorum*	86
	American Avocet	*Recurvirostra americana*	1
	American Bittern	*Botaurus lentiginosus*	2
	American Coot	*Fulica americana*	203
	American Crow	*Corvus brachyrhynchos*	39
	American Kestrel	*Falco sparverius*	3
	American Pipit	*Anthus rubescens*	1
	American Redstart	*Setophaga ruticilla*	53
	American Robin	*Turdus migratorius*	1133
	American Widgeon	*Anas americana*	65
	Bald Eagle	*Haliaeetus leucocephalus*	5
	Barred Owl	*Strix varia*	48
	Barrow's Goldeneye	*Bucephala islandica*	38
	Belted Kingfisher	*Ceryle alcyon*	1
	Black Tern	*Chlidonias niger*	113
	Black-backed Woodpecker	*Picoides arcticus*	54
	Black-capped Chickadee	*Poecile atricapillus*	805
	Blackpoll Warbler	*Dendroica striata*	4
	Blue Grouse	*Dendragapus obscurus*	2
	Blue-winged Teal	*Anas discors*	52
	Bohemian Waxwing	*Bombycilla garrulus*	6
	Bonaparte's Gull	*Larus philadelphia*	1
	Boreal Chickadee	*Poecile hudsonicus*	11
	Boreal Owl	*Aegolius funereus*	2
	Brewer's Blackbird	*Euphagus cyanocephalus*	3
	Brown Creeper	*Certhia americana*	366
	Brown-headed Cowbird	*Molothrus ater*	220
	Bufflehead	*Bucephala albeola*	238
	Calliope Hummingbird	*Stellula calliope*	4
	Canada Goose	*Branta canadensis*	305

Species	Scientific Name	Detections all years
Canvasback	*Aythya valisineria*	1
Cassin's Vireo	*Vireo cassinii*	1190
Cedar Waxwing	*Bombycilla cedrorum*	31
Chipping Sparrow*	*Spizella passerina*	1650
Cinnamon Teal	*Anas cyanoptera*	26
Clay-colored Sparrow	*Spizella pallida*	28
Common Goldeneye	*Bucephala clangula*	6
Common Loon	*Gavia immer*	174
Common Merganser	*Mergus merganser*	2
Common Nighthawk	*Chordeiles minor*	13
Common Raven	*Corvus corax*	358
Common Redpoll	*Carduelis flammea*	17
Common Snipe	*Gallinago gallinago*	109
Common Yellowthroat	*Geothlypis trichas*	178
Cooper's Hawk	*Accipiter cooperii*	2
Dark-eyed Junco*	*Junco hyemalis*	2403
Downy Woodpecker	*Picoides pubescens*	69
Dusky Flycatcher	*Empidonax oberholseri*	172
Eastern Kingbird	*Tyrannus tyrannus*	11
European Starling	*Sturnus vulgaris*	2
Evening Grosbeak*	*Coccothraustes vespertinus*	1209
Gadwall	*Anas strepera*	16
Golden Eagle	*Aquila chrysaetos*	1
Golden-crowned Kinglet	*Regulus satrapa*	734
Golden-crowned Sparrow	*Zonotrichia atricapilla*	2
Gray Catbird	*Dumetella carolinensis*	3
Gray Jay	*Perisoreus canadensis*	329
Great Blue Heron	*Ardea herodias*	1
Great Gray Owl	*Strix nebulosa*	9
Great Horned Owl	*Bubo virginianus*	30
Greater Scaup	*Aythya marila*	4
Greater Yellowlegs	*Tringa melanoleuca*	46
Green-winged Teal	*Anas crecca*	75
Hairy Woodpecker	*Picoides villosus*	239
Hammond's Flycatcher	*Empidonax hammondii*	147
Hermit Thrush	*Catharus guttatus*	1009
Herring Gull	*Larus argentatus*	2
Hooded Merganser	*Lophodytes cucullatus*	13
Horned Grebe	*Podiceps auritus*	2
Killdeer	*Charadrius vociferus*	82
Least Flycatcher	*Empidonax minimus*	213
Least Sandpiper	*Calidris minutilla*	1
Lesser Scaup	*Aythya affinis*	195
Lesser Yellowlegs	*Tringia flavipes*	7
Lincoln's Sparrow	*Melospiza lincolnii*	20

Species	Scientific Name	Detections all years
Long-eared Owl	*Asio otus*	2
MacGillivray's Warbler	*Oporornis tolmiei*	92
Magnolia Warbler	*Dendroica magnolia*	17
Mallard	*Anas platyrhynchos*	312
Marsh Wren	*Cistothorus palustris*	308
Merlin	*Falco columbarius*	4
Mountain Bluebird	*Sialia currucoides*	8
Mountain Chickadee	*Poecile gambeli*	1267
Nashville Warbler	*Vermivora ruficapilla*	10
Northern Flicker	*Colaptes auratus*	553
Northern Goshawk	*Accipiter gentilis*	12
Northern Harrier	*Circus cyaneus*	5
Northern Pintail	*Anas acuta*	3
Northern Pygmy Owl	*Glaucidium gnoma*	20
Northern Rough-winged Swallow	*Stelgidopteryx serripennis*	4
Northern Saw-whet Owl	*Aegolius acadicus*	29
Northern Shoveler	*Anas clypeata*	7
Northern Waterthrush	*Seiurus noveboracensis*	145
Olive-sided Flycatcher	*Contopus borealis*	488
Orange-crowned Warbler	*Vermivora celata*	689
Osprey	*Pandion haliaetus*	1
Pacific Slope Flycatcher	*Empidonax difficilis*	2
Pied-billed Grebe	*Podilymbus podiceps*	106
Pileated Woodpecker	*Dryocopus pileatus*	384
Pine Grosbeak	*Pinicola enucleator*	18
Pine Siskin*	*Carduelis pinus*	863
Purple Finch	*Carpodacus purpureus*	4
Red Crossbill	*Loxia curvirostra*	262
Red-breasted Merganser	*Mergus serrator*	5
Red-breasted Nuthatch*	*Sitta canadensis*	1868
Red-eyed Vireo	*Vireo olivaceus*	51
Redhead	*Aythya americana*	14
Red-naped Sapsucker	*Sphyrapicus nuchalis*	361
Red-necked Grebe	*Podiceps grisegena*	2
Red-tailed Hawk	*Buteo jamaicensis*	88
Red-winged Blackbird	*Agelaius phoeniceus*	286
Ring-billed Gull	*Larus delawarensis*	1
Ring-necked Duck	*Aythya collaris*	132
Ruby-crowned Kinglet*	*Regulus calendula*	2021
Ruddy Duck	*Oxyura jamaicensis*	145
Ruffed Grouse	*Bonasa umbellus*	350
Rufous Hummingbird	*Selasphorus rufus*	9
Rusty Blackbird	*Euphagus carolinus*	1
Sandhill Crane	*Grus canadensis*	279

	Species	Scientific Name	Detections all years
	Savannah Sparrow	*Passerculus sandwichensis*	55
	Say's Phoebe	*Sayornis saya*	6
	Semipalmated Plover	*Charadrius semipalmatus*	1
	Semipalmated Sandpiper	*Calidris pusilla*	5
	Sharp-shinned Hawk	*Accipiter striatus*	3
	Sharp-tailed Grouse	*Tympanuchus phasianellus*	3
	Short-billed Dowitcher	*Limnodromus griseus*	3
	Solitary Sandpiper	*Tringa solitaria*	58
	Song Sparrow	*Melospiza melodia*	113
	Sora	*Porzana carolina*	109
	Spotted Sandpiper	*Actitis macularia*	27
	Spruce Grouse	*Dendragapus canadensis*	35
	Swainson's Thrush*	*Catharus ustulatus*	1959
	Tennessee Warbler	*Vermivora peregrina*	3
	Three-toed Woodpecker	*Picoides tridactylus*	102
	Townsend's Solitaire	*Myadestes townsendi*	248
	Townsend's Warbler	*Dendroica townsendi*	135
	Tree Swallow	*Tachycineta bicolor*	157
	Varied Thrush	*Ixoreus naevius*	19
	Veery	*Catharus fuscescens*	26
	Vesper Sparrow	*Pooecetes gramineus*	9
	Violet-green Swallow	*Tachycineta thalassina*	16
	Warbling Vireo	*Vireo gilvus*	655
	Western Kingbird	*Tyrannus verticalis*	2
	Western Tanager	*Piranga ludoviciana*	1111
	Western Wood-Pewee	*Contopus sordidulus*	504
	White-crowned Sparrow	*Zonotrichia leucophrys*	19
	White-winged Crossbill	*Loxia leucoptera*	12
	Willow Flycatcher	*Empidonax traillii*	204
	Wilson's Phalarope	*Phalaropus tricolor*	26
	Wilson's Warbler	*Wilsonia pusilla*	150
	Winter Wren	*Troglodytes troglodytes*	103
	Wood Duck	*Aix sponsa*	2
	Yellow Warbler	*Dendroica petechia*	98
	Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*	168
	Yellow-rumped Warbler*	*Dendroica coronata*	1863
Mammals	Beaver	*Castor canadensis*	6
	Big Brown Bat	*Eptesicus fuscus*	6
	Black Bear	*Ursus americanus*	451
	Bushy-tailed Woodrat	*Neotoma cinerea*	3
	Columbian Ground Squirrel	*Spermophilus columbianus*	4
	Common Shrew	*Sorex cinereus*	4
	Cougar	*Puma concolor*	10

Species	Scientific Name	Detections all years
Coyote	*Canis latrans*	160
Deer Mouse	*Peromyscus maniculatus*	455
Dusky Shrew	*Sorex monticolus*	1
Ermine	*Mustela erminea*	29
Fisher	*Martes pennanti*	7
Grey Wolf	*Canis lupus*	10
Grizzly Bear	*Ursus arctos*	1
Heather Vole	*Phenacomys intermedius*	2
Hoary Bat	*Lasiurus cinereus*	11
Little Brown Myotis	*Myotis lucifugus*	21
Long Legged Myotis	*Myotis volans*	3
Long-tailed Weasel	*Mustela frenata*	78
Lynx	*Lynx canadensis*	42
Marten	*Martes americana*	10
Meadow Jumping Mouse	*Zapus hudsonius*	2
Meadow Vole	*Microtus pennsylvanicus*	97
Moose	*Alces alces*	876
Mule Deer*	*Odocoileus hemionus*	2255
Muskrat	*Ondatra zibethicus*	46
Northern Bog Lemming	*Synaptomys borealis*	3
Northern Flying Squirrel	*Glaucomys sabrinus*	24
Porcupine	*Erethizon dorsatum*	8
Red Fox	*Vulpes vulpes*	27
Red Squirrel*	*Tamiasciurus hudsonicus*	2449
Silver-haired Bat	*Lasionycteris noctivagans*	2
Snowshoe Hare	*Lepus americanus*	2218
Southern Red-backed Vole	*Clethrionomys gapperi*	2602
Striped Skunk	*Mephitis mephitis*	8
Western Jumping Mouse	*Zapus princeps*	2
Western Long-eared Myotis	*Myotis evotis*	163
Yellow-bellied Marmot	*Marmota flaviventris*	1
Yellow-pine Chipmunk	*Tamias amoenus*	317

* species not modelled because of commonness

Appendix III. List of vertebrate species used in non-metric multidimensional scaling ordination analysis (n = 66). Species were detected in the Williams Lake Study Area from 2001-2004 and ordination analysis was used in conjunction with cluster analysis to determine plots with similar species co-occurrence. Species detected at less than 5% of plots were omitted as were species that had high levels of spatial uncertainty associated with their detection (e.g., rarely detected not in flight, calls that travel long distances).

	Species	Scientific Name	Total detections all years
Amphibians	Western Toad	*Bufo boreas*	151
Birds	Alder Flycatcher	*Empidonax alnorum*	86
	American Crow	*Corvus brachyrhynchos*	39
	American Redstart	*Setophaga ruticilla*	53
	American Robin	*Turdus migratorius*	1133
	Black-backed Woodpecker	*Picoides arcticus*	54
	Black-capped Chickadee	*Poecile atricapillus*	805
	Brown Creeper	*Certhia americana*	366
	Brown-headed Cowbird	*Molothrus ater*	220
	Cassin's Vireo	*Vireo cassinii*	1190
	Chipping Sparrow	*Spizella passerine*	1650
	Clay-colored Sparrow	*Spizella pallida*	28
	Common Raven	*Corvus corax*	358
	Common Yellowthroat	*Geothlypis trichas*	178
	Dark-eyed Junco	*Junco hyemalis*	2403
	Downy Woodpecker	*Picoides pubescens*	69
	Dusky Flycatcher	*Empidonax oberholseri*	172
	Golden-crowned Kinglet	*Regulus satrapa*	734
	Gray Jay	*Perisoreus canadensis*	329
	Hairy Woodpecker	*Picoides villosus*	239
	Hammond's Flycatcher	*Empidonax hammondii*	147
	Hermit Thrush	*Catharus guttatus*	1009
	Least Flycatcher	*Empidonax minimus*	213
	MacGillivray's Warbler	*Oporornis tolmiei*	92
	Mountain Chickadee	*Poecile gambeli*	1267
	Northern Flicker	*Colaptes auratus*	553
	Northern Waterthrush	*Seiurus noveboracensis*	145
	Olive-sided Flycatcher	*Contopus borealis*	488
	Orange-crowned Warbler	*Vermivora celata*	689
	Pileated Woodpecker	*Dryocopus pileatus*	384
	Pine Siskin	*Carduelis pinus*	863
	Red-breasted Nuthatch	*Sitta canadensis*	1868
	Red-eyed Vireo	*Vireo olivaceus*	51
	Red-naped Sapsucker	*Sphyrapicus nuchalis*	361
	Red-tailed Hawk	*Buteo jamaicensis*	88

	Species	Scientific Name	Total detections all years
	Ruby-crowned Kinglet	*Regulus calendula*	2021
	Ruffed Grouse	*Bonasa umbellus*	350
	Song Sparrow	*Melospiza melodia*	113
	Spruce Grouse	*Dendragapus canadensis*	35
	Swainson's Thrush	*Catharus ustulatus*	1959
	Three-toed Woodpecker	*Picoides tridactylus*	102
	Townsend's Solitaire	*Myadestes townsendi*	248
	Townsend's Warbler	*Dendroica townsendi*	135
	Veery	*Catharus fuscescens*	26
	Warbling Vireo	*Vireo gilvus*	655
	Western Tanager	*Piranga ludoviciana*	1111
	Western Wood-Pewee	*Contopus sordidulus*	504
	Willow Flycatcher	*Empidonax traillii*	204
	Wilson's Warbler	*Wilsonia pusilla*	150
	Winter Wren	*Troglodytes troglodytes*	103
	Yellow Warbler	*Dendroica petechia*	98
	Yellow-rumped Warbler	*Dendroica coronata*	1863
Mammals	Black Bear	*Ursus americanus*	451
	Coyote	*Canis latrans*	160
	Deer Mouse	*Peromyscus maniculatus*	455
	Ermine	*Mustela erminea*	29
	Long-tailed Weasel	*Mustela frenata*	78
	Lynx	*Lynx canadensis*	42
	Meadow Vole	*Microtus pennsylvanicus*	97
	Moose	*Alces alces*	876
	Mule Deer	*Odocoileus hemionus*	2255
	Red Fox	*Vulpes vulpes*	27
	Red Squirrel	*Tamiasciurus hudsonicus*	2449
	Snowshoe Hare	*Lepus americanus*	2218
	Southern Red-backed Vole	*Clethrionomys gapperi*	2602
	Yellow-pine Chipmunk	*Tamias amoenus*	317

Appendix IV. Comparison of cluster analysis results for groupings of plots based on vertebrate-species co-occurrence (X, lettered groups) and structural characteristics (Y, numbered groups). Structure groups with the highest number of plots overlapping with species groups are in bold text (**Y**). Overlap for groups based on each method was minimal (range = 16.7% - 50.0%).

										Cluster Groups												
Plot	A	1	B	2	C	3	D	4	E	5	F	6	G	7	H	8	I	9	J	10	K	11
P1	X	Y																				
P17	X									Y												
P18	X													Y								
P19	X													Y								
P22	X													Y								
P38	X									Y												
P39	X									Y												
P40	X															Y						
P41	X							**Y**														
P44	X	Y																				
P45	X					Y																
P47	X							**Y**														
P48	X															Y						
P62	X									Y												
P74	X							**Y**														
P77	X							**Y**														
P78	X							**Y**														
P106	X									Y												
P107	X			Y																		
P120	X							**Y**														
P121	X							**Y**														
P124	X							**Y**														
P125	X															Y						
P127	X							**Y**														
P135	X																	Y				
P136	X							**Y**														
P137	X																	Y				
P139	X							**Y**														
P140	X							**Y**														
P169	X																			Y		
P170	X																	Y				
P179	X	Y																				
P127A	X							**Y**														
P127B	X							**Y**														
P2			X	Y																		
P3			X			Y																
P4		Y	X																			
P5		Y	X																			
P70			X											Y								
P71			X					Y														
P112			X							Y												
P113			X							Y												

	Cluster Groups																					
Plot	A	1	B	2	C	3	D	4	E	5	F	6	G	7	H	8	I	9	J	10	K	11
P117			X									**Y**										
P153			X									**Y**										
P156			X									**Y**										
P157			X									**Y**										
P158			X									**Y**										
P187			X			Y																
P192			X			Y																
P209			X					Y														
P178A		Y	X																			
P57A			X									**Y**										
P6		**Y**			X																	
P7					X			Y														
P9					X					Y												
P11					X	Y																
P13				Y	X																	
P16					X									Y								
P30					X			Y														
P31		**Y**			X																	
P43		**Y**			X																	
P46		**Y**			X																	
P58					X											Y						
P59					X											Y						
P76					X									Y								
P104					X					Y												
P108		**Y**			X																	
P109					X					Y												
P110		**Y**			X																	
P118					X							Y										
P119					X											Y						
P122					X									Y								
P128					X			Y														
P129					X			Y														
P130					X																	Y
P131				Y	X																	
P138					X											Y						
P150					X									Y								
P151					X									Y								
P155					X									Y								
P159					X							Y										
P190		**Y**			X																	
P210				Y	X																	
P110A					X					Y												
P114A					X			Y														
P118A					X											Y						
P8				**Y**			X															
P42		Y					X															
P72				**Y**			X															
P86						Y	X															
P97						Y	X															

Cluster Groups

Plot	A	1	B	2	C	3	D	4	E	5	F	6	G	7	H	8	I	9	J	10	K	11
P126							X									Y						
P188				Y			X															
P193				Y			X															
P10								Y	X													
P12						Y			X													
P14						Y			X													
P25						Y			X													
P53						Y			X													
P80									X	Y												
P82						Y			X													
P96						Y			X													
P114									X	Y												
P134								Y	X													
P141						Y			X													
P142									X									Y				
P145									X											Y		
P149									X									Y				
P171						Y			X													
P172		Y							X													
P173									X	Y												
P178								Y	X													
P184						Y			X													
P191		Y							X													
P199						Y			X													
P223									X			Y										
P224									X			Y										
P236									X											Y		
P243									X											Y		
P141A									X									Y				
P15											X	Y										
P54											X	Y										
P55											X	Y										
P56											X	Y										
P57											X	Y										
P67						Y					X											
P68						Y					X											
P87						Y					X											
P90						Y					X											
P92						Y					X											
P174		Y									X											
P176						Y					X											
P177						Y					X											
P181											X									Y		
P183											X	Y										
P202						Y					X											
P203											X									Y		
P206											X									Y		
P208											X									Y		
P222											X	Y										

											Cluster Groups											
Plot	A	1	B	2	C	3	D	4	E	5	F	6	G	7	H	8	I	9	J	10	K	11
P237											X							Y				
P238								Y			X											
P240											X							Y				
P241											X									Y		
P152A											X	**Y**										
P56B											X	**Y**										
P20				Y									X									
P21				Y									X									
P32													X			Y						
P33										Y			X									
P34		Y											X									
P35		Y											X									
P36													X			Y						
P37										Y			X									
P166								Y					X									
P23														Y	X							
P24														Y	X							
P27															X	**Y**						
P28															X			Y				
P49								Y							X							
P50														Y	X							
P60								Y							X							
P61															X	**Y**						
P63															X	**Y**						
P64															X	**Y**						
P65				Y											X							
P79						Y									X							
P81						Y									X							
P101															X	**Y**						
P102										Y					X							
P103										Y					X							
P105				Y											X							
P146															X	**Y**						
P147															X			Y				
P148															X			Y				
P160															X			Y				
P161															X			Y				
P180						Y									X							
P195						Y									X							
P207															X	**Y**						
P180A															X			Y				
P180B										Y					X							
P26														Y			X					
P88																	X			**Y**		
P89																	X			**Y**		
P91						Y											X					
P93																	X			**Y**		
P94																	X			**Y**		
P95												Y					X					

	Cluster Groups																					
Plot	A	1	B	2	C	3	D	4	E	5	F	6	G	7	H	8	I	9	J	10	K	11
P143																	X	Y				
P144																	X			**Y**		
P185												Y					X					
P196																	X			**Y**		
P201						Y											X					
P204																	X			**Y**		
P205																	X			**Y**		
P212						Y											X					
P230												Y					X					
P231								Y									X					
P232												Y					X					
P233																Y	X					
P239								Y									X					
P242																	X			**Y**		
P50A														Y			X					
P90A																	X			**Y**		
P29																			X	Y		
P51												**Y**							X			
P52												**Y**							X			
P69										Y									X			
P132																			X			Y
P133								Y											X			
P152												**Y**							X			
P154												**Y**							X			
P186						Y													X			
P198												**Y**							X			
P211						Y													X			
P220								Y											X			
P221								Y											X			
P234								Y											X			
P235																		Y	X			
P56A												**Y**							X			
P83										Y											X	
P84										Y											X	
P85														Y							X	
P111														Y							X	

Appendix V. Indicator species analysis to identify vertebrate species most closely associated with the 11 groups identified with cluster analysis of plots based on species co-occurrence in the Williams Lake Study Area from 2001-2004.

We used indicator species analysis (Dufrêne and Legendre, 1997) to determine species most associated with each of the 11 plot groups identified with cluster analysis (Table V.1). Indicator species analysis describes how well each species separates among groups by comparing the occurrence of each species within each group (McCune and Grace, 2002). A perfect match occurs when the species only occurs in one group, never others. The *p*-value is calculated based on the proportion of randomized trials with indicator values equal to or exceeding the observed value (McCune and Grace, 2002) and tests the hypothesis of no differences among groups. The table is provided only as supplemental information as we made no attempt to interpret relationships.

Table V.1. Species included in each group as determined by indicator species analysis. Groups were defined by cluster analysis of species co-occurrence for plots in the Williams Lake Study Area from 2001-2004.

Species	Latin	group	*p*-value
Coyote	*Canis latrans*	1	0.03
Cassin's Vireo	*Vireo cassinii*	1	0.01
Hermit Thrush	*Catharus guttatus*	1	0.02
Snowshoe Hare	*Lepus americanus*	1	0.02
Lynx	*Lynx canadensis*	1	0.01
Red Squirrel	*Tamiasciurus hudsonicus*	1	0.02
Black Bear	*Ursus americanus*	1	0.02
American Crow	*Corvus brachyrhynchos*	2	0.23
Gray Jay	*Perisoreus canadensis*	3	0.01
Spruce Grouse	*Dendragapus canadensis*	3	0.05
Western Tanager	*Piranga ludoviciana*	3	0.08
Willow Flycatcher	*Empidonax traillii*	3	0.04
Chipping Sparrow	*Spizella passerine*	4	0.01
Common Raven	*Corvus corax*	5	0.06
Mountain Chickadee	*Poecile gambeli*	5	0.05
Pileated Woodpecker	*Dryocopus pileatus*	5	0.09

Table V.1. Species included in each group as determined by indicator species analysis (continued).

Species	Latin	group	*p*-value
Alder Flycatcher	*Empidonax alnorum*	6	0.03
American Robin	*Turdus migratorius*	6	0.01
Black-capped Chickadee	*Poecile atricapillus*	6	0.01
Brown-headed Cowbird	*Molothrus ater*	6	0.02
Western Toad	*Bufo boreas*	6	0.05
Downy Woodpecker	*Picoides pubescens*	6	0.01
Dusky Flycatcher	*Empidonax oberholseri*	6	0.03
Hairy Woodpecker	*Picoides villosus*	6	0.02
Least Flycatcher	*Empidonax minimus*	6	0.01
Meadow Vole	*Microtus pennsylvanicus*	6	0.05
Long-tailed Weasel	*Mustela frenata*	6	0.04
Northern Flicker	*Colaptes auratus*	6	0.01
Orange-crowned Warbler	*Vermivora celata*	6	0.08
Olive-sided Flycatcher	*Contopus borealis*	6	0.01
Red-naped Sapsucker	*Sphyrapicus nuchalis*	6	0.02
Red-tailed Hawk	*Buteo jamaicensis*	6	0.03
Ruffed Grouse	*Bonasa umbellus*	6	0.03
Veery	*Catharus fuscescens*	6	0.08
Western Wood-Pewee	*Contopus sordidulus*	6	0.01
Pine Siskin	*Carduelis pinus*	7	0.01
Red-breasted Nuthatch	*Sitta canadensis*	7	0.16
Ruby-crowned Kinglet	*Regulus calendula*	7	0.02
Warbling Vireo	*Vireo gilvus*	7	0.02
Clay-colored Sparrow	*Spizella pallida*	8	0.29
Dark-eyed Junco	*Junco hyemalis*	8	0.01
MacGillivray's Warbler	*Oporornis tolmiei*	8	0.42
Yellow-pine Chipmunk	*Tamias amoenus*	8	0.01
Townsend's Solitaire	*Myadestes townsendi*	8	0.03
Yellow-rumped Warbler	*Dendroica coronata*	8	0.08
Hammond's Flycatcher	*Empidonax hammondii*	9	0.22
Northern Waterthrush	*Seiurus noveboracensis*	9	0.02
Red-eyed Vireo	*Vireo olivaceus*	9	0.02
Wilson's Warbler	*Wilsonia pusilla*	9	0.04
Yellow Warbler	*Dendroica petechia*	9	0.11

Table V.1. Species included in each group as determined by indicator species analysis (continued).

Species	Latin	group	p-value
Moose	*Alces alces*	10	0.12
American Redstart	*Setophaga ruticilla*	10	0.01
Common Yellowthroat	*Geothlypis trichas*	10	0.03
Deer Mouse	*Peromyscus maniculatus*	10	0.03
Song Sparrow	*Melospiza melodia*	10	0.04
Townsend's Warbler	*Dendroica townsendi*	10	0.01
Black-backed Woodpecker	*Picoides arcticus*	11	0.02
Brown Creeper	*Certhia americana*	11	0.01
Southern Red-backed Vole	*Clethrionomys gapperi*	11	0.01
Golden-crowned Kinglet	*Regulus satrapa*	11	0.01
Ermine	*Mustela erminea*	11	0.01
Mule Deer	*Odocoileus hemionus*	11	0.01
Swainson's Thrush	*Catharus ustulatus*	11	0.01
Three-toed Woodpecker	*Picoides tridactylus*	11	0.01
Red Fox	*Vulpes vulpes*	11	0.01
Winter Wren	*Troglodytes troglodytes*	11	0.01

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Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67, 345-366.

McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, OR.