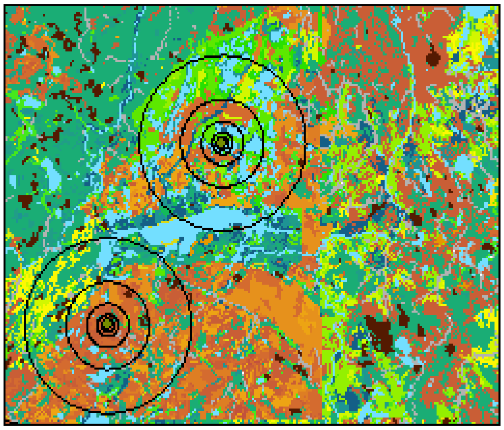
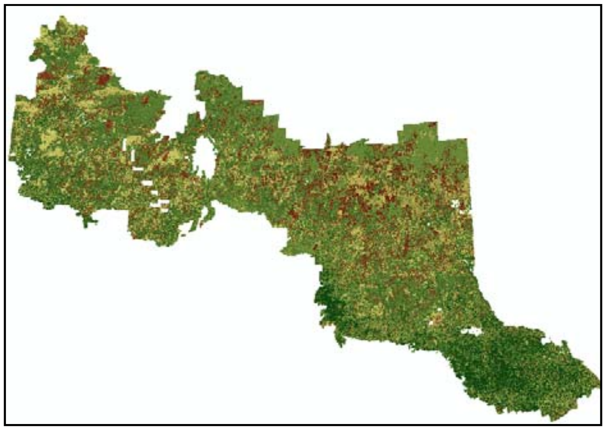
Integration of forest and wildlife inventories to identify indictors of biodiversity conservation in forest management planning





Final Report to the Forestry Futures Trust for KTTB-06B-2015

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Executive Summary

Identifying targets or reference conditions for monitoring indicators is critical to evaluate the effectiveness of forest management policies in meeting conservation objectives. The Forest Resource Inventory (FRI) is a key tool to support forest management planning, including mapping of wildlife habitat; however, the effectiveness of the FRI to adequately represent the range of habitat conditions important to wildlife remains uncertain. Further, many of the existing wildlife habitat models used in forest management planning were developed using data from limited geographic extents or other jurisdictions. Under a recently implemented Multiple Species Inventory and Monitoring (MSIM) program, the Ontario Ministry of Natural Resources and Forestry (MNRF) collects wildlife population and habitat information for terrestrial vertebrates at sites across the Area of the Undertaking (AOU) of forest management on Crown land. We assembled a dataset for songbirds, mammals and amphibians that captured variation in wildlife abundance and habitat condition across the AOU. A broad suite of environmental variables was considered, requiring assembly of a provincially consistent FRI classification, remote sensing products such as land cover classifications, roads, forest harvest, and climate data. The dataset provided a unique opportunity to assess appropriate species as indicators across a broader range of taxonomic groups and greater geographic-environmental gradient than previously possible.

In Chapter 1, we assess the ability of the enhanced understory and structural features of the FRI (eFRI) to characterize ground-based measurements of habitat at wildlife monitoring sites. We found that traditional eFRI-overstory variables performed better than eFRI-structure features in explaining variation in understorey features measured on the ground. Even so, the observed relationships for both variable sets were ecologically consistent. Using a bird community dataset, ground collected habitat information had greater explanatory power than eFRI overstory data, but both contributed independent information to the explained variance in bird species abundances. Findings suggest the eFRI has value to infer patterns in availability of wildlife habitat, although overall explanatory power was low. Inference can be improved by combining information at different levels and scales of forest structure.

In Chapter 2, individual-based modelling is used to measure the strength of response (relative abundance) and prominent patterns among wildlife taxa to variation in forest habitat conditions, ranging from understory site characteristics to landscape level patterns. Our findings revealed that forest understory was important in characterizing habitat. Stand level features and climate were generally more important than disturbance or landscape patterns in affecting wildlife response. Our work highlights that setting targets and monitoring for a diverse range of wildlife and habitat indicators at multiple scales, including understory features, may aid in the assessment of biodiversity response to forest management.

Chapter 3 describes evidence for the prevalence of thresholds in the response of wildlife to disturbance and habitat availability. Thresholds can aid in finding trade-offs in forest management for addressing biodiversity conservation and socio-economic benefits. Significant thresholds were evident among all taxa, although birds typically had the strongest relationships to environmental gradients and provided good representation of a range of forest conditions useful in assessing sustainability in forestry. We also demonstrate the value of identifying ecological community thresholds that can serve in target setting and characterizing dynamic community-habitat interactions that can be influenced through forest management.

The suite of science-based indicators and modelled wildlife habitat relationships described here are anticipated to enable better use of eFRI and provincial wildlife population monitoring data to support forest management planning and enhance the value of existing inventory and monitoring investment. These indicators can aid managers in interpreting wildlife trends in relation to manageable and unmanageable factors when conducting sustainability assessments.

Acknowledgements

Support for this project was provided by the Forestry Futures Trust under the auspices of project KTTB-06B-2015 to Brown, and the Ontario Ministry of Natural Resources' Wildlife Research and Monitoring Section. The authors also thank Denis Etiendem, Kyle Morrison, Ian Fife, Kiyoshi Sasaki, Lynn Landriault and Phil DeWitt for their assistance with various aspects of the project, as well as Neil Dawson, Dean phoenix, and the many operations staff who supported design and implementation of the MSIM program.

Acronyms

AIC – Akaike Information Criteria

AICw - Akaike Information Criteria weight

eFRI – enhance forest resource inventory, containing structural and understory attributes

FRI – Forest Resource Inventory

GAM – Generalized additive model

GLM – Generalized linear model

IndVal – Indicator value score

MNRF – Ministry of Natural Resource and Forestry

MSIM – Multiple species inventory and monitoring

PCA – Principal Component Analysis

PFT – Provincial Forest Type

RAC – Residuals autocovariate

TITAN - Threshold Indicator Taxa Analysis

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1.0 Can enhanced forest resource inventory characterize understory habitat structure for wildlife?

1.1 Introduction

Current understanding of wildlife–habitat relationships in managed forests have highlighted the importance of a range of spatial scales to many wildlife species (Baillie *et al.* 2000; Rettie & Messier 2000; Venier & Pearce 2007; Sauder & Rachlow 2015). In recent decades forest managers has given much attention to broad landscape scales of management (OMNR 2014). Such emphasis has created increased demand to map wildlife habitat at large spatial extents while still capturing the multiple scales of habitat condition that may affect wildlife distribution and abundance, including forest stand and understory features (OMNR 2010a). Wildlife managers and researchers often rely on land cover inventories to map habitat across large extents. In jurisdictions with commercial forestry operations, aerial photography-based forest resource inventory (FRI) data have been used, as they are ecologically meaningful and cover a large extent at a relatively fine grain (Poole *et al.* 2004). Traditionally, FRI has focused on inventory of merchantable timber, with limited or no information available regarding stand understory features important to wildlife. More recently, inventories have sought to include additional information about stand structure and managers would benefit from assessment of how well this information can serve to characterize wildlife habitat.

In Ontario, Canada, an enhanced Forest Resource Inventory (eFRI) is used to support forest management planning, including mapping of wildlife habitat as an indicator of sustainability. The eFRI contains traditional information about the forest canopy (e.g. age, height, tree stocking, species composition), as well as additional “enhanced” variables (e.g. understory crown closure, horizontal stand structure, and stand vertical structure). Our objective was to assess the ability of the eFRI to account for habitat features relevant to wildlife. We employed a spatially extensive wildlife monitoring dataset that spanned the entire area of undertaking of forest management in Ontario to assess how well eFRI characterized canopy and understory features at wildlife monitoring sites, compared to actual ground measures of vegetation. We conducted a series of constrained ordinations and hierarchical variance decomposition to compare the explanatory power of the ground collected vegetation data at wildlife survey sites to the eFRI. We then used the ground-collected habitat information and eFRI to assess habitat associations and relative explanatory power of each dataset to account for observed variation in the bird community. We focused on the forest song bird community as we suspected the nesting strategy of birds in trees, shrubs and ground may make them sensitive to the effects of forest management on habitat structure.

1.2 Methods

1.2.1 Study Area, Forest and Wildlife Inventories

We used forest and wildlife inventories collected by the Ministry of Natural Resources and Forestry (MNRF) in the province of Ontario, Canada. The study area encompassed diverse vegetation communities, including temperate deciduous forest in the south and boreal forest in the north. Mean annual temperature ranged from 2 to 6 °C and moist conditions were more prevalent in the south and east because of the moderating effects of the Great Lakes (MacKey *et al.* 1996).

Ground-based inventories of forest vegetation composition and structure were collected at 141 sites distributed randomly across the area of Crown forest managed by the province of Ontario, between 2013 and 2015 (Figure 1.1). The sample design was intended to support the Ontario Wildlife Population Monitoring Program and included a set of 3-4 habitat survey stations at each site. Details of the sample design are described in Brown *et al*. (2015). Sampling was centered on the wildlife plots and included multiple circular buffer extents appropriate for each wildlife survey and habitat component. Understory vegetation was measured within 1 m radius circular plots, including 5 plots per bird audio station, one centered on the station and four offset by 30 m and 50 m to the east and west. Measurements included litter depth and the percentage cover of ground vegetation, leaf litter, coarse woody debris, and vertical vegetation structure between 0 m and 10 m above ground for deciduous and conifer woody vegetation (Appendix 1). Vegetation variables were averaged among 1 m radius plots at each station for subsequent analysis.

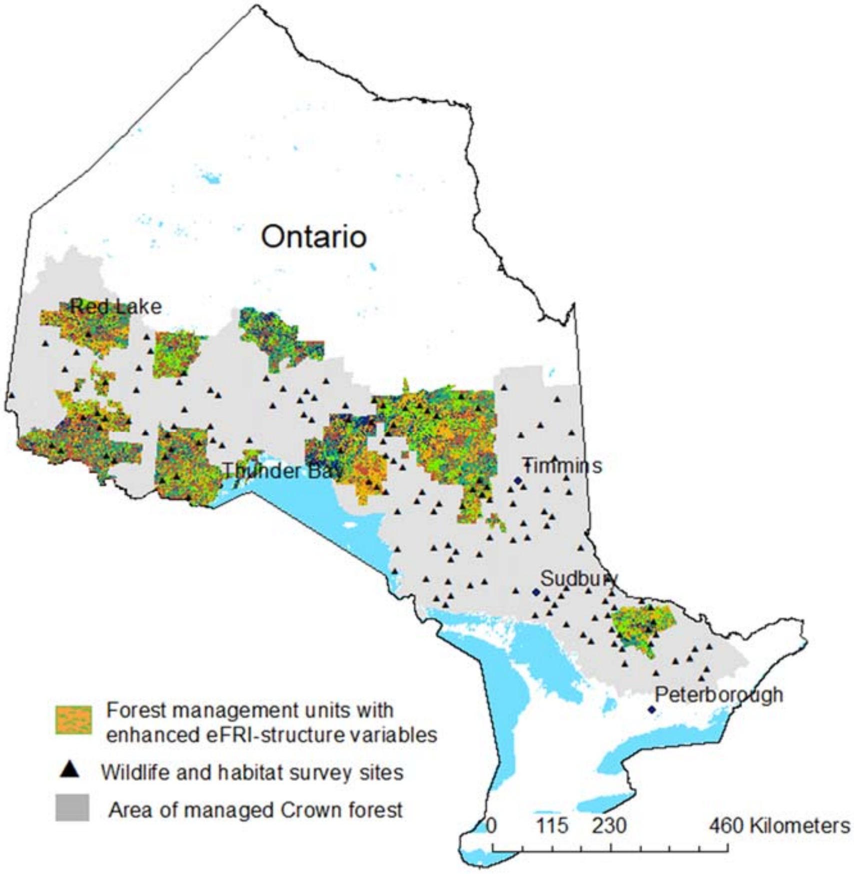

Figure 1.1 Study area showing the overlap of ground-based wildlife and habitat survey sites (black triangles) in relation to the available coverage of eFRI containing the understory, horizonal, and vertical structural attributes. Only canopy information was available for the eFRI overlapping the remaining sites (not shown).

Overstory information was collected within 11.28 m radius circular tree plots during ground sampling. Tree plots were located at each wildlife station and offset 50 m in an east and west direction (up to 3 plots per station). Measurements within each tree plot included species composition, tree height, tree diameter, tree density, visual percentage of canopy cover, and abundance of cavity trees (Appendix 1). Measurements of individual trees included the species and diameter at breast height (d.b.h.) (1.3 m above base of tree) for all trees that were >= 8 cm d.b.h., whether dead or alive, and whether there were one or more cavities present. Vegetation variables were averaged among tree plots at each station for subsequent analysis.

Bird stations at each site were spaced approximately 346 m apart to ensure independence and reduce potential double-counting of individual birds during surveys. During the summers of 2013 to 2015, audio point counts (10-minute duration) were recorded daily, 30 minutes before to 30 minutes after sunrise (local time), using a Song Meter SM2 or SM2+ (Wildlife Acoustics Inc., Concord, MA.). A single 10-minute point count was selected for each of 6 equal duration sessions between May 20 and July 7. Point count recordings were interpreted by a single person to record the number of unique individuals of each species. The mean number of individuals among sessions at each station was used as an index of relative abundance for each species and stations were treated as independent samples for subsequent analysis (n = 364).

The eFRI produced by the MNRF is based on digital aerial photo interpretation and field surveys and contains both overstory tree composition and understory structure information (https://www.ontario.ca/page/forest-resources-inventory, OMNR 2009). Overstory canopy variables derived from the eFRI included the proportion of conifer in the overstory, overstory height (m), stocking (%), overstory age (years), and the percentage composition of each combination of eight Provincial Forest Types (PFT) by three age classes (PFT x young, immature, mature) (OMNR 2003). Additional "enhanced" variables obtained from the eFRI included understory crown closure (%), horizonal stand structure (HORIZ, 6 classes), and stand vertical structure (VERT, 7 classes) that described the number of distinct layers of the canopy, ranging from single story, two-tiered, to complex (wide range of heights and ages). Site class (0-4) was also included in this dataset (Appendix 1). Hereafter, we refer to these two datasets as the eFRI-overstory and eFRI-structure datasets. The eFRI variables were extracted in a geographic information system (GIS) using 150 m radius buffers centered on each ground-based sampling station. Continuous variables were averaged within the buffer and the value at the centroid of the buffer was used for class variables, based on the resolution of FRI relative to the buffer size. At the time of this study, availability of the eFRI understory structural variables was limited to 8 forest management units (Figure 1.1), resulting in a total sample of 136 stations with both ground and eFRI-structure data for subsequent multivariate analysis. The vintage of FRI ranged from 2008 – 2013.

1.2.2 Statistical Analysis

Constrained ordination was used to assess the ability of the eFRI to explain variation in understory vegetation structure relevant to wildlife. Specifically, redundancy analysis (RDA) (Borcard, Gillet & Legendre 2011) was used to conduct ordinations of the ground-collected understory vegetation data (response matrix) constrained by the eFRI variables (explanatory matrix). To aid in interpreting how the enhanced features of eFRI can improve explanatory power beyond the canopy features historically available, we ran separate RDA's using the eFRI-overstory and eFRI-structure variables as the explanatory matrices. Analysis was limited to the ground survey stations that overlapped forest management units containing the eFRI-structure attributes (n = 136). Prior to running the RDA's, the ground-based understory variables were standardized to zero mean and unit variance to place variables with different units of measure on a common scale. Forward selection of explanatory variables was used due to expected linear dependencies in the eFRI variables, desire to improve parsimony, and to highlight key eFRI variables that may serve as useful indicators for assessing vegetation structure relevant to wildlife habitat assessment. Linear dependencies among explanatory variables were identified using variance inflation factors (VIF) and variables were excluded where VIF's were >= 20.

Hierarchical variance decomposition was used to provide insight into the relative explanatory power of the eFRI-overstory and eFRI-structure datasets (Brown, Rettie & Mallory 2006; Borcard, Gillet & Legendre 2011). The decomposition required measuring the variation explained by the eFRI-overstory and eFRI-structure variables separately, the variation jointly explained by both variable sets, and the total variation explained by all eFRI-overstory and eFRI-structure variables together, using adjusted R^2 values and subtractive procedures (Borcard, Gillet & Legendre 2011).

To explore the ability of the eFRI to account for habitat features relevant to birds we conducted a series of ordinations using the multiple bird species relative abundance data as the response matrix, constrained using the ground-collected vegetation data and the eFRI-overstory variables as explanatory datasets. Due to the limited availability of structural variables in the eFRI dataset across the full extent of our available bird dataset, we could only assess overstory variables at the time of this study. However, this trade-off permitted using more of the ground-collected vegetation and bird data (n = 364), as well as the overlapping eFRI spanning the full extent of forest management units in the province (Figure 1.1). The RDA methods described above were employed for these comparisons, including the hierarchical variance decomposition to quantify the explanatory power of the eFRI relative to the ground-collected data. Non-linear relationships between the response data and explanatory variables were assessed and quadratic polynomial terms were fit for explanatory variables when needed. All statistical analyses were conducted using R version 3.5.1 (R Development Core Team 2018) and the RDA was performed using the vegan package (Version 2.5-4, J. Oksanen).

1.3 Results

1.3.1 eFRI Comparison to Ground-based Inventory

The eFRI-structure variables explained a significant but smaller proportion of the variation in the ground-based understory structure at our field sites (adjusted R^2 = 0.106), compared to eFRI-overstory variables (adjusted R^2 = 0.205). Permutation tests indicated that the global RDA model for eFRI- understory was significant (*pseudo-F* = 2.1168, *P* = 0.001), but only the first canonical axis was significant (RDA1: *pseudo-F* = 15.8730, *P* = 0.002). The global RDA model for eFRI-overstory was significant (*pseudo-F* = 2.2607, *P* = 0.001), with a significant amount of variation explained by the first two canonical axes (RDA1: *pseudo-F* = 31.6631, *P* = 0.001; RDA2: *pseudo-F* = 16.4757, *P* = 0.017). Forward selection of eFRI-understory explanatory variables supported retaining variables that identified four structural conditions and a site class (HorizMP, HorizSS, VertTO, VertSV, VertSI, and SC2) (see Appendix 1 for variable descriptions). Forward selection of eFRI-overstory explanatory variables supported retaining variables describing canopy height, stocking, percentage conifer, and two forest type-age class combinations (HT, stkg, pconif, Y_MCL, and I_TOL). Permutation tests indicated that the parsimonious RDA model for eFRI-structure was significant (*pseudo-F* = 3.5131, *P* = 0.001, adjusted $R^2 = 0.103$), and only the first canonical axis was significant (RDA1: *pseudo-F* = 13.1704, *P* = 0.001). The parsimonious RDA model for eFRI-overstory was significant (*pseudo-F* = 5.6949, *P* = 0.001, adjusted $R^2 = 0.151$), with a significant amount of variation explained by the first two canonical axes (RDA1: *pseudo-F* = 16.8557, *P* = 0.001; RDA2: *pseudo-F* = 8.2829, *P* = 0.001).

Inspection of the triplot for the ordination constrained by eFRI-structure revealed that HorizSS (single stem canopy) and HorizMP (several distinct patches) played an important role in the distribution of sites along the RDA1 axis (Figure 2). Greater amounts of woody conifer structure in the low (WCL, 0 – 1.5 m) and medium (WCM, 0.5 – 2 m) vertical strata were associated with greater horizontal stand complexity as inferred from the eFRI (HorizMP), as well as stands with a single layer and the presence of veteran trees (VertSV). Large percentage cover of deciduous in the high vertical stratum (WHH, 2 – 10 m) and the canopy (TH, > 10 m) was associated with VertTO, which characterized stand canopies with two distinct layers. Greater amount of woody conifer at 2 – 10 m (WCH) was associated with single story stands (VertSI) as represented in the eFRI (Figure 1.2).

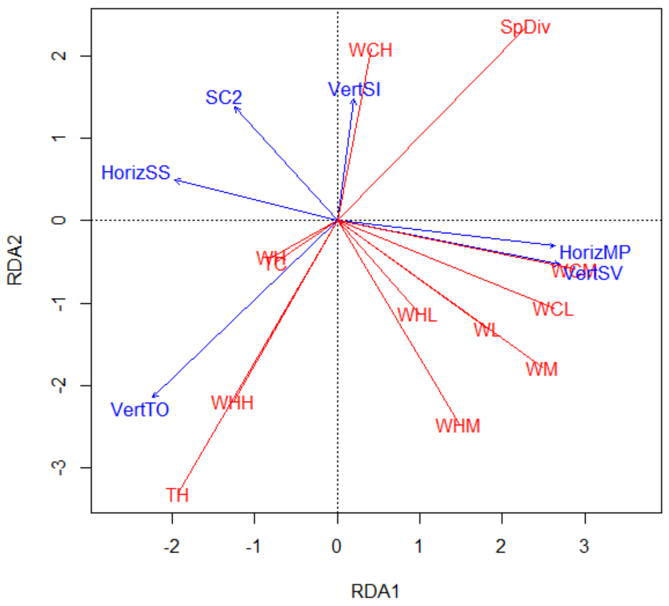

Figure 1.2 Redundancy analysis (RDA) triplot of ground-collected vegetation structure variables (red, response) constrained by six eFRI-structure variables (blue, explanatory) retained following forward selection. Variable codes are described in Appendix 1. The angles between response and explanatory variables reflect their correlations and the length of the arrow represents the relative importance of each variable.

The triplot for eFRI-overstory illustrated that the RDA1 contrasted sites with young conifer (pconif, Y_MCL) and canopy height (HT), and RDA2 captured a gradient in the amount of intermediate-aged tolerant hardwood stands (I_TOL) (Figure 1.3). Understory species diversity was correlated with greater amount of conifer as measured in the eFRI. Woody conifer in the medium and low strata were correlated with greater amounts of the mixed conifer lowlands PFT in the young age class (Y_MCL); whereas, deciduous in the high stratum and canopy was correlated with intermediate aged tolerant hardwood stands (I_TOL) in the eFRI (Figure 1.3).

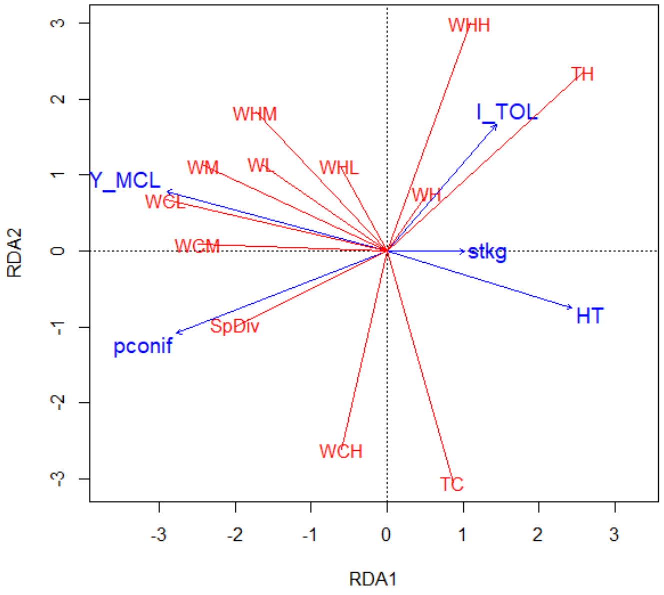

Figure 1.3 RDA triplot of ground-collected vegetation structure variables (red) constrained by five eFRI-overstory variables (blue) retained following forward selection. Variable codes are described in Appendix 1. The angles between response and explanatory variables reflect their correlations.

Variance decomposition revealed that eFRI-structure variables explained a small but significant amount of the observed variation in ground-based structure information, independent of the eFRI-overstory (*pseudo-F* = 3.5131, *P* = 0.001, adjusted R^2 = 0.085) (Figure 1.4). The independent effect of eFRI-overstory was also significant, but with smaller explanatory power than eFRI-structure (*pseudo-F* = 3.6243, *P* = 0.001, adjusted R^2 = 0.036). There was overlap in the explained variation of both datasets (adjusted R^2 = 0.066); however, combining these datasets improved overall explanatory power (adjusted R^2 = 0.187). There was a high amount of residual variation in the response variables that could not be explained by the eFRI (adjusted R^2 = 0.813).

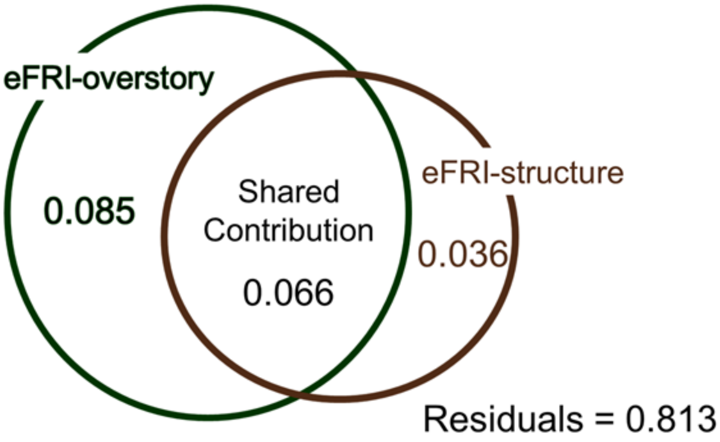

Figure 1.4 Variance decomposition of ground-collected vegetation structure variables (response) constrained by eFRI-structure and eFRI-overstory variables (explanatory). Values represent the independent and shared proportions of total variation in the ground data that could be explained using the eFRI variables. All RDA ordinations were significant at P < 0.05.

1.3.2 Bird Community Ordination

The eFRI-overstory variables explained a significant but smaller proportion of the variation in the bird community (adjusted R^2 = 0.165), compared to ground-collected variables (adjusted R^2 = 0.207). Permutation tests indicated that the global RDA model for ground-collected data was significant (*pseudo-F* = 3.1979, *P* = 0.001), including the first seven canonical axes (*pseudo-F's* = 4.449 – 46.575, *P* < 0.05 in all cases). The global RDA model for eFRI-overstory was significant (*pseudo-F* = 3.0449, *P* = 0.001), with a significant amount of variation explained by the first five canonical axes (*pseudo-F's* = 4.697 – 38.908, *P* = 0.05 in all cases). Forward selection of ground-collected explanatory variables supported retaining 22 variables that characterized canopy, understory and ground-level vegetation structure (Appendix 2 for variable descriptions). Forward selection of eFRI-overstory explanatory variables supported retaining 20 variables, including age, stocking, and various combinations of forest type (PFT) by age class. Permutation tests indicated that the parsimonious RDA model for ground-collected data was significant (*pseudo-F* = 4.3717, *P* = 0.001, adjusted R^2 = 0.200), and the first seven canonical axes were significant (*pseudo-F's* = 3.527 – 45.735, *P* < 0.05

in all cases). The parsimonious RDA model for eFRI-overstory was significant (*pseudo-F* = 4.358, $P < 0.05$ in all cases, adjusted $R^2 = 0.156$), with a significant amount of variation explained by the first five canonical axes (*pseudo-F's* = 3.943 – 37.201, $P < 0.05$ in all cases).

The triplot for the bird community constrained by the ground-collected explanatory variables captured a gradient in deciduous, mixed, and conifer forests along RDA1 and forest age along RDA2 (Figure 1.5). Birds associated with mature mixed forests included red-breasted nuthatch (*Sitta canadensis*, RBNU), blackburnian warbler (*Setophaga fusca*, BLBW), and black-capped chickadee (*Poecile atricapillus*, BCCH). Species associated with greater amount of conifer in the canopy and an understory of sphagnum mosses and lichen included nashville warbler (*Oreothlypis ruficapilla*, NAWA), Tennessee warbler (*Oreothlypis peregrina*, TEWA), and ruby-crowned kinglet (*Regulus calendula*, RCKI). Alder flycatcher (*Empidonax alnorum*, ALFL), Lincoln's sparrow (*Melospiza lincolnii*, LISP), and common yellowthroat (*Geothlypis trichas*, COYE) were correlated with greater amounts of gramminoids, and ovenbird (*Seiurus aurocapilla*, OVEN), yellow-bellied sapsucker (Sphyrapicus varius, YBSA), and black-throated green warbler (*Setophaga virens*, BTNW) were correlated with greater amounts of cavity trees (Figure 1.5).

Similar to the ground-collected ordination, the triplot for the bird community constrained by the eFRI-overstory variables captured a gradient in conifer and deciduous forests along RDA1 and forest age along RDA2 (Figure 1.6). Similar patterns in bird species associations with vegetation communities were apparent, including an association of RBNU, BLBW, and BCCH with stand age, canopy height and abundance of mixed forest PFT's. NAWA, TEWA, and RCKI were correlated with greater amounts of mature mixed conifer lowlands (M_MCL); whereas, ALFL, LISP and COYE were associated with young mixed conifer lowlands (Y_MCL), and the veery (VEER), scarlet tanager (SCTA), and blue jay (*Cyanocitta cristata*, BLJA) were associated with mature tolerant hardwoods (M_TOL)(Figure 1.6).

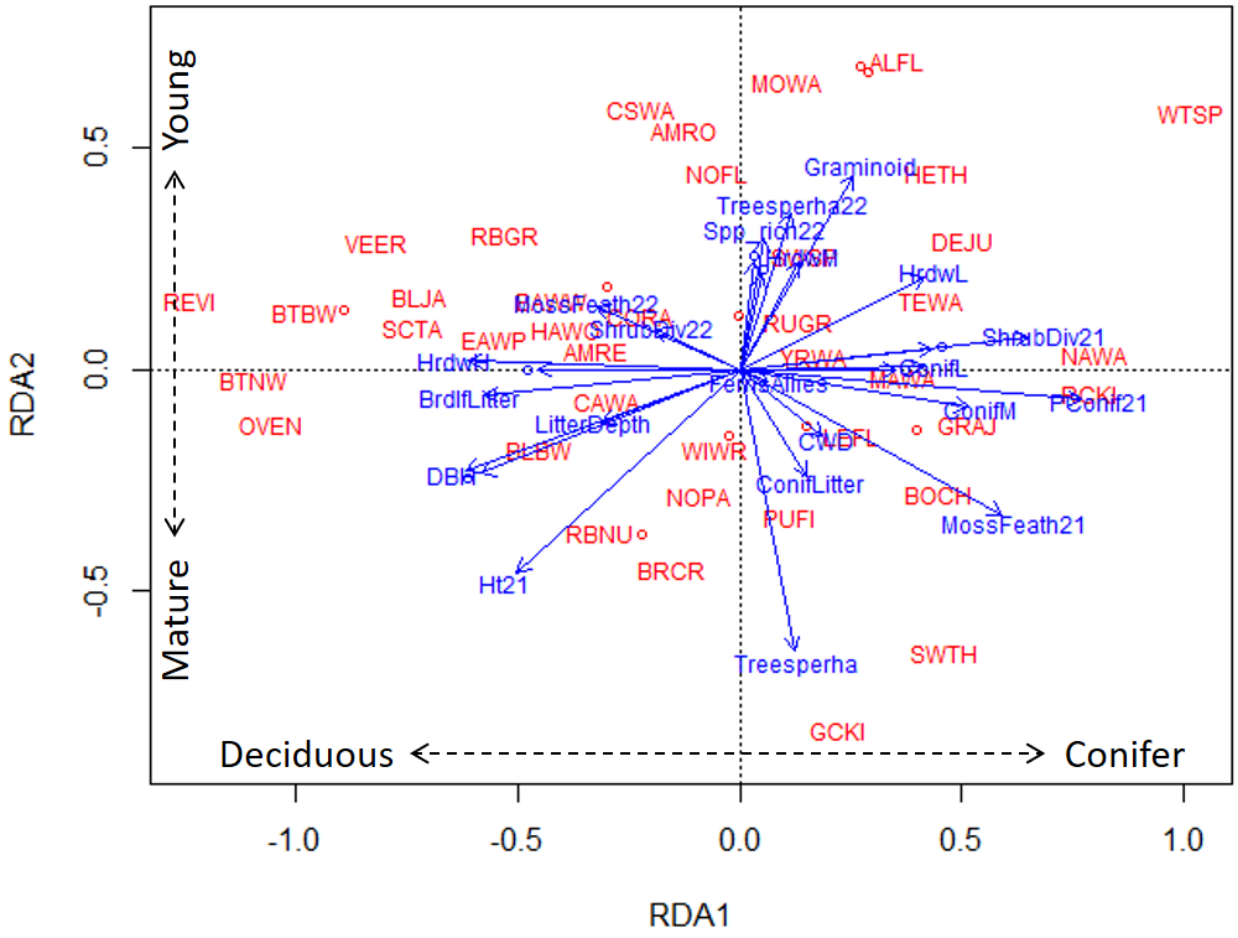

Figure 1.5 RDA triplot of forest songbird relative abundances (red) constrained by ground-collected vegetation structure variables (blue, with arrows) retained following forward selection. Explanatory variables, bird species codes, and variable labels omitted to avoid overlap clutter (circles) are described in Appendix 2. Variables with two arrows, and codes ending in "21" or "22", represent quadratic terms used to reflect their non-linear relationships to the response data. The angles between response and explanatory variables reflect their correlations (Species response lines omitted to avoid clutter).

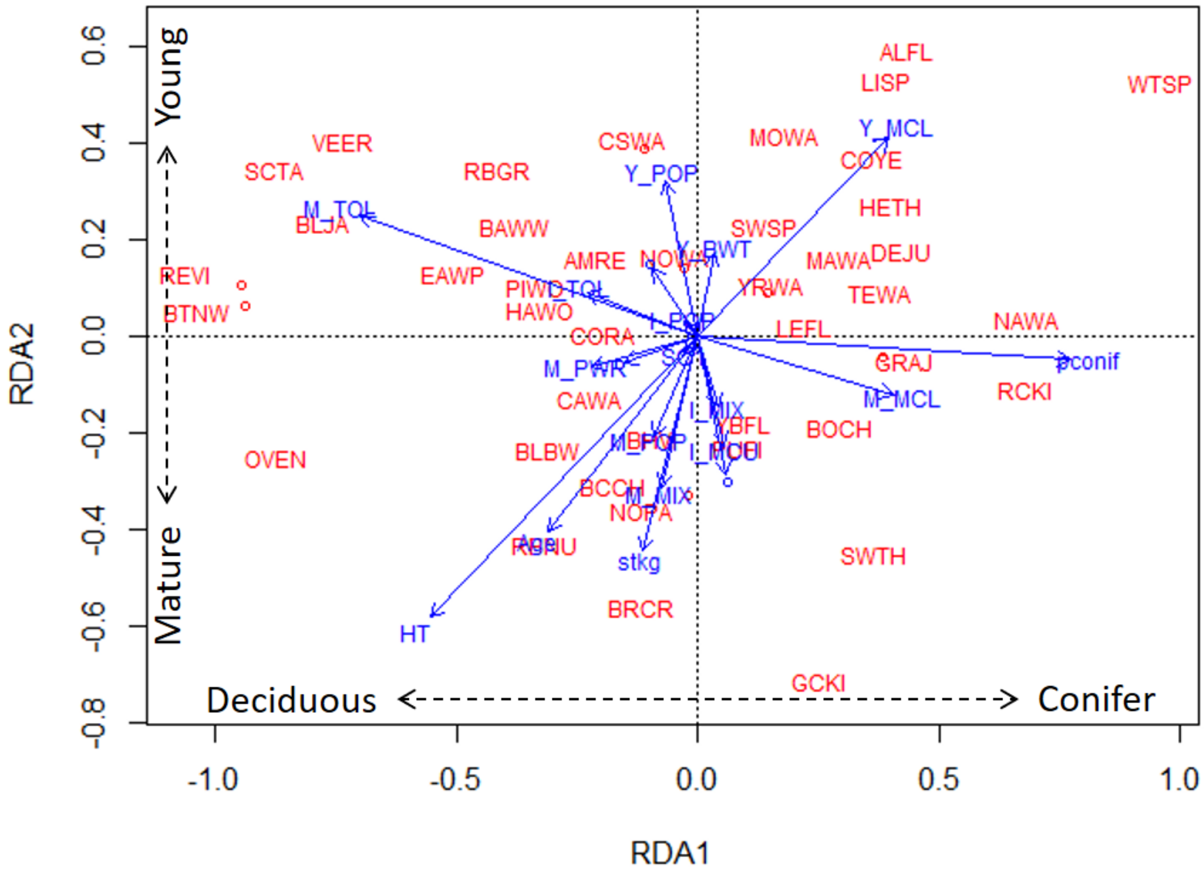

Figure 1.6 RDA triplot of forest songbird relative abundances (red) constrained by eFRI-overstory variables (blue) retained following forward selection. Explanatory variables, bird species codes, and variable labels omitted to avoid overlap clutter (circles) are described in Appendix 2. The angles between response and explanatory variables reflect their correlations (Species response lines omitted to avoid clutter).

Variance decomposition revealed that the ground-collected vegetation data explained a significant amount of the observed variation in the bird community, independent of the eFRI-overstory (*pseudo-F* = 2.3791, *P* = 0.001, adjusted R^2 = 0.083) (Figure 1.7). The independent effect of eFRI-overstory was also significant, but with smaller explanatory power than ground-collected data (*pseudo-F* = 1.8459, *P* = 0.001, adjusted R^2 = 0.036). There was overlap in the explained variation of both datasets (adjusted R^2 = 0.118); however, combining these datasets improved overall explanatory power (adjusted R^2 = 0.237). There was a high amount of residual variation in the response variables that could not be explained by the ground and eFRI (adjusted R^2 = 0.763).

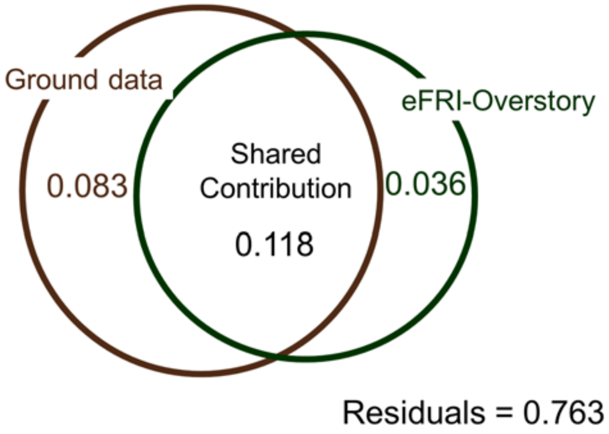

Figure 1.7 Variance decomposition of bird species relative abundances (response) constrained by eFRI-overstory variables (explanatory). Values represent the independent and shared proportions of total variation in the bird community that could be explained using the eFRI variables. All RDA ordinations were significant at P < 0.05.

1.4 Discussion

1.4.1 eFRI Comparison to Ground-based Inventory

Contrary to expectations, the eFRI-overstory variables performed better than eFRI-structure in explaining variation in understory features measured on the ground (approx. 2 x better). The observed pattern could potentially result from the strong environmental influence of canopy to affect understory structure, as well as classification inaccuracy in the relatively new structure variables; however, clarifying sources of discrepancies would require further investigation. Even so, the relationships among ground-measured vegetation structure and elements in the eFRI characterizing canopy composition, vertical and horizontal structure were ecologically consistent. For example, the eFRI accurately represented the simpler single layer canopy structure of conifer dominated stands (e.g. VertSI) in contrast to more complex structured deciduous stands (e.g. VertTO). Findings suggest potential to further exploit the eFRI for inferring wildlife habitat.

Both eFRI-structure and eFRI-overstory datasets explained independent variation in ground-collected understory, that was not explained or represented by the other dataset. Our findings indicate that overall power to characterize understory vegetation structure can be improved by combining information at different scales or levels of forest structure. Similarly, Brown et al. (2006) found that combining FRI and information from Landsat TM remote sensing data could improve explanatory power of forest structure relevant to wildlife. Ecological land classifications (ELC) are another information source that have potential to describe wildlife habitat features (Bowman, Robitaille & Watt 1996). ELC typically characterize a range of vegetation attributes (from ground to canopy). Such classifications are derived from information about surficial geology, climate (temperature, precipitation), physiography (soils, slope, aspect) and corresponding vegetation. Despite the broad suite of information, such approaches are necessarily generalizations that may still not capture the local site level variation in conditions that can affect wildlife detected at survey sites. Although ELC can provide detailed understory species composition (Taylor *et al.* 2000), the finer variation in vertical vegetation structure and growth patterns that relate to stand age and productivity may not be well characterized. Evidently, our findings highlight the importance of such features to wildlife (Chapter 2). As well, ELC are data hungry and where classes are built or inferred from more limited information (e.g. FRI and other coarse scale mapped products), there may be greater uncertainty in fine scale features. However, further studies that can integrate information from ELC or other inventory products may strengthen inferences about habitat for wildlife.

Despite the significance of constrained ordinations, there was high residual variation in ground vegetation that could not be explained by the eFRI. Overall, the available inventory did a limited job of characterizing major patterns in understory vegetation. In contrast, Brown *et. al* (2006) found that FRI explained higher amounts of observed variation in forest stand and understory structure (31.3%, compared to 18.1% in this study). The lower explanatory power in this study may reflect the greater forest complexity across the large environmental gradient, ranging from temperate deciduous forest in the south to boreal shield forest in the north. Improvements in classification accuracy can be expected in homogeneous habitats with lower structural complexity (Hyyppä *et al.* 2000). Further investigation that characterizes variation in explanatory power across landscapes with different forest community complexity may prove useful.

1.4.2 Bird Community Ordination

Our analysis of the bird community revealed that species are influenced by forest conditions at multiple scales, including understory and overstory structure. Like other studies (Rempel 2007; Mahon *et al.* 2016), we found that the bird community was influenced by forest height, forest age, and area of deciduous and conifer forest. In addition, we also found a significant influence of tree density, the density of cavity trees, the area of mature tolerant hardwoods, ground cover (e.g. litter, moss), understory shrub cover and shrub diversity.

Many bird species were located in the central region of the ordination space, indicative of associations with common habitat conditions, or lacking strong associations with habitat variables. Mahon et. al (2016) suggested a generalist strategy may be a common adaptation for species in the boreal forest where disturbances such as fire create heterogeneity and unstable environments. However, many species in our study were distributed along the outer areas of the first two RDA axes and demonstrated strong associations with specific habitat variables, such as the oven bird, red-eyed vireo, golden-crowned kinglet, and white throated sparrow. Our study area also included lowland black spruce forest in the eastern portion of the province with long fire cycles (Bergeron *et al.* 2001), and thus more stable environments. Temperate hardwood forests dominated in the south where human fire suppression limits natural disturbances. Such diversity of forests communities in combination with more stable environments may facilitate greater frequency of species specialization, although this hypothesis remains to be tested in our study area.

Our variance decomposition revealed that the ground collected habitat information and eFRI overstory data contributed independently to the explained variance in the distribution of species abundances. Not surprisingly, the habitat data collected directly at each wildlife station, which included ground-level understory and canopy information, explained more of the observed variation in the bird community. Variables describing understory conditions, including leaf litter and shrub structure, were highly correlated with the first two ordination axes. In addition to the more obvious canopy features (e.g. cavity trees as nesting substrate), understory features can affect nesting habitat, foraging, and predation risk, depending on the life history strategies of individual bird species. Robinson and Holmes (1982) found that there are limitations in the ways in which birds can search for and capture prey among foliage. As a result, vegetation structure may impose constraints that effect foraging traits of birds, and in turn, patterns in habitat selection and community structure.

The large amount of unexplained variation in the bird community in relation to the forest habitat information considered here may be due to the omission of important variables, including climate (Keith *et al.* 2008), food (Robinson & Holmes 1982), predators, landscape features (Terraube *et al.* 2016), or more explicit parameterization of functional habitat conditions related to vegetation features. Inclusion of such features was beyond the scope of this study. The nature of the bird community ordination may also limit characterization of species-specific habitat associations and contribute to lower observed explanatory power. The benefits of synthesizing complex information into a reduced number of dominant patterns (axes) across the entire bird community, where the axes characterize the strongest gradient (maximal independent variation), may not be effective to characterize the unique habitat associations of individual species. Some multivariate methods are unduly influenced by rare species (Kenkel 2006), although redundancy analysis may be less sensitive to rare species in ordination results (Mahon *et al.* 2016). RDA also assumes linear relationships among response and explanatory variables. Although we attempted to included quadratic terms in models, non-linear relationships for the birds in our analysis could have reduced overall explanatory power.

1.4.3 Conclusions

Our variance decomposition method illustrates the conceptual advantages of explicitly quantifying the independent and confounded components of explained variation when assessing the value of habitat inventories. Findings suggest the eFRI has value to infer patterns in availability of wildlife habitat. When possible, combining multiple datasets (e.g. ground collected, aerial-based inventories, remote sensing) is expected to strengthen modelled relationships and interpretations. The eFRI provides a valuable spatially extensive inventory suitable for applications in wildlife habitat mapping. We suggest that further development of eFRI structural indices, including understory information, could improve the application potential of the inventory with respect to adequately characterizing habitat for wildlife.

2.0 Response of terrestrial vertebrates to forest composition, structure and landscape reveals implications for forest management

2.1 Abstract

Assessing the impacts of forest harvest on biodiversity is a key mandate for demonstrating sustainable forest management in many jurisdictions, yet the identification of an appropriate suite of wildlife and habitat indicators remains a challenge. We used individual-based modelling and a spatially extensive dataset of forest-dependent bird, amphibian, and mammal species to measure the strength of response and prominent patterns among taxa to variation in forest habitat conditions, ranging from understory site characteristics to landscape level patterns. Our findings revealed that understory habitat was a significant contributor to species occupancy or relative abundance. Stand level features and climate were generally more important than disturbance or landscape patterns in affecting wildlife response. There was much variability among species in the specific habitat conditions and scales of importance, consistent with the inherent complexity and diversity of forest ecosystems. Our work highlights that setting targets and monitoring for a diverse range of wildlife and habitat indicators at multiple scales, including understory features, may be needed to adequately assess biodiversity response to sustainable forest management activities.

2.2 Introduction

Mangers responsible for conducting forestry on public lands are under increasing pressure to address multiple conservation and sustainable resource management objectives, such as maintaining a diversity of wildlife in forest communities. Identifying the best suite of species and forest conditions to serve as indicators remains a challenge due to the complexity of forest ecosystems and diverse taxa that may need to be sustained. Harvesting of timber is typically a stand level process yet wildlife may respond to forest conditions at a range of scales. Further, extraneous conditions such as climate change may have cumulative or interacting effects on wildlife populations.

Managers would benefit from better understanding of the relative importance of forest condition at multiple scales (understory, canopy, landscape), and commonalities and differences among a range of wildlife, to identify useful indicators of sustainable forest management.

Forest management can affect wildlife through the direct removal of habitat or alteration of forest communities with subsequent changes to trophic interactions and predator-prey relationships. Landscape level effects are widely recognized and inherently variable among species (Brown *et al.* 2007; Venier & Pearce 2007; Houle *et al.* 2010). Understory forest features may also be influential and interact with other scales of forest structure to affect wildlife. For example, salamanders are highly sensitive to soil conditions (Frisbie & Wyman 1991), which, in turn, are affected by the structure and composition of the shrub and forest canopy (Shear & Stewart 1934; Finzi, Canham & Breemen 1998). Vegetation cover may simultaneously provide food, shelter, visual cover from predators, and substrate for breeding birds that nest in the ground, shrub or canopy layers. The density or biomass of understory foliage can be positively correlated with arthropod abundance or seed crop mass, which in turn, may provide food for birds and small mammals (Greene & Johnson 1994). As such, vegetation composition and structure represent dynamic components of ecosystems that can be manipulated to assist in meeting wildlife population objectives.

Despite the potential importance of understory features to wildlife, mangers are often limited to assessment of habitat using canopy-level information available in forest inventories designed to support tree harvesting (OMNR 2010a; OMNR 2014). Understory and ground-level habitat information is often cost-prohibitive to collect over the large geographic extent typical of forest operations planning. Although fine scale habitat features may often not be explicitly managed during forestry activities (exceptions include cavity trees, OMNR 2010a), understanding the relative influence and interactions among different scales of habitat alteration may help clarify the mechanisms of population change in wildlife. Addressing such uncertainties can aid in evaluating the effectiveness of forest management activities with respect to manageable and unmanageable factors.

We employ an individual-based modelling approach for a range of species, using data that captures variation in wildlife-habitat associations across the entire area of forest management on Crown land in Ontario, and at scales explicitly tailored to planning processes. Although multi-scale habitat analysis are common for a range of forest dependent species (Rempel 2007; Venier & Pearce 2007), we are not aware of studies that assess the importance of understory forest attributes relative to larger scale habitat features, for a wide range of birds and mammals. Further, our dataset spans a broad bioclimatic gradient, allowing us to consider the effects of climate and forest community (spanning temperate hardwood to northern boreal) in shaping the response of wildlife.

Our objective was to assess the relative importance of a suite of factors hypothesized to affect wildlife occupancy or relative abundance, including disturbance, climate and forest structural attributes at multiple scales (understory, overstory, landscape). In doing so, we sought to clarify the importance of understory attributes to accurately characterize wildlife response to forest alteration, as well as, whether wildlife are more sensitive to disturbance related features or the actual forest conditions they select. We discuss our findings in relation to useful indicators for applications in sustainability assessments of forest management. Evidence for variation among species in the strength of relationships between species and habitat conditions can improve the basis for prioritization of wildlife indicators.

2.3 Methods

2.3.1 Study Area and Wildlife Inventories

We used inventories of forest habitat condition and biodiversity collected by the Ministry of Natural Resources and Forestry (MNRF) in the province of Ontario, Canada. The study area encompassed diverse vegetation communities, including temperate deciduous forest in the south and boreal forest in the north. Mean annual temperature ranged from 2 to 6 °C and moist conditions were more prevalent in the south and east because of the moderating effects of the Great Lakes (MacKey *et al.* 1996).

The wildlife inventories were collected at 141 sites distributed randomly across the area of Crown forest managed by the province of Ontario (Figure 2.1). All sites included up to 5 camera stations to detect medium-large sized mammals and 3 audio recorder stations to detect bird species. A portion of sites included 3 small mammal trap lines and a rectangular grid of cover boards to sample salamanders (Plethodontid species), both co-located at the audio recorder stations. Details of the sample design are described in Brown *et al*. (2015). A single season of survey data was available for each site, collected between 2013 and 2015.

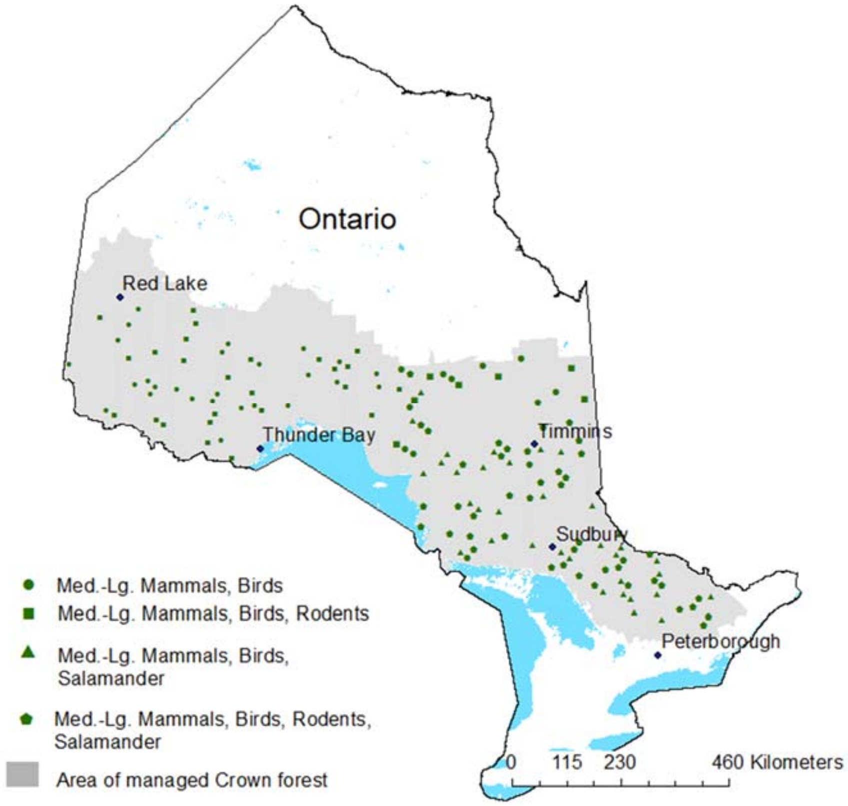

Figure 2.1 Study area in Ontario, showing the distribution of wildlife and habitat sampling sites.

Bird stations at each site were spaced approximately 346 m apart to ensure independence and reduce potential double-counting of individual birds during surveys. Audio point counts (10-minute duration) were recorded daily, 30 minutes before to 30 minutes after sunrise (local time), using a Song Meter SM2 or SM2+ (Wildlife Acoustics Inc., Concord, MA.). A single 10-minute point count was selected for each of 6 equal duration sessions between May 20 and July 7. Point count recordings were interpreted by a single person to record the number of unique individuals of each species. The mean number of individuals among sessions at each station was used as an index of relative abundance for each species and stations were treated as independent samples for subsequent analysis (n = 387).

Small mammal trap lines consisted of 11 trapping stations spaced 10 m apart. Each station contained one large trap (XLF15, 10.16 cm x 11.43 cm x 38.1 cm, H.B. Sherman Traps Inc.) and one smaller trap (XLK, 7.62 cm x 9.525 cm x 30.48 cm, H.B. Sherman Traps Inc.). Trapping was conducted for three consecutive nights between mid-July and the end of August and the projected number of unique individuals per 1000 trap nights was used as an index of relative abundance for each trap line (n = 206).

Cameras were placed at the center of each site and 500 m away in each of the four cardinal directions. Cameras were deployed between May and August for a minimum of 100 days. The total deployment period for each camera was partitioned into a maximum of seven 15-day sessions. A relative abundance index for each species and site was calculated as the number of days in each session with a detection divided by the number of active camera days (max of 15), averaged for all sessions. The mammal species under consideration were assumed able to move among all cameras at a site, so the index was averaged among all stations for use in statistical analysis (n = 140).

Abundance of red-backed salamander (*Plethodon cinereus*) was surveyed at each site using grids of 20 or 30 coverboards placed 8 m apart. Additional boards were deployed in the northern portion of range where densities were expected to be lower. Counts of salamanders at each board were conducted between May and July for up to three repeat surveys. The maximum of the average count per board among repeat surveys at each site was used to create a projected count per 20 boards for use as a relative abundance index (n = 71 sites). Salamander board grid locations were paired with one of the bird stations at each site.

2.3.2 Habitat Inventories

We characterized habitat according to five primary explanatory datasets, including forest UNDERSTORY, forest OVERSTORY, forest LANDSCAPE pattern, anthropogenic DISTURBANCE, and CLIMATE (Appendix 3). Sampling was centered on the wildlife plots and included multiple circular buffer extents appropriate for each wildlife survey and habitat component. UNDERSTORY was measured within 1 m radius circular plots, including 1 plot per salamander board and 5 plots per bird audio station, one centered on the station and four offset by 30 m and 50 m to the east and west. Measurements included litter depth and the percentage cover of ground vegetation, leaf litter, coarse woody debris, and vertical vegetation structure between 0 m and 10 m above ground (Appendix 3). A preliminary assessment of the availability of understory structure variables in the enhanced Forest Resource Inventory (eFRI) maintained by the MNRF revealed that these variables were not available for enough of our wildlife survey sites to enable inclusion in our analysis.

OVERSTORY information was collected from ground sampling and the eFRI, including stand age, tree species composition, tree height, tree diameter, canopy cover, and abundance of cavity trees (Appendix 3). Circular tree plots (11.28 m radius) were located at each bird audio station and offset 50 m in an east and west direction (3 in total). Measurements within each tree plot included the species and diameter at breast height (d.b.h.) (1.3 m above base of tree) for all trees that were >= 8 cm d.b.h., whether dead or alive, and whether there were one or more cavities present. The FRI-derived overstory variables were extracted in a geographic information system (GIS) using 150 m radius buffers centered on each wildlife station.

DISTURBANCE variables included the mean distance to roads (m) and percentage cover of forest harvest <= 10 years and <= 20 years since disturbance within 150 m and 500 m buffers of each wildlife station (Appendix 3). Mapped layers for roads and year-specific forest harvest blocks were available from the MNRF. Euclidean distance analysis was used to determine the mean distance within buffered station polygons (rasterized) to the nearest road segment (highway, primary or secondary road).

LANDSCAPE metrics describing patterns in forest patches included average total edge, ratio of total edge to patch area, and forest patch contiguity using 500 m buffers centered on the wildlife stations (Appendix 3). The patch metrics were calculated for conifer, mixed and deciduous forest cover types, as well as young, immature and mature age classes of these three forest types using the software Fragstats (Version 4.0, McGarigal 2015).

CLIMATE variables included long-term averages (1984 – 2010) for mean temperature and precipitation of the warmest and coldest quarters of the year, Julian day number of the start of the growing season, temperature seasonality (standard deviation of monthly mean temperature), and an index of cumulative snow depth (winter prior to wildlife survey year and 18-year average, 1994-2015). Spatial grids of historical climate data were obtained from Natural Resources Canada (McKenney *et al.* 2006; McKenney *et al.* 2007), and the resolution of grids was approximately 4.5 km. The snow depth index was obtained from the MNRF as 500 m by 500 m raster grids derived from the MNRF snow course network (SNOW 4.0, Snow Network for Ontario Wildlife, http://www.wildliferesearch.ca). Details of the field-based sampling methods and locations are described by Smith, Voigt & Bisset (1998), and involved empirical Bayesian kriging of snow depth index values for stations located across the province (Oliver & Webster 2014). Given the broad-scale nature of the bioclimatic patterns and resolution of the source data (approx. 4 km), mean values for each climate variable were generated within 8 km buffers for each wildlife inventory site. All spatial analyses were conducted using ArcGIS desktop 10.3 (ESRI Inc., Redlands, California, USA).

2.3.3 Statistical Analyses

Due to the large number of habitat variables, we used Principle Component Analysis (PCA) to create a reduced set of ordination axes for use as independent variables in statistical modelling of wildlife relative abundance. PCA was performed using the full set of explanatory variables for each of the habitat categories (UNDERSTORY, OVERSTORY, DISTURBANCE, LANDSCAPE, CLIMATE) and the Kaiser–Guttman criterion was used to identify the ordination axes whose eigenvalues were greater than the mean of all eigenvalues (Borcard, Gillet & Legendre 2011) (Appendix 3). To facilitate comparisons among species and across all the habitat categories, ordinations were performed using the station-level habitat summaries. PCA scores were applied to individual stations for birds, small mammals, and the red-backed salamander. All available PCA-habitat scores were averaged among stations to represent site-level habitat conditions for analysis of camera-derived mammal abundance indices.

Generalized additive models (GAMs) were constructed to test the hypotheses that relative abundance of each wildlife species was related to the habitat explanatory datasets. GAMs allowed nonlinear response shapes (Guisan, Edwards & Hastie 2002) that better represented the underlying ecological relationships. To avoid over-fitting and to retain more easily interpretable relationships in the GAM smoothing functions (thin plate regression spline), an upper of limit of 3 degrees of freedom was set for each explanatory variable when fitting the models. Wildlife response values were skewed near zero and we used a Tweedie error distribution to account for evidence of overdispersion (Dunn & Smyth 2005). To assess the relative importance of explanatory variables, we developed models containing all possible variable combinations to ensure a balance in the number of models that contained each variable. Models were limited to a maximum of 5 variables to avoid issues of overfitting. Variable relative importance was estimated by summing the Akaike Information Criteria weights (AICw) across all models in the set that contained each variable (Burnham & Anderson 2002). To account for evidence of spatial autocorrelation, we included a residuals autocovariate (RAC) term in each model (Crase, Liedloff & Wintle 2012). The autocovariate represents the spatial autocorrelation in the residuals of an environment only global model that included all explanatory variables.

The form of habitat associations for species was interpreted by inspecting GAM response shapes for PCA-derived explanatory variables and the correlations of the original explanatory habitat variables with each PCA axis. Following inspection of GAM model selection results and the PCA axis correlations, we also developed standardized coefficients for key original explanatory variables using univariate generalized linear models with a binomial distribution (response = presence/absence). These coefficients were used to help identify and visualize the directional effects of shrub understory and forest harvest. All statistical analyses were conducted using R version 3.5.1 (R Development Core Team 2018), PCA was performed using the vegan package (Version 2.5-4, J. Oksanen), GAMs were constructed using the mgcv package (Version 1.8-27, S. Wood, Wood & Augustin 2002), and AICw values for each model set were compiled using the MuMIn package (Version 1.42.1, K. Bartoń)

2.4 Results and Discussion

2.4.1 Habitat

Five UNDERSTORY PCA axes were retained that captured significant variation in shrub cover in the low (0 – 0.5 m), intermediate (0.5 – 2 m) and high (2 m – 10 m) vertical strata, and ground cover of broadleaf litter, herbs, lichen, coarse woody debris, and moss (Appendix 3). Four OVERSTORY axes described variation in tree age, conifer, deciduous, and abundance of standing dead trees. Two DISTURBANCE axes were retained that described variation in forest harvest and roads and two LANDSCAPE axes captured variation in the amount of edge and contiguity of forest patches. Two CLIMATE axes captured the primary gradients in summer precipitation and seasonal phenology, including snow and start of the summer growing season.

2.4.2 Wildlife Habitat Associations

Sufficient data were available to develop models for 61 species, including 44 birds, 7 rodents, 9 medium-large mammals, and 1 salamander. AICw scores demonstrated the strongest support for UNDERSTORY, CANOPY and CLIMATE. Cavity-nesting birds generally showed greater support for CANOPY features than UNDERSTORY, while the reverse was evident for ground-nesting birds. Tree-nesting birds showed a range of support for CANOPY and UNDERSTORY variables among species (Figure 2.2). The red-backed salamander and rodents showed relatively high support for UNDERSTORY while medium-large mammals appeared more strongly influenced by the broad scale effects of CLIMATE. There was less model support among species for DISTURBANCE and LANDSCAPE patch effects on relative abundance; however, DISTURBANCE received slightly higher support among some birds than other taxonomic groups and LANDSCAPE had the strongest support for medium-large mammals and the red-backed salamander (Figure 2.2 & Figure 2.3).

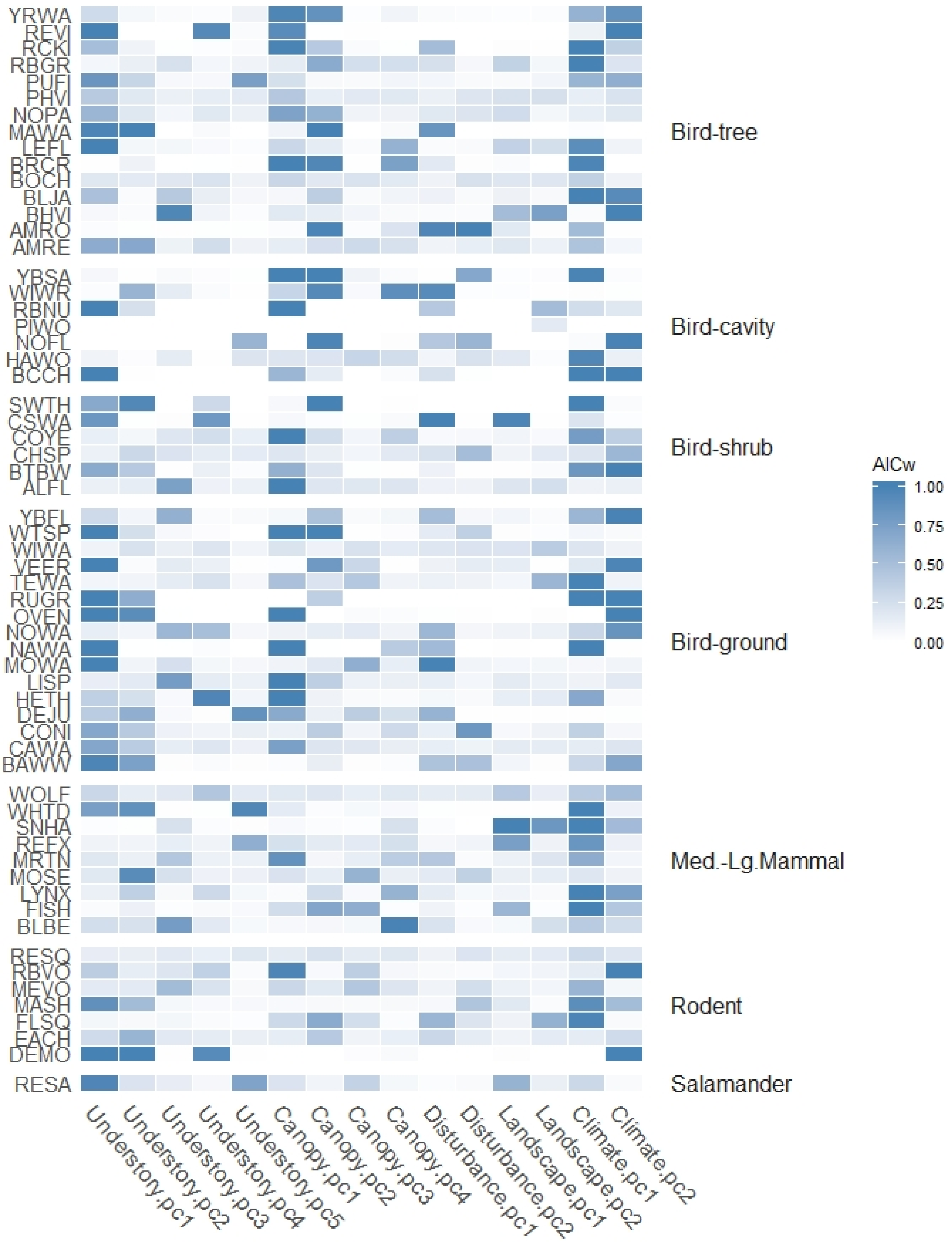

Figure 2.2 AIC weights characterizing the strength of support for each of the PCA-derived habitat variables for each wildlife species. Birds are grouped according to their nesting strategy and species codes are defined in Appendix 4.

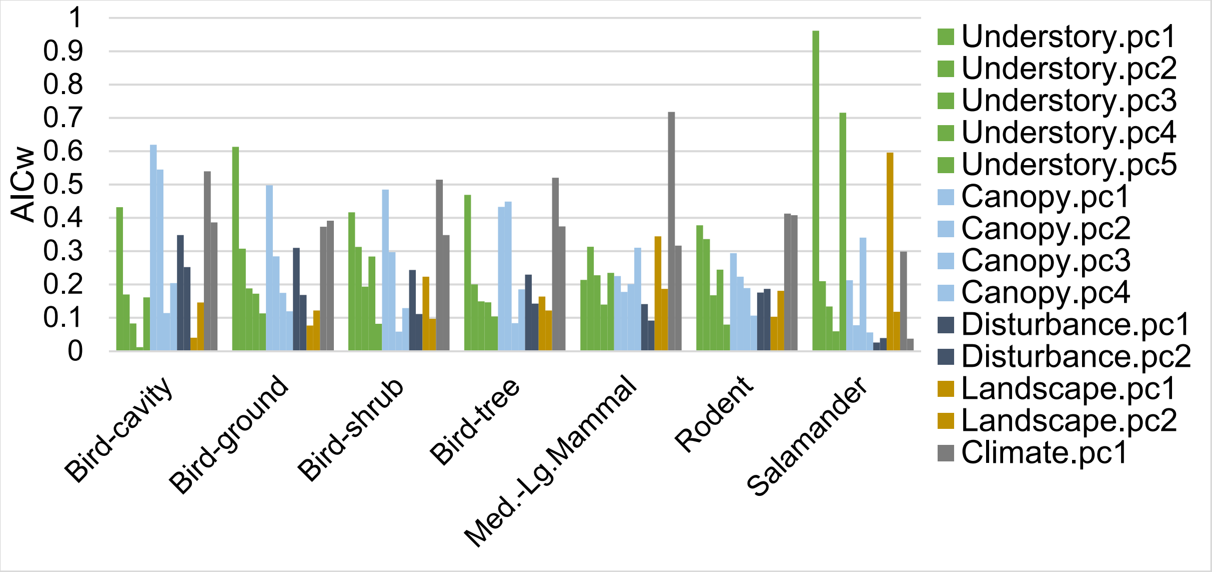

Figure 2.3 Mean AIC weights among taxonomic groups and species guilds for PCA-derived habitat variables. AIC weights characterize the strength of support for each of the habitat variables. Raw habitat variable loadings for each PCA axis are described in Appendix 4.

To help clarify patterns in specific habitat associations for species, we inspected GAM response shapes for explanatory variables (response = relative abundance), as well as standardized coefficients for key original explanatory variables derived from univariate generalized linear models with a binomial distribution (response = presence/absence). Ground-nesting birds with positive relationships to UNDERSTORY.pc1 (e.g. white-throated sparrow [*Zonotrichia albicollis*, WTSP], Nashville warbler [*Oreothlypis ruficapilla*, NAWA]) in GAM's were associated with greater shrub diversity and shrub cover in the understory, evident from the factor loadings for those original variables on the ordination axis (Appendix 3, Figure 2.4). These ground-nesting birds also tended to have positive relationships to CANOPY.pc1, consistent with greater amounts of young open forest. Conversely, for species like the ovenbird (*Seiurus aurocapilla*, OVEN), which nest and feed in leaf litter (Porneluzi, Van Horn & Donovan 2011), GAM models demonstrated a negative relationship to UNDERSTORY.pc1 and CANOPY.pc1, consistent with more closed canopy deciduous forests containing an open understory with abundant leaf litter (Figure 2.4).

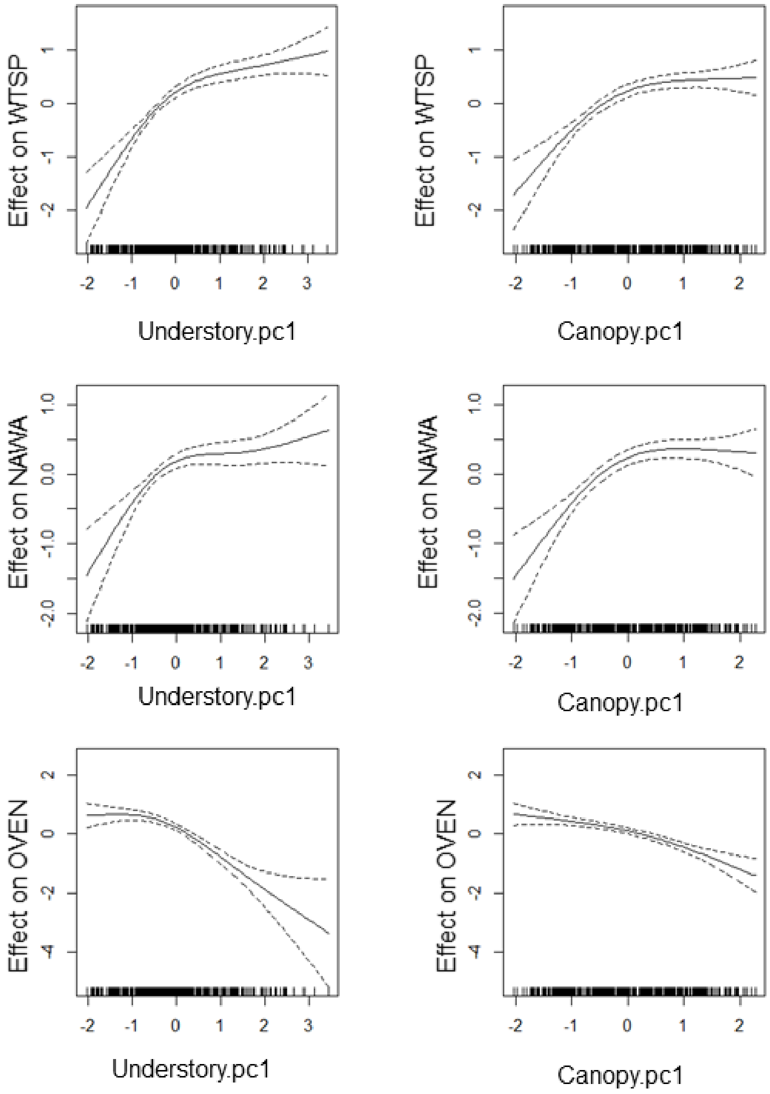

Figure 2.4 Generalized additive model response curves for Understory.pc1 and Canopy.pc1 effects on relative abundance of white-throated sparrow (WTSP), Nashville warbler (NAWA), and the ovenbird (OVEN). Positive values for Understory.pc1 are associated with boreal forests (moss cover, shrub diversity) while negative values capture temperate forest conditions (broadleaf litter, deciduous understory). The Canopy.pc1 axis differentiates conifer (positive scores) from mature deciduous forest (negative scores) (Appendix 3). The y-axis is centred on the response scale by subtracting a weighted mean to ensure valid pointwise 95% confidence intervals (Hastie & Tibshirani 1990). Zero on the y-axis corresponds to no effect of the predictor variable. Solid curves are the thin plate regression spline fits for the predictor variable. The broken lines correspond to 95% Bayesian confidence limits for the smooth. Ticks on the x-axis indicate the locations of observations.

Inspection of GLM-derived coefficients for original understory structure variables revealed that ground and shrub-nesting birds showed mixed response to shrub understory, likely dependent on their unique life history strategies (e.g. feeding behviours). Ground nesters that were also ground foragers tended to show negative relationships to a shrubby understory (e.g. ovenbird, northern waterthrush [Parkesia noveboracensis, NOWA] (Whitaker & Eaton 2014), veery [Catharus fuscescens, VEER] (Heckscher et al. 2017)) (Figure 2.5). Conversely, species such as Nashville warbler, white-throated sparrow, and alder flycatcher (Empidonax alnorum, ALFL) that nest on the ground under low dense vegetation or in bushes, had positive relationships to shrub cover. Cavity nesters (e.g. yellow-bellied sapsucker [Sphyrapicus varius, YBSA] showed a negative relationship to shrub understory, consistent with a preference for mature closed canopy forests (Figure 2.5) (Canterbury et al. 2000). Medium-large mammals that had negative relationships to low shrub cover included white-tailed deer

(Odocoileus virginianus, WHTD) for deciduous cover (Figure 2.5) and red fox (Vulpes Vulpes, REFX) for conifer cover (not plotted, std. coeff. = -0.917, SE = 0.369, P=0.013). The Canada lynx (Lynx canadensis, LYNX) was positively associated with conifer cover in the understory (not plotted, std. coeff. = 0.446, SE = 0.186, P = 0.016). Meadow vole (Microtus pennsylvanicus, MEVO) and masked shrew (Sorex cinereus, MASH) were positively associated with shrub cover (Figure 2.5).

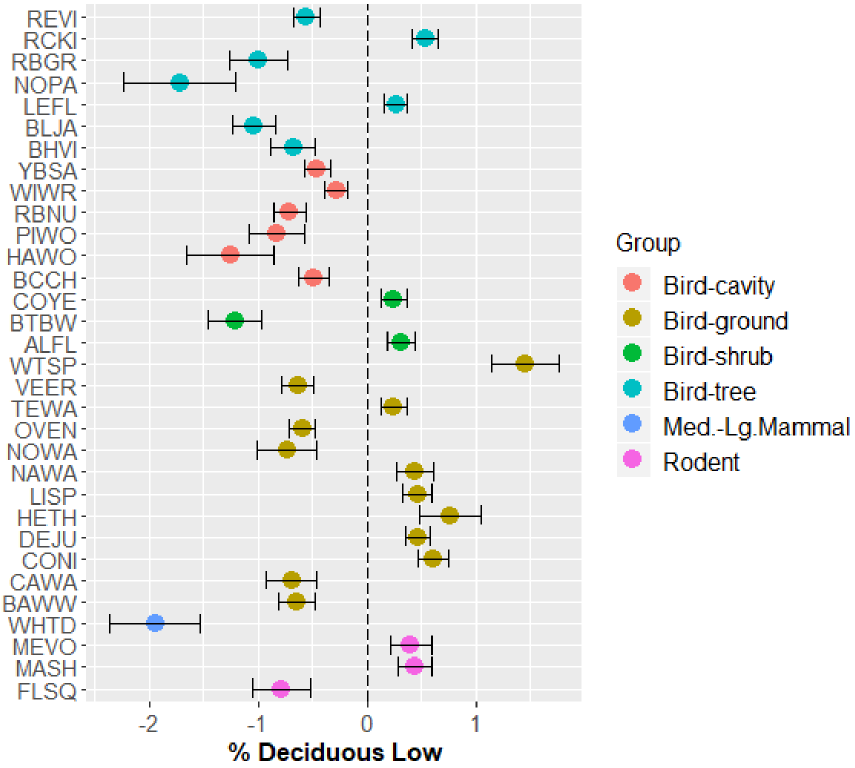

Figure 2.5 Effect size of the mean percentage cover of deciduous shrub cover between 0 and 0.5 m above ground within 1 m radius vegetation plots at wildlife stations. Values are standardized coefficients with standard errors from univariate generalized linear models with binomial distribution for wildlife presence-absence. Only species with significant coefficients in the model (p < 0.05) are shown. Species codes are defined in Appendix 4.

Evidence here identified the importance of understory to affect the wildlife community, including variation in vertical vegetation structure and ground cover (e.g. leaf litter, moss, shrub species diversity). Consistent with our findings, Venier and Pearce (2007) also found strong support for the importance of overstory and understory structure to affect boreal land birds. Conversely, their evidence for the importance of landscape context for birds was less well supported in our study, however, we found stronger support for its affects on mammals and our single salamander species. Importantly, our study characterized landscape with respect to forest edge metrics, whereas they characterized amounts of forest age and cover classes. Our findings highlight that partitioning of birds by breeding guilds can reveal important ecological patterns. Canterbury *et al*. (2000), also using a guild approach, reported negative relationships between shrub-nesting birds and canopy cover and positive relationships for cavity- and canopy-nesting birds. Here, we show greater complexity and variation in response, potentially related to trade-offs in nesting and feeding strategies. For example, Smith and Shugart (1987) demonstrated that arthropod food availability can be positively associated with habitat structure in ovenbird territories, yet we found a negative association with shrub cover and relative abundance of ovenbird.

As noted by Venier and Pearce (2007) in their study, none of the understory variables we assessed are available as mapped features across the large study area. Forest managers require the ability to map habitat at broad spatial extents to permit integration of wildlife-habitat mapping into planning processes and to assess outcomes of potential harvesting scenarios (Venier & Pearce 2007). Some understory features may be correlated with canopy and other features available in FRI and remote sensing products, permitting inferences about understory habitat features (Brown, Rettie & Mallory 2006). However, there is likely independent variation in understory that cannot be inferred from available eFRI and there are mixed results as to the ability of aerial imagery-based forest inventories to accurately map canopy level features (Thompson *et al.* 2007; Maxie *et al.* 2010). Our findings suggest that effort to improve characterization of understory structure in the eFRI will be of considerable value when evaluating biodiversity objectives in forest management planning. Alternative inventory methods, such as remote sensing, high spatial resolution airborne imagery and LiDAR (Light Detection and Ranging), also hold great promise for mapping understory habitat (Martinuzzi *et al.* 2009; Zhang *et al.* 2017). If available, field-based sampling that can compliment inventories derived from aerial imagery and remote sensing, as available in our study system through a broad scale monitoring program, may greatly augment the ability to infer wildlife-habitat relationships and track changes in response to management.

Climate received moderate to high support among all taxa considered but ranked much greater in importance than the other habitat groups for medium to large mammals (Figure 2.3). Relationships were generally consistent with broad bioclimatic patterns, including latitudinal gradients in productivity, winter snow conditions, and forest cover, relative to the habitat niche space of species (Powell 1981; Tumlison 1987; Smith 1991; Raine 2011). White-tailed deer, red fox, and fisher (*Pekania pennant*) were negatively associated with CLIMATE.pc1, consistent with greater temperature seasonality, snow accumulation and a later start to the summer growing season (Figure 2.6, see PCA factor loadings in Appendix 3). Lynx and snowshoe hare (*Lepus americanus*) were positively associated with northern climate conditions (i.e. greater snow accumulation and later start of the growing season).

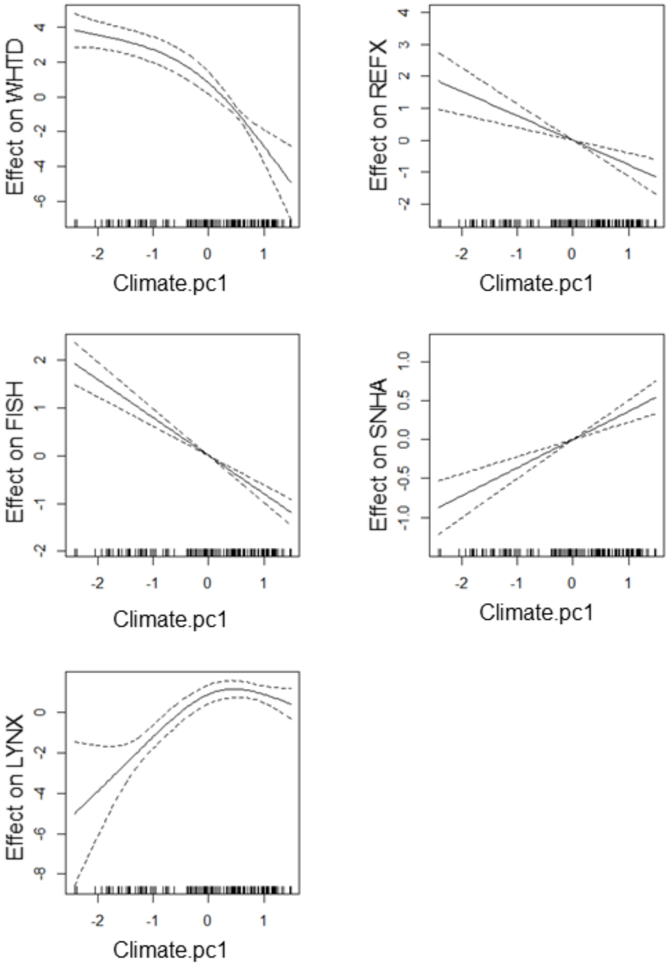

Figure 2.6 Generalized additive model response curves for Climate.pc1 effects on relative abundance of white-tailed deer (WHTD), red fox (REFX), fisher (FISH), Canada lynx (LYNX), and snowshoe hare (SNHA). Positive values for Climate.pc1 are associated with greater seasonality and winter snow accumulation (Appendix 3). The y-axis is centred on the response scale by subtracting a weighted mean to ensure valid pointwise 95% confidence intervals (Hastie & Tibshirani 1990). Zero on the y-axis corresponds to no effect of the predictor variable. Solid curves are the thin plate regression spline fits for the predictor variable. The broken lines correspond to 95% Bayesian confidence limits for the smooth. Ticks on the x-axis indicate the locations of observations.

Positive or negative relationships to forest harvest disturbance were more evident among birds than mammals. Several shrub- and ground-nesting bird species showed positive relationships to Disturbance.pc1, consistent with selection for young open stands with an abundant shrub understory (Figure 2.7). Examples include the mourning warbler (*Geothlypis philadelphia*, MOWA), Lincoln's sparrow (*Melospiza lincolnii*, LISP), hermit thrush (*Catharus guttatus*, HETH), veery, alder flycatcher, black-throated blue warbler (*Setophaga caerulescens*, BTBW), common yellowthroat (*Geothlypis trichas*, COYE) and chestnut-sided warbler (*Setophaga pensylvanica*, CSWA). Other ground- and shrub-nesting birds, such as the Nashville warbler, yellow-bellied flycatcher (*Empidonax flaviventris*, YBFL), and Swainson's thrush (*Catharus ustulatus*, SWTH) had negative relationships to Disturbance.pc1. Cavity- and canopy-nesting birds that had negative relationships to Disturbance.pc1 included northern parula (*Setophaga americana,* NOPA), brown creeper (*Certhia Americana*, BRCR), red-breasted nuthatch (*Sitta canadensis*, RBNU) and black-capped chickadee (*Poecile atricapillus*, BCCH), while rose-breasted grosbeak (*Pheucticus ludovicianus*, RBGR), American robin (*Turdus migratorius*, AMRO), American redstart (*Setophaga ruticilla*, AMRE), and northern flicker (*Colaptes auratus*, NOFL) were positively related to DISTURBANCE.pc1. Among mammals, the meadow vole and white-tailed deer were positively related to DISTURBANCE.pc1, and the red squirrel (*Tamiasciurus hudsonicus*, RESQ) eastern chipmunk (*Tamias striatus*, EACH), lynx and American marten (*Martes americana*, MRTN) were negatively related.

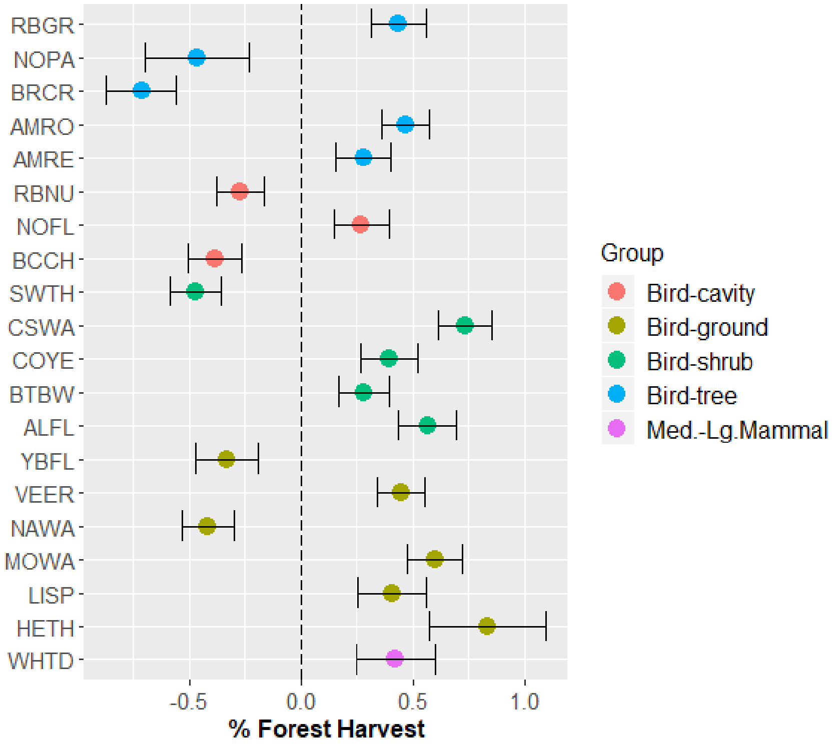

Figure 2.7 Effect size of percentage of forest harvest within 500 m of wildlife stations. Values are standardized coefficients with standard errors from univariate generalized linear models with a binomial distribution for wildlife presence-absence. Only species with significant coefficients in the model ($p < 0.05$) are shown. Species codes are defined in Appendix 4.

Conservation targets may focus on anthropogenic disturbance related conditions (e.g. the amount of cut forest and roads). Such negative affects might operate through the absence of a needed resource or increased mortality risk (Carroll & Miquelle 2006; Houle *et al.* 2010; DeCesare *et al.* 2012). Alternatively, wildlife habitat selection should fundamentally reflect the need to access resources that meet various life history requirements (e.g. availability of nest sites or food), where wildlife is positively associated with specific desired or suitable habitat conditions. The two aspects are inherently related, yet little is known as to whether general mechanisms exist that may affect sensitivities among species and thus optimal approaches to habitat management. Here, we assessed the relative contributions of apparently negative (disturbance) and positive (resource-providing) habitat conditions. We found that resource-providing habitat conditions received greater support in models than the direct characterization of disturbance-related land cover features. Disturbance effects received the greatest support for species whose breeding substrate may be directly impacted by tree harvest, such as cavity- and ground-nesting birds. Notably, seven species of bird all showed negative response to forest harvest (Figure 2.7, northern parula, brown creeper, black-capped chickadee, red-breasted nuthatch, Swainson's thrush, yellow-bellied flycatcher, Nashville warbler), which may support their value as indicators in forest management. Some, but not all of these species have been identified in prior assessments of boreal songbird indicators (Rempel 2007). Of the species identified by Rempel (2007), only the bay-breasted warbler (*Setophaga castanea*) lacked sufficient detections within the provincial monitoring program dataset to develop statistical models in our study.

Landscape features had relatively high support for snowshoe hare and chestnut-sided warbler GAMs, exhibiting positive associations with forest edge; whereas, fisher and red fox were associated with more contiguous patches of forest with less edge (Figure 2.8, see PCA factor loadings in Appendix 3). The wolf GAM had a quadratic response shape for LANDSCAPE.pc1, indicative of a positive effect of forest edge (negative correlation with LANDSCAPE.pc1) and contiguous patches (positive correlation with LANDSCAPE.pc1). Gregarious species, such as wolves, may benefit from a mixture of habitat features in meeting life history needs, such as hunting in areas with openings and edge, while selecting for remote forest at broader scales (Jędrzejewski *et al.* 2004; McPhee, Webb & Merrill 2012). We caution that our scale of forest habitat metric estimation (e.g. 500 m buffer width) was small for species that range widely, such as large mammals. We prioritized selection of habitat metrics and sampling buffer extents to facilitate comparisons among the broad suite of species and environmental conditions in an integrated analysis while attempting to minimize the inclusion of too many predictor variables. Further investigation at a range of spatial extents that better capture habitat features potentially influential to wide-ranging species may be beneficial.

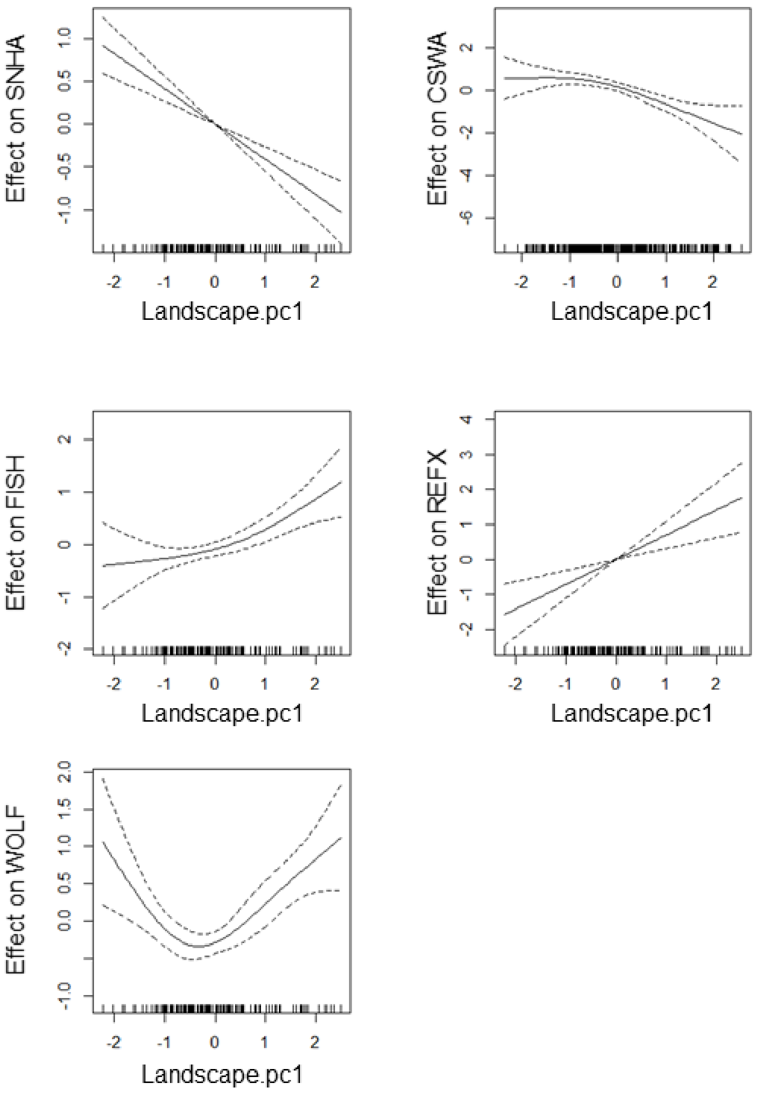

Figure 2.8 Generalized additive model response curves for LANDSCAPE.pc1 effects on relative abundance of snowshoe hare (SNHA), chestnut-sided warbler (CSWA), fisher (FISH), red fox (REFX), and wolf (WOLF). Positive values for LANDSCAPE.pc1 are associated with greater contiguity of forest patches and negative values are associated with greater edge (Appendix 3). Solid curves are the thin plate regression spline fits for the predictor variable. The broken lines correspond to 95% Bayesian confidence limits for the smooth. Ticks on the x-axis indicate the locations of observations.

2.4.3 Conclusions and Recommendations

Our findings provide new information about broad patterns among taxonomic groups as to the relative importance of understory and overstory forest habitat conditions, disturbance, landscape patterns, and climate. These five categories captured multiple scales of habitat that may affect wildlife response, ranging from breeding site selection (e.g. nesting song birds) to broad patterns in abundance that may be driven by landscape level processes. Our individual-based habitat modelling provides quantitative measures of species response to different habitat conditions that can be integrated into ongoing forest management planning processes. We observed differences among taxonomic groups, such as breeding strategy in birds, that may explain observed differences in response to habitat at different scales; for example, the importance of understory to ground-nesting birds. Managers often focus on stand or landscape level objectives for the maintenance of wildlife habitat (OMNR 2010b; OMNR 2010a; OMNR 2014), yet our work highlights the importance of understory vegetation as a significant contributor to explain variation in relative abundance of wildlife. We found considerable variation among species in the habitat conditions of importance, and our work highlights that managing for a diverse range of wildlife and habitat indicators at multiple scales, including understory features, may be needed to assess biodiversity response to sustainable forest management. Our findings also highlight the important scales for monitoring habitat and revealed patterns that may help prioritize effort in field surveys, where resources are limited.

In many cases, wildlife habitat models used in forest management planning may be developed using data from other jurisdictions or limited geographic extents. Given evidence that wildlife-habitat associations can vary in relation to resource availability across landscapes (Holbrook *et al.* 2019), we suggest it is essential that monitoring tools be derived from empirical data collected at scales and geographic extents consistent with the scales of forest management. Forest management may benefit from explicit integration of management and monitoring of wildlife and habitat indices that enable direct evaluation of effectiveness (Lindenmayer & Likens 2009). Habitat monitoring parameters should reflect the conditions hypothesized to potentially affect wildlife populations, consistent with the adaptive management paradigm. Our findings demonstrate the benefits of an approach to identify monitoring indicators using wildlife-habitat models built from monitoring data collected at scales consistent with the intended scale of management decision-making. Such matching of scales in management, monitoring, and model parameterization provides efficiency in effectiveness evaluation and update of management tools used in planning.

3.0 Prevalence of threshold responses in a vertebrate wildlife community to variation in managed forest condition

3.1 Abstract

Monitoring biodiversity to evaluate management policies is a major challenge with respect to identifying sensitive indicators that provide adequate community representation. Conservation of communities of wildlife that rely on a range of forest conditions may conflict with forestry due to the impacts of habitat alteration to wildlife and desire by the public for economic development. Identification of thresholds to disturbance and habitat availability may improve our ability to find compromises between conservation and industrial development, while also identifying sensitive indicators. We used the multivariate Threshold Indicator Taxa Analysis (TITAN) to assess the response of a vertebrate wildlife community to variation in disturbance from forest harvest, roads, and a suite of forest-related habitat indices that may be affected by forest management. Our species-environment dataset spanned the entire area of commercially managed forest in Ontario, Canada, capturing variation in wildlife abundance and habitat for forest song birds, mammals, and a single salamander. Significant thresholds were evident among all taxa, although birds typically had the strongest relationships to environmental gradients and provided good representation of a range of forest conditions useful in assessing sustainability in forestry. We found that negative indicator responses to forest habitat gradients were often more precise and consistent in community response than positive indicator responses, potentially affected by the diversity of habitat niche space among species. Stronger responses among a greater range of taxa were evident for resource-providing habitat conditions than direct measures of disturbance (i.e. forest cuts and roads). Our approach demonstrates the value of identifying ecological community thresholds that can serve to set targets for conserving biodiversity and to characterize community dynamics in response to habitat change mediated by forest management.

3.2 Introduction

Land use managers are increasingly required to identify management alternatives that balance competing objectives for both industrial development and biodiversity conservation. Habitat loss is implicated as one of the leading causes of population decline (Fahrig 1997; Bender, Contreras & Fahrig 1998) and identification of thresholds to habitat alteration, below which the impact to wildlife can be minimized, may help in achieving sustainable resource management. Ecological thresholds can be defined as transition points of relatively rapid change in an ecosystem state in response to potentially small changes in an influential environmental condition (Groffman *et al.* 2006; Nichols, Eaton & Martin 2014).

Habitat alteration from anthropogenic disturbance may directly influence distribution or abundance of wildlife by contributing to a functional loss of habitat, including landscape scale fragmentation, loss of structural features, and indirectly by changing vegetation community dynamics and predator-prey relationships (Butler *et al.* 2004; Wittmer *et al.* 2007).Understory forest vegetation may simultaneously provide food, shelter, and visual cover from predators. The density or biomass of understory foliage can be positively correlated with plant and animal-based food sources for birds and mammals (Greene & Johnson 1994). With respect to birds, a focal group of our study, vegetation provides substrate for breeding birds that nest in the ground, shrub or canopy layers. As such, vegetation represents a dynamic component of ecosystems that can be readily manipulated through forest management in meeting wildlife habitat objectives.

Forestry is an important source of economic revenue in many jurisdictions and managers would benefit from knowing the extent of habitat alteration, if any, that can be tolerated without compromising the habitat value of an area. Although ecological thresholds are widely recognized as a potential tool for sustainable management (Groffman *et al.* 2006; Qian & Cuffney 2012; Richmond *et al.* 2015), the actual prevalence of thresholds among wildlife community inhabiting forests is not well documented. Further, where managers take a landscape-scale approach to the maintenance of wildlife habitat (OMNR 2014), managing for separate individual threshold targets for a large suite of species may prove problematic. Under such circumstances, identification of ecological community thresholds may be appropriate, based on the hypothesis that communities of species may show synchronous responses to shared environmental pressures (Økland, Skarpaas & Kausrud 2009).

Conservation targets may focus on anthropogenic disturbance related conditions (e.g. the amount of cut forest and roads) under the hypothesis that negative effects drive distributions. Such negative affects might operate through the absence of a needed resource or increased predation risk (Butler *et al.* 2004; DeCesare *et al.* 2012). Alternatively, wildlife habitat selection should fundamentally reflect the need to access resources that meet various life history requirements, where wildlife are positively associated with specific desired or suitable habitat conditions. The two aspects are inherently correlated, yet little is known as to whether general mechanisms exist that may affect sensitivities among species and thus optimal approaches to habitat management. Here, we assess evidence of thresholds among taxa to apparently negative (disturbance) and positive (resource-providing) habitat conditions.

Assessments of threshold responses frequently use single-species approaches or aggregate community data into synthetic metrics of community condition or species richness (King & Richardson 2003; Butler *et al.* 2004; Brown 2011); however, such methods may fail to accurately characterize the joint community level and individual species responses, including non-liner relationships of one or more species to environmental gradients. We employ Threshold Indicator Taxa Analysis (TITAN) to identify abrupt changes in both the occurrence frequency and relative abundance of individual species along environmental gradients in forest condition (Baker & King 2010). We used a wildlife monitoring dataset that captured variation in relative abundance and wildlife-habitat associations across the entire area of forest management on Crown land in Ontario, Canada and at scales explicitly tailored to forest management planning processes.

Our objective was to identify the prevalence and patterns among wildlife species in threshold response in relative abundance to variation in managed forest condition. We focused on environmental gradients in disturbance from forest tree harvest, roads, and availability of habitat features known to be important to wildlife and that may be affected by forestry. We specifically targeted vegetation features in the canopy, understory and ground-level, as well as a landscape-scale estimate of forest edge. We were interested in identifying the relative importance of disturbance versus the availability of suitable habitat in characterizing thresholds. Ultimately, our goal is to provide information as to the safe biological limits (i.e. thresholds), benchmarks and indicators that can be defined for use in forest management planning and biodiversity conservation. Our findings are discussed in relation to anticipating potential shifts in communities in response to environmental change and the biodiversity and habitat that may be most sensitive, and thus useful as indicators.

3.3 Methods

3.3.1 Study Area and Wildlife Inventories

We used forest and wildlife inventories collected by the Ministry of Natural Resources and Forestry (MNRF) in the province of Ontario, Canada. The study area encompassed diverse vegetation communities, including temperate deciduous forest in the south and boreal forest in the north. Mean annual temperature ranged from 2 to 6 °C and moist conditions were more prevalent in the south and east because of the moderating effects of the Great Lakes (MacKey *et al.* 1996). Wildlife inventories were collected at 141 sites distributed randomly across the area of Crown forest managed by the province of Ontario (Figure 2.1). The sample design was intended to support a wildlife population monitoring program that included habitat surveys and each site contained a set of 3-4 survey stations. Details of the sample design are described in Brown *et al*. (2015).

Bird stations at each site were spaced approximately 346 m apart to ensure independence and reduce potential double-counting of individual birds during surveys. Audio point counts (10-minute duration) were recorded daily, 30 minutes before to 30 minutes after sunrise (local time), using a Song Meter SM2 or SM2+ (Wildlife Acoustics Inc., Concord, MA.). A single 10-minute point count was selected for each of 6 equal duration sessions between May 20 and July 7. Point count recordings were interpreted by a single person to record the number of unique individuals of each species. The mean number of individuals among sessions at each station was used as an index of relative abundance for each species and stations were treated as independent samples for subsequent analysis (n = 364).

Small mammal trap lines were co-located at bird stations and consisted of 11 trapping sub-stations spaced 10 m apart. Each sub-station contained one large trap (XLF15, 10.16 cm x 11.43 cm x 38.1 cm, H.B. Sherman Traps Inc.) and one smaller trap (XLK, 7.62 cm x 9.525 cm x 30.48 cm, H.B. Sherman Traps Inc.). Trapping was conducted for three consecutive nights between mid-July and the end of August and the projected number of unique individuals per 1000 trap nights was used as an index of relative abundance for each trap line (n = 206).

Cameras were placed at the center of each site and 500 m away in each of the four cardinal directions. Cameras were deployed between May and August for a minimum of 100 days. The total deployment period for each camera was partitioned into a maximum of seven 15-day sessions. A relative abundance index for each species and site was calculated as the number of days in each session with a detection divided by the number of active camera days (max of 15), averaged for all sessions. The mammal species under consideration were assumed able to move among all cameras at a site, so the index was averaged among all stations for use in statistical analysis (n = 140).

Abundance of red-backed salamander (*Plethodon cinereus*) was surveyed at each site using grids of 20 or 30 coverboards placed 8 m apart and co-located with one of the bird stations. Additional boards were deployed in the northern portion of range where densities were expected to be lower. Counts of salamanders at each board were conducted between May and July for up to three repeat surveys. The maximum of the average count per board among repeat surveys at each site was used to create a projected count per 20 boards for use as a relative abundance index (n = 71 sites).

3.3.2 Forest Habitat Inventories

Ground-based inventories of forest vegetation composition and structure were collected at 141 wildlife survey sites. Sampling was centered on the wildlife plots and included multiple circular buffer extents appropriate for each wildlife survey and habitat component. Understory vegetation was measured within 1 m radius circular plots, including 5 plots per bird audio station, one centered on the station and four offset by 30 m and 50 m to the east and west. Measurements employed in our study included the percentage cover of leaf litter, coarse woody debris, and vertical vegetation structure between 0 m and 10 m above ground for deciduous and conifer woody vegetation (Appendix 1).

Overstory information collected during ground sampling included stand tree species composition, tree height, tree density, and abundance of cavity trees (Appendix 1). Circular tree plots (11.28 m radius) were located at each wildlife station and offset 50 m in an east and west direction (up to 3 plots per station). Measurements within each tree plot included the species and diameter at breast height (d.b.h.) (1.3 m above base of tree) for all trees that were >= 8 cm d.b.h., whether dead or alive, and whether there were one or more cavities present. Vegetation variables were averaged among plots at each station (separately for 1 m radius and tree plots) for subsequent analyses for birds, rodents, and the salamander. Plot information was averaged at a site level for the camera-derived mammal analysis.

The Forest Resource Inventory (FRI) maintained by the MNRF is based on digital aerial photo interpretation and field surveys and contains both overstory tree composition and understory structure information (https://www.ontario.ca/page/forest-resources-inventory; OMNR 2009). Overstory canopy variables derived from the FRI included the overstory age (years) and the percentage composition of conifer and deciduous forest derived from pooling of Provincial Forest Types (Conifer = Mixed conifer lowland + Mixed conifer upland + Jack Pine, Deciduous = Poplar + Tolerant hardwoods + White birch; definitions in OMNR 2003). The FRI-derived overstory variables were extracted in a geographic information system (GIS) using 150 m radius buffers centered on each bird, small mammal, and salamander station, and 500 m buffers around each site centroid for the camera-derived mammal analysis.

Disturbance variables included the mean distance to roads (m) and percentage cover of forest harvest (<= 20 years old) within 500 m circular buffers of each wildlife station. Mapped layers for roads and year-specific forest harvest blocks were available from the MNRF. Euclidean distance analysis was used to determine the mean distance within buffered station polygons (rasterized) to the nearest road segment (highway, primary or secondary road). Landscape-scale pattern in forest patches was characterized as the average total edge using 500 m buffers centered on the wildlife stations. Total edge was calculated using conifer, mixed and deciduous forest cover classes and the software Fragstats (Version 4.0, McGarigal 2015).

3.3.3 Statistical Analysis

We used the TITAN method described by Baker and King (2010) to identify abrupt changes in both the occurrence frequency and relative abundance of individual wildlife species along environmental gradients in forest condition. Thresholds were assessed separately for each of the habitat and disturbance metrics. The approach combines methods of change point analysis (King & Richardson 2003) and indicator species analysis (IndVal, Dufrêne & Legendre 1997). Change point analysis was used to order and partition observations along each environmental gradient, similar to regression trees (Elith, Leathwick & Hastie 2008). TITAN uses taxon-specific IndVal scores and deviance reduction to identify an optimal change point. IndVal scores integrate information about occurrence frequency and abundance to produce a measure of association that is unbiased by group size (Dufrêne & Legendre 1997). TITAN distinguishes negative and positive responses of individual species and cumulative responses of taxa in the community. Bootstrapping was used to estimate indicator reliability as well as uncertainty around the location of individual species and community change points.

The quality of each indicator response for each species was assessed using TITAN’s diagnostic measures of purity and reliability (Baker & King 2010). Pure indicators were identified as those where >= 95% of the bootstrap replicates (n = 500) indicated change-point response directions that agreed with the observed response. Reliable indicators were those that achieved >= 95% of bootstrap replicates with a P-value <=

0.05, with repeatable and consistently large IndVal maxima (Baker & King 2010). IndVal scores were rescaled as z scores by subtracting the mean of randomized permutations from the observed IndVal scores and dividing by the standard deviation. Standardized taxa responses increasing at the change point (z+) were distinguished from those decreasing (z-) and those showing no response. Evidence for community-level thresholds among negative and positive taxa was assessed by summing all z- and z+ scores for each candidate change-point value and identifying the change-point with the maximum summed values. Large values of sum(z) scores occur when many taxa have strong responses at a similar value of the environmental gradient (Baker & King 2010). Evidence of community thresholds was assessed using bootstrapped confidence intervals of the sum(z) scores and evidence of a distinct local maxima in the cumulative frequency of sum(z) scores along the environmental gradient. All statistical analyses were conducted using R version 3.5.1 (R Development Core Team 2018) and threshold analysis was performed using the TITAN2 package (Version 2.1, M. Baker, R. King, & D. Kahle).

3.4 Results

Thresholds were evident among all taxa, including positive and negative effects for landscape, stand canopy, understory, and disturbance related forest condition. Of the individual species and habitat interactions considered, roughly 50% yielded no reliable threshold responses, and the remainder of reliable thresholds were distributed evenly among negative and positive indicator responses (Figure 3.1). Not surprisingly, the uncertainty in threshold identification (i.e. precision), inferred from the range of 90% bootstrapped confidence intervals (0.05 and 0.95 quantiles), was greater for unreliable metrics. The precision was significantly better (smaller range) for negative indicator thresholds than positive indicators (F-test 249.7, $P<0.05$, Tukey post-hoc comparisons) (Figure 3.1). Among taxa, only birds had a significant difference in precision of thresholds between negative and positive effects, with negative effects more precise (F-test 184.7, $P<0.05$, with Tukey post-hoc comparisons). Responses to cavity trees (positive and negative), coarse woody debris (negative), and low shrub cover (negative) typically had narrow distributions along the environmental gradients, and narrower bootstrap frequency distributions, suggestive of a more consistent and distinct community level response for these variables. Responses to other gradients were often distributed widely along the environmental gradient, indicating variability among species in thresholds. Species with relatively wide bootstrap frequency distributions, such as evident for the FRI-derived measures of conifer and deciduous tree cover, suggested substantial uncertainty about the existence of a threshold.

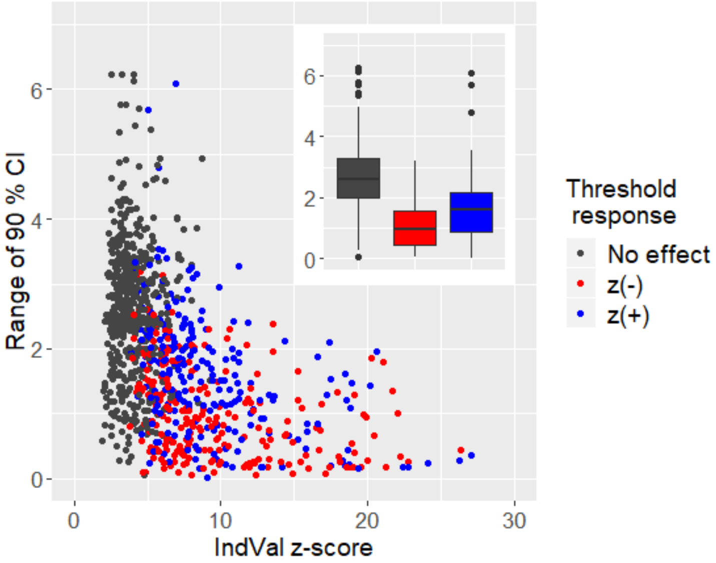

Figure 3.1 Range of 90% bootstrap confidence intervals of change points relative to observed indicator value (IndVal) z scores for each combination of species and habitat gradient. All habitat variables were standardized (to zero mean and unit variance) prior to analysis to permit comparisons among variables with different original units of measure. Unreliable indicators are displayed in grey, and reliable indicators (purity >=0.95 and reliability >= 0.95) are distinguished by whether they represented a negative (z-) or positive (z+) repsponse to the respective habitat gradient. The boxplot insert illustrates the the distribution of CI ranges among groups.

Birds showed the strongest evidence of change point responses to forest harvest and roads and no mammals had a significant negative response to harvest. More bird species had positive response thresholds to harvest than negative responses – most notably shrub- and ground-nesting bird species (Figure 3.2a). In contrast, more birds had a positive response to greater distances from roads (i.e. a negative effect of roads) (Figure 3.2b). There was limited evidence of a community level negative response by birds to percentage cover of forest harvest, but greater support for a positive community response, as evidenced by the flat and moderate peaks in cumulative frequency distributions, respectively (Figure 3.3). The TITAN sum(z+) peaked at a mean of 30% cover of forest harvest (inferred community level threshold response) across 500 iterations and the cumulative change-point frequency distributions for bootstrap replicates ranged between 20 – 53% at the 90% level (Table 1). A single bird community response to roads was not evident, although some tree nesters appeared to exhibit positive thresholds near approximately 1.7 km distance from roads (e.g. olive-sided flycatcher [*Contopus cooperi*] and common grackle [*Quiscalus quiscula*]), while other species clustered near the community mean positive response of approximately 5.8 km distance from roads (Figure 3.2b). Among rodents, the red-backed vole (*Myodes gapperi*, RBVO), northern flying squirrel (*Glaucomys sabrinus*, NFSQ), and short tailed shrew (*Blarina brevicauda*, STSH) had negative responses to distance to roads (i.e. more abundant closer to roads), whereas, the reverse was true for the masked shrew (*Sorex cinereus*, MASH).

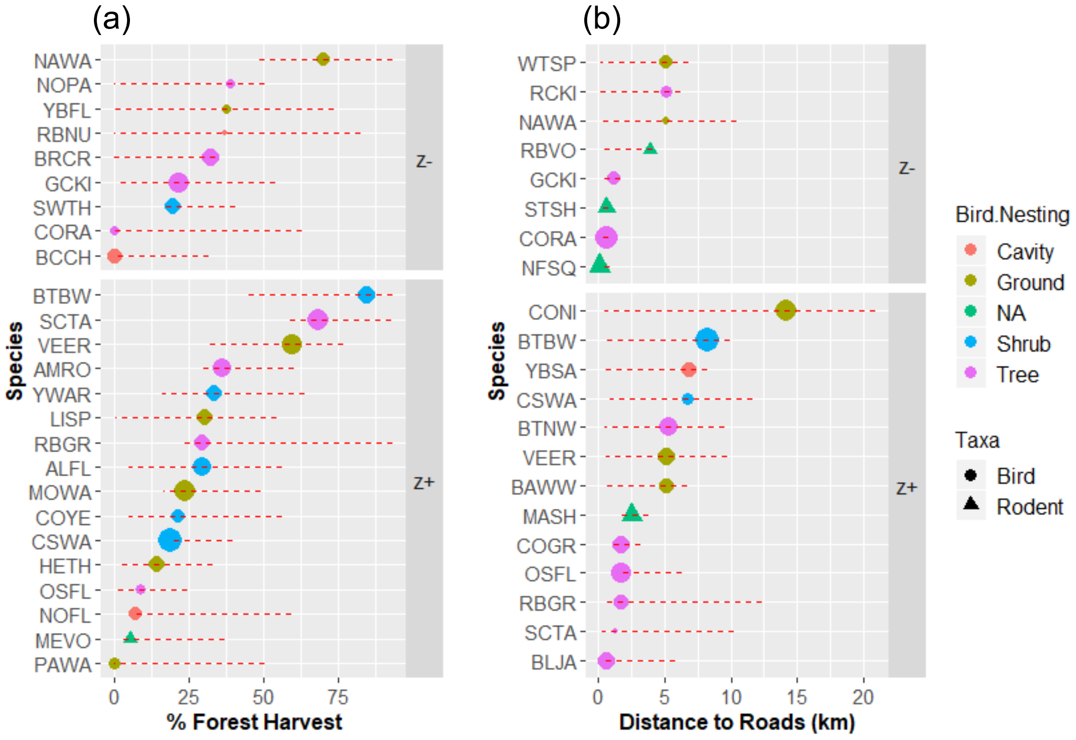

Figure 3.2 Threshold indicator taxa analysis (TITAN) of vertebrate community response to gradients in (a) forest harvest and (b) roads in 500 m radius circular wildlife and habitat survey plots in managed forest of Ontario. Reliable indicator taxa (purity >=0.95 and reliability >= 0.95) are plotted in increasing order with respect to their observed environmental change point. Negative (z-) indicator taxa are plotted in the top block and positive (z+) taxa in the lower block. Symbols are sized in proportion to z scores representing stregth of indicator value. Dashed horizontal red lines overlapping each symbol represent 5th and 95th percentiles in change point estimates among 500 bootstrap replicates. Species codes are defined in Appendix 4.

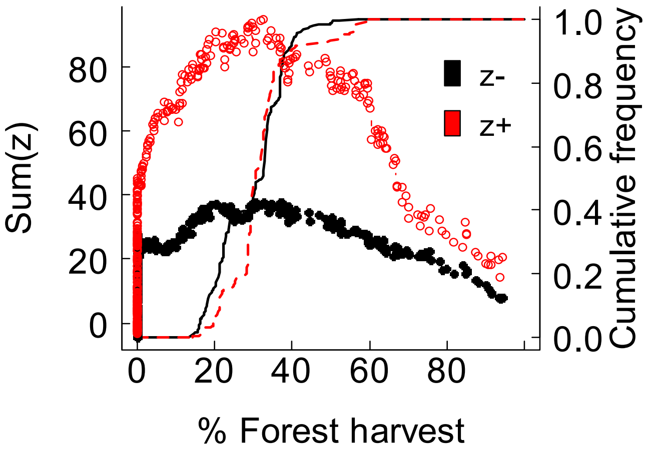

Figure 3.3 TITAN sum(z-) and sum(z+) values (circles) for the bird community corresponding to all candidate change points along the forest harvest gradient. Black and red vertical lines represent the cumulative frequency distribution of change points (thresholds) among 500 bootstrap replicates for sum(z-) and sum(z+), respectively. Prominent peaks in sum(z) suggest stronger evidence of a consistent community response among birds.

A wide range of taxa showed threshold responses to vegetation cover within 0 to 0.5 m above ground (Conifer low and Deciduous low). More species had negative responses to low deciduous cover and many ground-nesting birds exhibited positive responses (Figure 3.4a). Dark-eyed junco (*Junco hyemalis*, DEJU), common nighthawk (*Chordeiles minor*, CONI), hermit thrush (*Catharus guttatus*, HETH), and the white-throated sparrow (*Zonotrichia albicollis*, WTSP) had high IndVal z scores (indicator strength). Bird community level responses were strong and demonstrated a negative response at mean percentage low deciduous cover of 9.2% (8.69 – 13.3%) and a positive threshold among species at 21% (12.4 – 22.9%) (Table 1). Cavity-nesting birds typically had negative threshold responses to low conifer or deciduous in the understory. Ground or shrub nesters that were also ground foragers tended to show negative thresholds to a shrubby understory (e.g. ovenbird [*Seiurus aurocapilla*, OVEN], northern waterthrush [*Parkesia noveboracensis*, NOWA] (Whitaker & Eaton 2014), veery [*Catharus fuscescens*, VEER] (Heckscher *et al.* 2017)). Birds had a strong community level response to any amount of low conifer cover and thresholds had narrow ranges of uncertainty: 1.5% (0.5 – 2.0%) and 1.5% (1.0 – 5.7%) for negative and positive thresholds, respectively (Figure 3.4b) (Table 3.1). Medium – large mammals exhibited a community-level negative response to low deciduous cover at a threshold of 8% (6 – 10%). Among mammals, the white-tailed deer (*Odocoileus virginianus*, WHTD) and masked shrew had relatively high IndVal z scores, showing negative and positive threshold responses to low conifer, respectively.

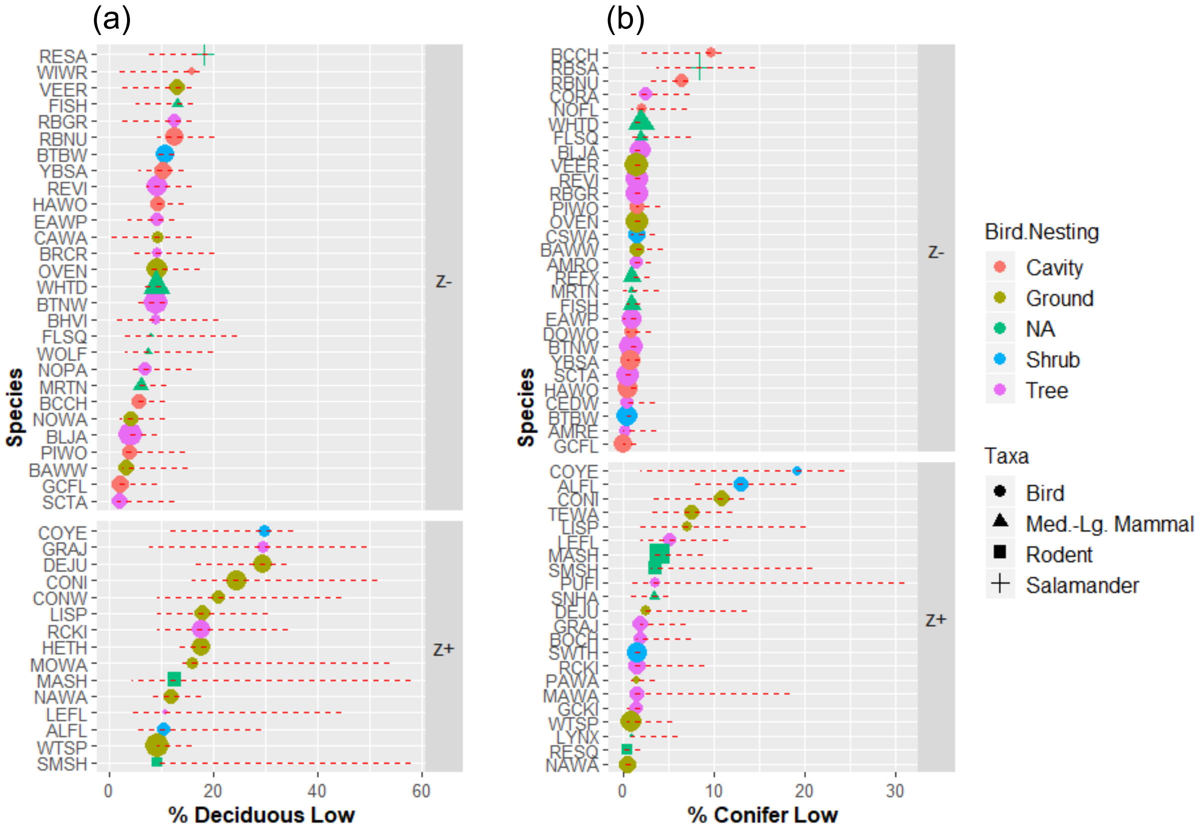

Figure 3.4 Threshold indicator taxa analysis (TITAN) of vertebrate community response to gradients in (a) percentage cover of low deciduous and (b) low coniferous vegetation occurring 0 – 0.5 m above ground at wildlife survey sites. Reliable indicator taxa (purity >=0.95 and reliability >= 0.95) are plotted in increasing order with respect to their observed environmental change point. Negative (z-) indicator taxa are plotted in the top block and positive (z+) taxa in the lower block. Symbols are sized in proportion to z scores representing stregth of indicator value. Dashed horizontal red lines overlapping each symbol represent 5th and 95th percentiles in change point estimates among 500 bootstrap replicates. Species codes are defined in Appendix 4.

Rodents had a positive community threshold response to coarse woody debris at a mean% cover of 2.6% (2.1 – 6.7%) and no significant negative effects among species (Figure 3.5a, Table 3.1). Birds showed mixed responses, with a slightly stronger negative community response (2.1%, 1.0 – 4.2%) than positive response (7.4%, 2.6 – 7.6%). Surprisingly, the red-backed salamander (RESA) had a negative threshold response to coarse woody debris. Although Plethodontids are known to use dead decaying wood has habitat, and the cover broad method is considered a viable sampling technique (Marsh & Goicochea 2003), the method could potentially cause bias if salamanders preferentially use natural objects instead of artificial cover boards when the former is highly abundant.

Many tree- and cavity-nesting birds had negative threshold responses to shrub species diversity (mean community threshold of 2 – 3 shrub species), and positive threshold responses were more typical of ground- and shrub-nesting birds (community threshold of 3 - 4 shrub species) (Figure 3.5b). Mammals such as the white-tailed deer, American marten (*Martes americana*, MRTN) and fisher (*Pekania pennant*, FISH) had negative threshold responses to shrub diversity and the Canada lynx (*Lynx canadensis*, LYNX) and snowshoe hare (*Lepus americanus*, SNHA) had positive responses, although the IndVal z scores were small for these species.

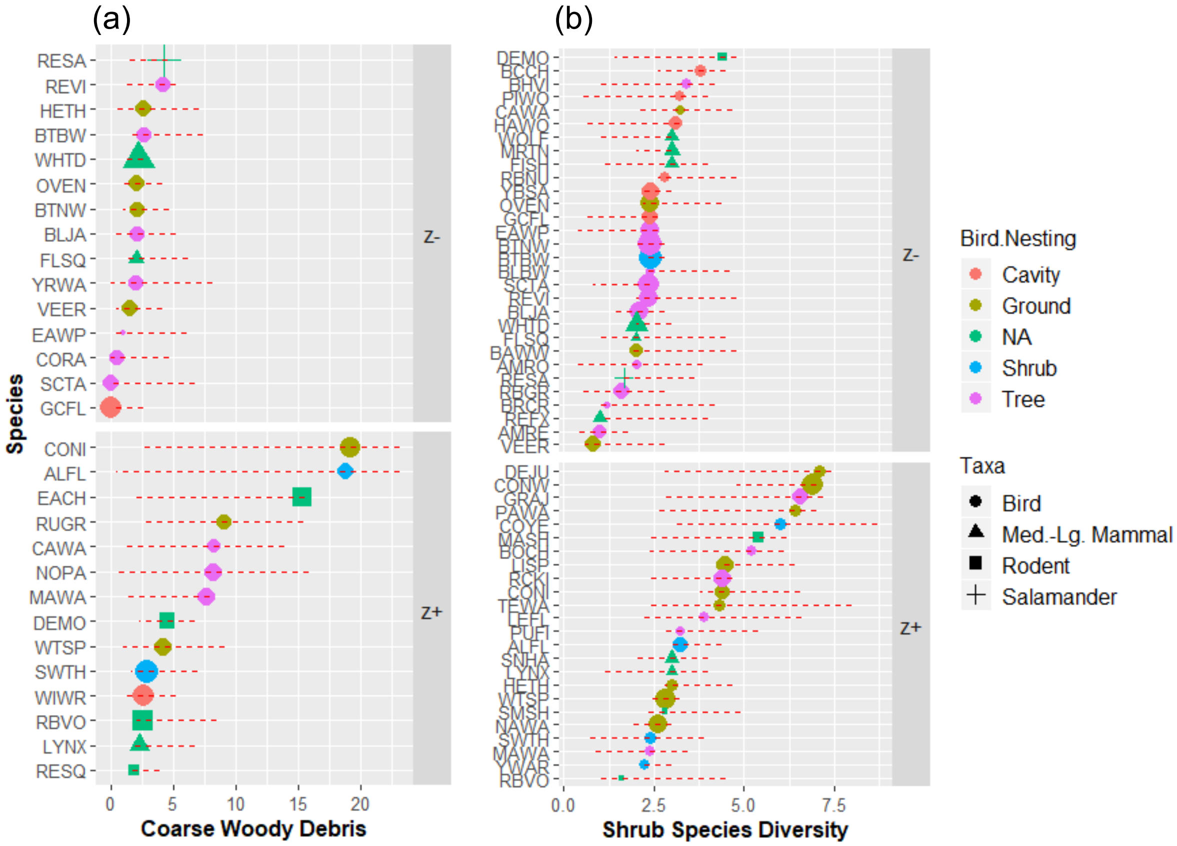

Figure 3.5 Threshold indicator taxa analysis (TITAN) of vertebrate community response to gradients in (a) percentage cover of coarse woody debris and (b) shrub species diversity at wildlife survey sites. Reliable indicator taxa (purity >=0.95 and reliability >= 0.95) are plotted in increasing order with respect to their observed environmental change point. Negative (z-) indicator taxa are plotted in the top block and positive (z+) taxa in the lower block. Symbols are sized in proportion to z scores representing stregth of indicator value. Dashed horizontal red lines overlapping each symbol represent 5th and 95th percentiles in change point estimates among 500 bootstrap replicates. Species codes are defined in Appendix 4.

Table 3.1 TITAN community-level thresholds estimated from taxa responses to gradients in forest condition across the area of managed forest in Ontario, Canada.*

Taxa	Variable	Effect	Change point	5%	95%
Bird	Forest age	sum(z-)	22	18	22
Bird	Forest age	sum(z+)	56	51	73
Bird	Cavity trees	sum(z-)	8.3	0	16.7
Bird	Cavity trees	sum(z+)	10.4	8.3	25
Bird	Conif. low	sum(z-)	1.5	0.5	2
Bird	Conif. low	sum(z+)	1.5	1	5.7
Bird	CWD	sum(z-)	2.1	1	4.2
Bird	CWD	sum(z+)	7.5	2.6	7.6
Bird	Edge	sum(z-)	8.9	6.3	10.7
Bird	Edge	sum(z+)	9.7	9.1	14.3
Bird	Harvest	sum(z-)	30.7	16	41.2
Bird	Harvest	sum(z+)	33	20.3	53
Bird	Decid. low	sum(z-)	9.2	8.9	13.3
Bird	Decid. low	sum(z+)	21	12.4	22.9
Bird	Conif. canopy	sum(z-)	17.6	0.5	56.4
Bird	Conif. canopy	sum(z+)	23.5	19.2	98.2
Bird	Decid. canopy	sum(z-)	40	0	82.7
Bird	Decid. canopy	sum(z+)	78.7	45.9	99.1
Bird	Roads	sum(z-)	424.3	282.8	5344.2
Bird	Roads	sum(z+)	5849.2	750.4	8342.7
Bird	Shrub divers.	sum(z-)	2.4	2.2	2.8
Bird	Shrub divers.	sum(z+)	4.4	2.8	4.4
Bird	Trees per ha	sum(z-)	241.8	191.8	601.2
Bird	Trees per ha	sum(z+)	1054.9	716.7	1150.8
M.-Lg. Mammal	Forest age	sum(z-)	122.5	65.5	124.5
M.-Lg. Mammal	Forest age	sum(z+)	73.5	62	122.5
M.-Lg. Mammal	Cavity trees	sum(z-)	21.5	11	26.5
M.-Lg. Mammal	Cavity trees	sum(z+)	11.5	7	21.5
M.-Lg. Mammal	Conif. low	sum(z-)	2	1	2.5
M.-Lg. Mammal	Conif. low	sum(z+)	0	0	4
M.-Lg. Mammal	CWD	sum(z-)	2.1	1.5	3.5
M.-Lg. Mammal	CWD	sum(z+)	1.9	1.8	4
M.-Lg. Mammal	Edge	sum(z-)	11.4	7	12.1
M.-Lg. Mammal	Edge	sum(z+)	6.7	6.8	14.9
M.-Lg. Mammal	Decid. low	sum(z-)	8	6	10
M.-Lg. Mammal	Conif. canopy	sum(z-)	14.8	8.7	44.3
M.-Lg. Mammal	Conif. canopy	sum(z+)	49.8	10.6	98.2
M.-Lg. Mammal	Decid. canopy	sum(z-)	40.5	8.9	85.3
M.-Lg. Mammal	Decid. canopy	sum(z+)	85.3	74.9	90.8
M.-Lg. Mammal	Shrub divers.	sum(z-)	2	2	3
M.-Lg. Mammal	Shrub divers.	sum(z+)	3	1	4
M.-Lg. Mammal	Trees per ha	sum(z-)	871	865.5	1233.6
M.-Lg. Mammal	Trees per ha	sum(z+)	1328.5	828.8	1331
Rodent	Forest age	sum(z-)	113	79.4	115.6

Taxa	Variable	Effect	Change point	5%	95%
Rodent	Cavity trees	sum(z-)	16.7	8.3	29.2
Rodent	Conif. low	sum(z+)	5.2	3.6	9
Rodent	CWD	sum(z+)	2.6	2.1	6.7
Rodent	Edge	sum(z+)	9.5	9	16.4
Rodent	Harvest	sum(z+)	5.1	4.1	36.7
Rodent	Decid. low	sum(z+)	9.2	7	58
Rodent	Conif. canopy	sum(z-)	63.8	31.8	86.1
Rodent	Conif. canopy	sum(z+)	0	0	100
Rodent	Decid. canopy	sum(z-)	83.8	0	100
Rodent	Decid. canopy	sum(z+)	81.7	36	100
Rodent	Roads	sum(z-)	604.2	100	932.7
Rodent	Roads	sum(z+)	2524.8	1916	3827.5
Rodent	Shrub divers.	sum(z-)	4.4	1.6	4.8
Rodent	Shrub divers.	sum(z+)	4.6	1.8	5.3
Rodent	Trees per ha	sum(z+)	1034	1004.9	2026.4

* TITAN community-level analysis performed separately for birds, medium to large mammals, and rodents. Observed change points correspond to the value of the candidate change point (*x*) resulting in the largest sum of indicator value (IndVal) z scores among all negative (z-) and positive (z+) species, respectively. Quantiles (5% and 95%) correspond to change points from 500 bootstrap replicates. Units of measure include: edge (km of roads per km^2), age (years), cavity trees (count per hectare), shrub species diversity (count per 1 m radius circular plot), and percentage cover for tree harvest, coarse woody debris (CWD), conifer and deciduous in the canopy (Conif. & Decid. canopy) and 0 – 0.5 m above ground (Conif. & Decid. low).

For both forest stand age and tree density, ground- and shrub-nesting birds had relatively high IndVal z scores and negative threshold responses, whereas several tree- and cavity-nesting birds had positive responses (Figure 3.6a, b). Likewise, tree- and cavity-nesting birds had positive responses to the number of cavity trees per hectare and many ground and shrub nesters had negative responses (Figure 3.6c). The marten and red-backed salamander also had positive threshold responses to forest age, and the red squirrel (*Tamiasciurus hudsonicus*, RESQ) and woodland jumping mouse (*Napaeozapus insignis*, WJMO) were positively associated with tree density. Community level thresholds were evident for bird response to trees per hectare, forest age, and cavity trees per hectare (Table 3.1). Distinct community level responses among mammals was not evident based on wide confidence bands of sum(z) scores (Table 3.1) and inspection of cumulative frequency distribution plots (not shown). However, the snowshoe hare, red squirrel and deer mouse (*Peromyscus maniculatus*, DEMO) all had negative response thresholds to forest age at 113 – 122 years.

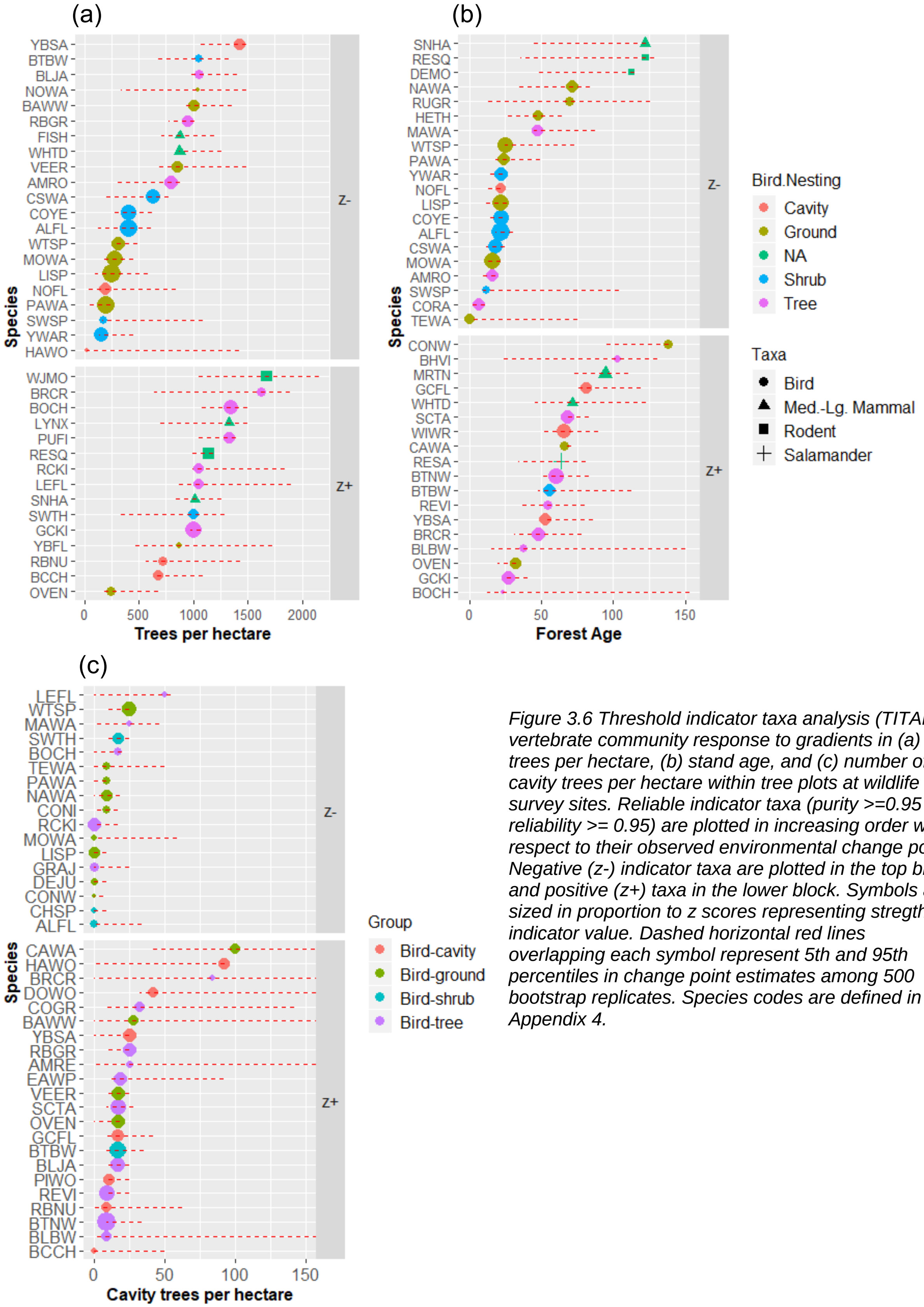

Figure 3.6 Threshold indicator taxa analysis (TITAN) of vertebrate community response to gradients in (a) trees per hectare, (b) stand age, and (c) number of cavity trees per hectare within tree plots at wildlife survey sites. Reliable indicator taxa (purity >=0.95 and reliability >= 0.95) are plotted in increasing order with respect to their observed environmental change point. Negative (z-) indicator taxa are plotted in the top block and positive (z+) taxa in the lower block. Symbols are sized in proportion to z scores representing stregth of indicator value. Dashed horizontal red lines overlapping each symbol represent 5th and 95th percentiles in change point estimates among 500 bootstrap replicates. Species codes are defined in Appendix 4.

Positive and negative threshold responses to the amount of conifer or deciduous trees in stand canopies were evident among all taxonomic groups; however, the bootstrapped confidence intervals were typically wide suggesting weak support for thresholds (Figure 3.7a, b). Distinct community thresholds were not evident, although, the great crested flycatcher (*Myiarchus crinitus*, GCFL) and scarlet tanager (*Piranga olivacea*, SCTA) had high positive thresholds near 100% for deciduous cover, with narrow confidence intervals. Several tree-nesting birds had positive responses to deciduous cover, while many ground-nesting birds had high positive thresholds to conifer cover (Figure 3.7a, b). The fisher, deer mouse, white-tailed deer, and marten had positive thresholds to deciduous and negative thresholds to conifer, while the snowshoe hare, lynx and masked shrew had positive thresholds to conifer.

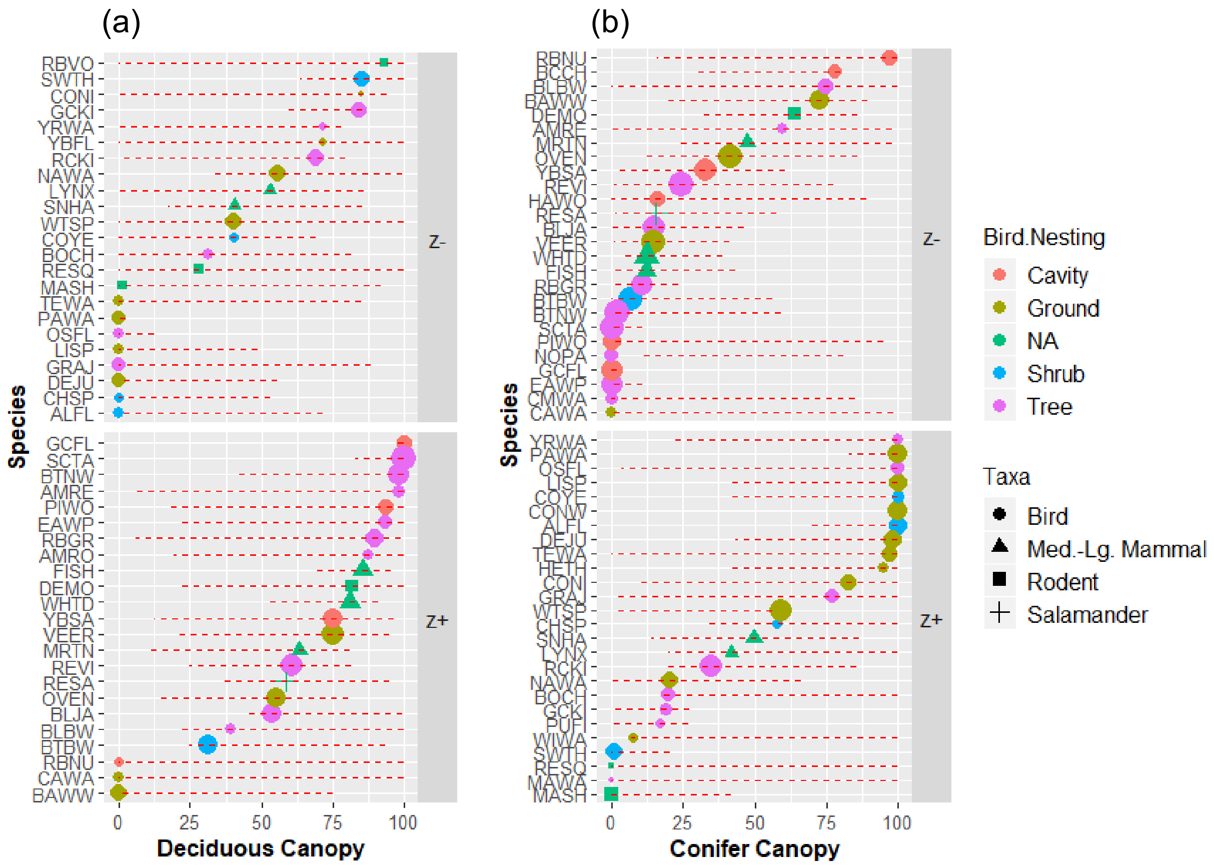

Figure 3.7 Threshold indicator taxa analysis (TITAN) of vertebrate community response to gradients in percentage of (a) deciduous and (b) coniferous trees within tree plots at wildlife survey sites. Reliable indicator taxa (purity >=0.95 and reliability >= 0.95) are plotted in increasing order with respect to their observed environmental change point. Negative (z-) indicator taxa are plotted in the top block and positive (z+) taxa in the lower block. Symbols are sized in proportion to z scores representing stregth of indicator value. Dashed horizontal red lines overlapping each symbol represent 5th and 95th percentiles in change point estimates among 500 bootstrap replicates. Species codes are defined in Appendix 4.

More species had a positive threshold response to forest edge than negative response, with mostly ground- and shrub-nesting birds showing positive responses and tree-nesting birds having negative responses (Figure 3.8a). The snowshoe hare and rodents, including the masked shrew, red-backed vole, and deer mouse benefited from greater amounts of forest edge, while the marten and red fox (REFX, *Vulpes vulpes*) had negative responses to edge. Community level thresholds for birds were 8.9 km of edge per km^2 (negative response) and 9.7 km of edge per km^2 (positive). Rodents had a positive community response at 9.4 km per km^2. Although medium to large mammals did not demonstrate a significant community level threshold response, inspection of the sum (z) cumulative frequency distribution plot revealed multiple peaks that suggest more than one shift in community structure may exist along the forest edge gradient (Figure 3.8b). Such secondary structure was apparent for other taxa and environmental gradients but was not explored further in the present analysis.

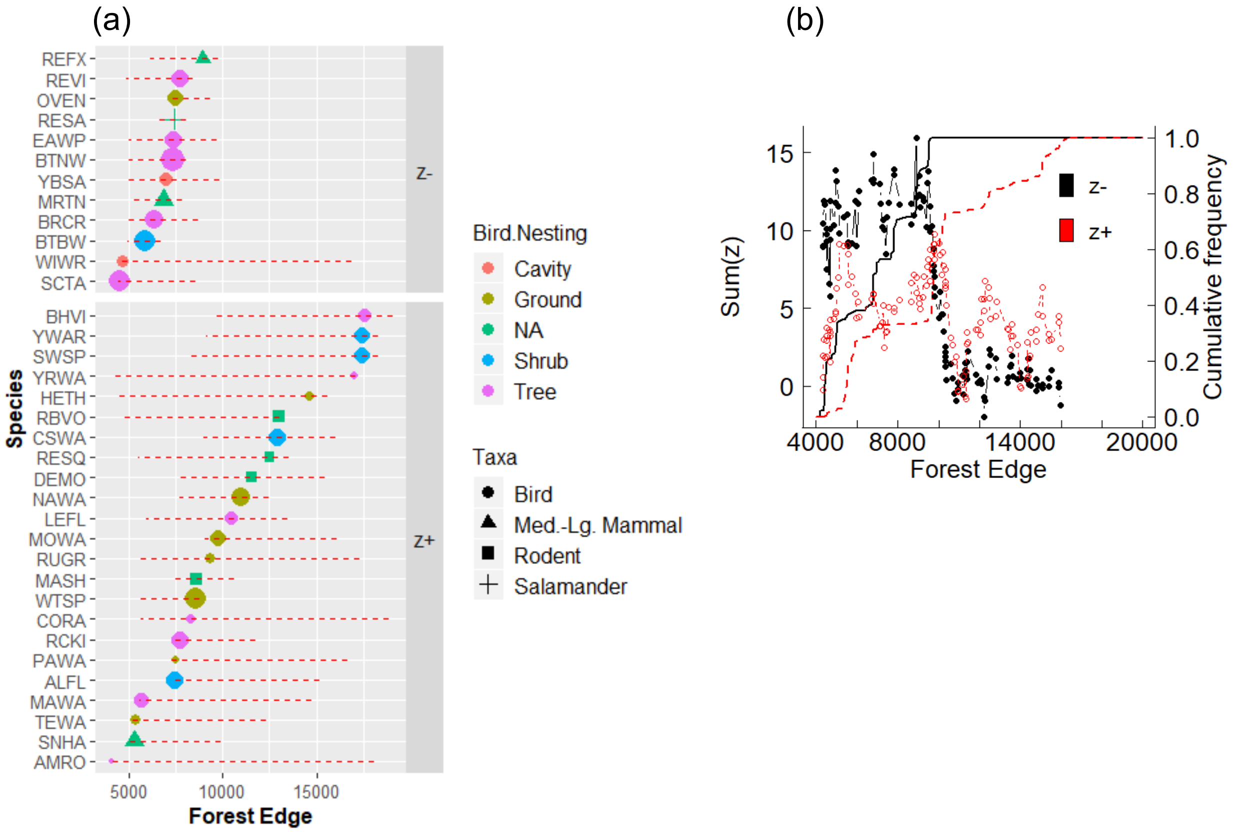

Figure 3.8 Threshold indicator taxa analysis (TITAN) of vertebrate community response to gradients in (a) total edge (m) defined by forest stands of conifer, mixed, or deciduous within 500 m buffers at wildlife survey sites. Reliable indicator taxa (purity >=0.95 and reliability >= 0.95) are plotted in increasing order with respect to their observed environmental change point. Negative (z-) indicator taxa are plotted in the top block and positive (z+) taxa in the lower block. Symbols are sized in proportion to z scores representing stregth of indicator value. Dashed horizontal red lines overlapping each symbol represent 5th and 95th percentiles in change point estimates among 500 bootstrap replicates. Species codes are defined in Appendix 4. (b) TITAN sum(z-) and sum(z+) values (circles) for the bird community corresponding to all candidate change points along the forest edge gradient, indicating a lack of a single peak in community response. Black and red vertical lines represent the cumulative frequency distribution of change points (thresholds) among 500 bootstrap replicates for sum(z-) and sum(z+), respectively.

3.5 Discussion

Our findings of a diverse range of positive and negative threshold responses among taxa to forest habitat condition is consistent with the expectation that species have unique life history adaptations within a complex and diverse forest community. Even so, there were patterns of similar responses among wildlife that can help identify indicators species and targets in forest management. Where jurisdictions take an ecosystem approach to biodiversity conservation (OMNR 2014; Raum 2017), confusion in how to implement concepts of biodiversity and sustainability remains a challenge (Hagan & Whitman 2006). Further, monitoring of general species richness or even long-term trends in target wildlife may be inadequate to inform management response (Yoccoz, Nichols & Boulinier 2001). Here, we identify a range of species and their habitat associations of high indicator value and evidence of thresholds in habitat conditions affected by forest management. Such considerations can help monitoring programs differentiate among factors affecting wildlife populations.

Evidence of disturbance impacts to wildlife are widespread and often considered in the assessment of sustainable forest management (Bayne & Hobson 1998; Niemi *et al.* 1998; Brown *et al.* 2007; Houle *et al.* 2010). In our study, responses to anthropogenic disturbance were more prominent among birds than other taxa; however, the essentially linear response of change-points along the gradients for harvest and roads suggested they do not represent cohesive communities of species. Among mammals, only the masked shrew had a strong negative response threshold to roads (positive response to greater distance). Evidence elsewhere suggests small mammal response to roads can vary with habitat specialization, individual mobility and home-range location (Grilo *et al.* 2018). We found that several small mammal species had negative thresholds associated with greater distances to roads. Downing, Rytwinski and Fahrig (2015) proposed that such positive effects of roads could result from reduced predation rates for species whose predators are reduced in proximity to roads (the predator release hypothesis). Further research is needed to test this hypothesis in our study system.

Broadly speaking, our findings suggest that direct measures of habitat have potentially greater application in setting indicator targets than disturbance factors, based on the greater frequency of significant thresholds among the suite of environmental variables considered. Negative indicators for forest harvest were limited to a small number of bird species and most had wide quantile intervals for identified thresholds. Community level responses and greater certainty in threshold change points were more evident for the direct measures of habitat structure. Where approaches to biodiversity conservation in forest management are focused on emulation of natural disturbance (OMNR 2014), and under the assumption that wildlife are adapted to forests that include stand-replacing processes (e.g. fire), resource-providing habitat features may better serve sustainability assessments than negative indicators for disturbance.

There was greater support for community level responses in birds than other taxa, consistent with evidence elsewhere for the value of birds as forest indicators (Rempel 2007; Venier & Pearce 2007). Our study offers additional insight into the relative importance of indicator thresholds for birds alongside other taxa and assessed under a consistent monitoring and management regime. The greater species richness of birds may have affected this perceived pattern and result from greater ecological niche representation and possible redundancy or niche overlap among birds. Regardless, the strongest evidence for a synchronous taxonomic shift in community structure was evident in the bird community. Minimal overlap in community thresholds, based on narrowness of quantile intervals and distances between community sum(z) values illustrate that declines in negative indicator species may occur prior to observing increases in positive indicator species with increasing low shrub cover, tree density and age. For species-habitat combinations that failed to show evidence of distinct community thresholds (i.e. wide confidence bands for sum(z) scores), other responses may be more plausible, including random (no relationship), modal or liner (Baker & King 2013).

We found that additional insights can be gained about community structure in thresholds by partitioning species according to key life history traits, such as nesting strategy in birds. The strength of IndVal z scores and precision of thresholds provide support for the specific suite of species within different guilds that may be most sensitive to gradients in forest conditions. Canterbury *et al*. (2000) reported negative relationships between shrub-nesting birds and canopy cover and positive relationships for cavity and canopy-nesting birds. Our findings provide additional insight as to the magnitudes of threshold responses among individual species and guilds, and for a range of habitat features that impact nesting substrate (e.g. low shrubs, tree density, abundance of cavity trees). At a landscape scale, forest edges can be associated with higher bird species richness, but there can be important trait- and species-specific responses (Terraube *et al.* 2016). In our study, several tree-nesting species had a negative threshold response to forest edge and a consistent community level response; whereas, positive responses to edge were distributed more widely among nesting guilds, with less precise thresholds and the absence of a distinct community response.

Understory vegetation structure can serve an important habitat function with respect to substrate for feeding, nests, and shelter for wildlife (Van Vuren *et al.* 2006; Burke, Chamberlain & Geaghan 2008). Ground-nesting birds notably showed a positive response to understory deciduous cover. We found that the negative indicator response to low shrub cover had a more consistent community response, with similar thresholds within a narrower range among species. In contrast, the positive indicator response to shrub cover varied more widely along the percentage cover gradients. Such patterns are consistent with the hypothesis that positive features vary among species in relation to habitat niche, where competition may act to separate species niches. Negative indicator effects may be less dependent on selection for resources or competitive interactions, possibly dependent more on the omission of one or more critical resources. Further study would be needed to test such hypotheses.

The utility of small mammals as indicators of sustainable forest management is hindered by strong year-to-year variation in population abundance, independent of forest management disturbance. Our evidence for threshold responses to forest condition among several rodent species may provide a means to establish targets that can aid in interpreting the effectiveness of habitat management for species with high annual variation in abundance. Pearce and Venier (2005) found that red-backed vole abundance was linearly related to stand age and the volume of downed logs. Our study spanned a much greater geographic extend and gradient in habitat, and we found a strong positive threshold response of red-backed voles to coarse woody debris (high IndVal and narrow CI), but not stand age. Those authors also found that deer mice were associated with recent forest clearcuts and declined in abundance in stands greater than 5-15 years in age. We found a strong positive response of deer mice to coarse woody debris, and although positively associated with forest harvest, there was no threshold evident. We identified additional rodent species that may serve as potential indicators. The masked shrew had relatively high IndVal z scores and narrow confidence intervals for multiple threshold responses, including low shrub cover, forest edge, and proximity to roads. The red-backed vole and deer mouse also had positive thresholds to forest edge, and the smoky shrew was positively associated with low shrubs and coarse woody debris. Gagné, Bélanger and Huot (1999) also found a positive association of red-backed voles with shrub cover, as well as evidence that post-harvest regeneration strategies affected abundance. Our findings suggest habitat associations, in addition to forest age and harvest, may be useful to interpret patterns in rodent abundance in assessment of sustainable forest management.

Medium to large mammals had threshold responses to a variety of habitat conditions, from understory to landscape, with more precise thresholds for low conifer shrub and forest edge. Understory structural features may provide a mixture of shelter and feeding habitat for various mammals and interspersion or heterogeneity in habitat can provide multiple resources in close proximity (Ferron & Ouellet 1992; Hagar 2007; Stirnemann *et al.* 2015). For example, we identified a positive threshold response by lynx to low conifer, consistent with findings by Squires *et al.* (2010) that lynx selected multilayered conifer forests and kill sites had more horizontal cover. Medium to large mammals with relatively high indicator value (IndVal scores) included white tailed deer (- understory structure), marten (+ forest age, - forest edge) and snowshoe hare (+ forest edge).

Surprisingly, no threshold responses to roads were evident in medium to large mammals. Negative impacts of roads are often cited for mammals (Fahrig & Rytwinski 2009), especially considering their mobility and home range size relative to the scale of human infrastructure. Benítez-López, Alkemade and Verweij (2010) found that mammals appeared to avoid infrastructure in forested areas less than in open areas, speculating that the greater tolerance of roads could be due to the reduced visibility of the infrastructure in forested areas. Impacts could have been masked in our study given that the wildlife monitoring plots were always located within 1 to 2 km of roads to facilitate accessibility. Thus, our study would underrepresent the low gradient extent of roads. Even so, our sampling focused on forested stands and covered a wide range of road densities associated with the north-south gradient in human settlements and infrastructure in the province.

Although the TITAN approach has been identified as a useful tool for assessment of community responses to environmental gradients (Suarez-Rubio *et al.* 2013; Khamis *et al.* 2014; Morissette *et al.* 2019), we suggest caution when searching for patterns among a broad suite of taxonomic groups and forest conditions. Species-habitat associations under consideration should have clear ecological rationale as binary partitioning techniques will typically identify change points in a dataset, which could lead to identification of indirect or spurious relationships. The use of IndVal z scores and measures of reliability and purity through boostrapping aid in minimizing such problems (Baker & King 2010; Baker & King 2013). Forest vegetation communities are inherently complex and species responses may be correlated to other habitat conditions that were not measured, which could explain some of our observed relationships. TITAT can be used to identify secondary and tertiary limiting factors in a hierarchical fashion (Baker & King 2013); however, such evaluation was beyond the scope of our current study. We were explicitly interested in assessing community patterns among taxa in relation to each forest condition metric identified *a priori* as relevant in representing or affecting habitat. We suggest that where individual species with known relationships of interest are identified, the threshold responses we report have value for applications in both community level and individual species management and monitoring.

3.5.1 Conclusions and Recommendations

In summary, the identification of thresholds in forest harvest or habitat condition where the loss of species, prominent declines in abundance, or shifts in community composition can be expected is an important task in the assessment of sustainable forest management. We identify thresholds that can be used to set targets for habitat management and note that responses can be expected to vary among species and taxonomic groups or functional guilds in relation to unique life history adaptations.

Forest managers often set targets for the retention of key forest attributes using factors other than wildlife habitat supply (e.g. wood supply, emulation of natural disturbance). In such cases, our study provides evidence for a suite of indicators that can be used to inform the interpretation of outcomes of sustainability policies for biodiversity, including anticipated shifts in community response. Although much emphasis is placed on stand and landscape level management in recent years, we recommend that managers consider important understory conditions that may affect wildlife response. Our study focused on the identification of single thresholds for each environmental gradient; however, the sum(z) community level analysis revealed instances of secondary peaks in cumulative frequencies. We suggest that further investigation is warranted into whether multiple change point responses exist along environmental gradients that might reveal additional community structure.

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Appendix 1. RDA scores for two separate ordinations of ground-collected vegetation structure variables (response) constrained by eFRI-structure and eFRI-overstory explanatory variables. Only RDA scores for significant explanatory variables retained using forward selection are included. The ground-collected response scores in each cell include those from the separate eFRI-structure and eFRI-overstory RDA's, respectively (separated by a forward slash)

Group	Code	Description	RDA1	RDA2	RDA3
eFRI-structure	VertTO	The stand canopy is composed of mainly two distinct layers that have at least 3 meters in height difference or 20 years of age difference, and each layer represents at least 10% of the total canopy crown closure for the stand.	-0.429	-0.793	-0.247
eFRI-structure	HorizMP	Several distinct patches	0.508	-0.115	0.138
eFRI-structure	HorizSS	Mainly single stem canopy structure	-0.378	0.181	-0.27
eFRI-structure	VertSV	Mainly a single story stand with a veteran (super canopy) component representing less than 10% of the total crown closure for the stand.	0.518	-0.197	-0.137
eFRI-structure	SC2	Site class 2	-0.239	0.509	-0.126
eFRI-structure	VertSI	Mainly a single story stand	0.038	0.545	-0.712
eFRI-overstory	Y_MCL	Lowland conifers, <= 29 years*	-0.793	0.307	-0.076
eFRI-overstory	pconif	Conifer% in canopy	-0.759	-0.424	0.194
eFRI-overstory	HT	Canopy height (m)	0.667	-0.293	0.423
eFRI-overstory	I_TOL	Tolerant hardwoods, <= 9 years*	0.394	0.647	0.366
eFRI-overstory	stkg	Stocking	0.278	-0.002	0.76
Ground	SpDiv	Shrub species diversity (count)	0.684 / -0.658	0.364 / -0.227	0.284 / -0.162
Ground	WCH	Woody conifer 2-10 m above ground (%)	0.122 / -0.196	0.324 / -0.603	0.295 / 0.341
Ground	WCL	Woody conifer 0-0.5 m above ground (%)	0.788 / -0.96	-0.164 / 0.155	0.15 / 0.167

Group	Code	Description	RDA1	RDA2	RDA3
Ground	WCM	Woody conifer 0.5-2 m above ground (%)	0.862 / -0.82	-0.091 / 0.021	0.091 / 0.169
Ground	WHH	Woody deciduous 2-10 m above ground (%)	-0.378 / 0.362	-0.341 / 0.692	0.39 / 0.115
Ground	WHL	Woody deciduous 0-0.5 m above ground (%)	0.294 / -0.201	-0.175 / 0.257	-0.204 / 0.091
Ground	WHM	Woody deciduous 0.5-2 m above ground (%)	0.443 / -0.566	-0.384 / 0.422	-0.021 / -0.022
Ground	TC	Conifer % cover in canopy (>10 m above ground) in 1 m radius circular plots	-0.221 / 0.287	-0.078 / -0.704	0.01 / 0.299
Ground	TH	Deciduous % cover in canopy (>10 m above ground) in 1 m radius circular plots	-0.577 / 0.849	-0.515 / 0.542	0.096 / 0.26
Ground	WH	Woody 2-10 m above ground (%)	-0.237 / 0.173	-0.068 / 0.174	0.532 / 0.33
Ground	WM	Woody 0.5-2 m above ground (%)	0.745 / -0.794	-0.277 / 0.26	0.039 / 0.082
Ground	WL	Woody 0-0.5 m above ground (%)	0.548 / -0.542	-0.204 / 0.265	-0.101 / 0.139

* Tree-based habitat descriptions refer to Provincial Forest Types (PFT) partitioned according to three PFT-specific age classes (young, immature, mature) (OMNR 2003).

Appendix 2. RDA scores for two separate ordinations of bird species (response variables) constrained by ground-collected and eFRI explanatory variables. Only RDA scores for significant explanatory variables retained using forward selection are included. The bird RDA scores in each cell include those from the separate ground-based and eFRI based RDA's, respectively (separated by a forward slash)

Group	Code	Description	RDA1	RDA2	RDA3
Ground	PConif21	Conifer % of species composition in 11.28 m radius circular tree plots	0.810	-0.072	0.036
Ground	PConif22	Conifer % of species composition in 11.28 m radius circular tree plots	0.034	0.255	-0.636
Ground	Treesperha	No. of trees per hectare for trees > 8.0 cm d.b.h.	0.130	-0.665	-0.179
Ground	DBH	Mean d.b.h. (diameter at breast height) of trees	-0.648	-0.238	0.193
Ground	MossFeath 21	Feather moss (%)	0.619	-0.345	-0.100
Ground	MossFeath 22	Feather moss (%)	-0.340	0.151	-0.123
Ground	MossSphag	Sphagnum moss (%)	0.456	0.051	-0.506
Ground	Graminoid	Graminoids (%)	0.270	0.459	0.258
Ground	Treesperha 22	No. of trees per hectare for trees > 8.0 cm d.b.h.	0.121	0.368	0.005
Ground	CavityTrees perha	No. cavity trees per hectare	-0.478	0.001	-0.109
Ground	BrdlfLitter	Broadleaf litter (%)	-0.606	-0.063	0.154
Ground	Spp_rich21	No. tree species in canopy	-0.612	-0.247	0.229
Ground	Spp_rich22	No. tree species in canopy	0.058	0.311	-0.317
Ground	ShrubDiv21	Shrub species diversity (count)	0.685	0.077	-0.018
Ground	ShrubDiv22	Shrub species diversity (count)	-0.200	0.096	-0.389
Ground	ConifL	Woody conifer 0-0.5 m above ground (%)	0.438	0.006	-0.008
Ground	ConifM	Woody conifer 0.5-2 m above ground (%)	0.541	-0.090	0.060
Ground	HrdwL	Woody deciduous 0-0.5 m above ground (%)	0.440	0.219	-0.267
Ground	HrdwM	Woody deciduous 0.5-2 m above ground (%)	0.140	0.256	0.145
Ground	HrdwH	Woody deciduous 2-10 m above ground (%)	-0.644	0.021	-0.033
Ground	ConifLitter	Conifer litter (%)	0.160	-0.253	0.214
Ground	Ht21	Mean height (m) of trees for trees > 8.0 cm d.b.h.	-0.528	-0.481	0.022
Ground	Ht22	Mean height (m) of trees for trees > 8.0 cm d.b.h.	0.054	0.225	0.004
Ground	CWD	Coarse woody debris (%)	0.196	-0.157	0.363
Ground	FernsAllies	Ferns & fern allies (%)	0.068	-0.027	0.311
Ground	Lichen	Lichen (%)	0.371	-0.002	-0.151

Group	Code	Description	RDA1	RDA2	RDA3
Ground	LitterDepth	Litter depth (mm)	-0.328	-0.123	0.094
eFRI	pconif	Conifer % in canopy	0.813	-0.053	-0.129
eFRI	HT	Canopy height (m)	-0.583	-0.613	-0.085
eFRI	stkg	Stocking	-0.120	-0.470	-0.296
eFRI	Age	Age of canopy (years)	-0.328	-0.428	-0.531
eFRI	Y_BWT	White birch, <= 9 years*	0.036	0.179	0.175
eFRI	Y_MCL	Lowland conifers, <= 29 years*	0.415	0.432	0.060
eFRI	Y_MCU	Upland conifers, <= 29 years*			
eFRI	Y_MIX	Mixedwoods, <= 29 years*			
eFRI	Y_PJK	Jack pine, <= 29 years*			
eFRI	Y_POP	Poplar, <= 9 years*	-0.069	0.337	0.382
eFRI	Y_PWR	Excluded - data deficient, White pine & red pine, <= 19 years*			
eFRI	Y_TOL	Tolerant hardwoods, <= 9 years*	-0.098	0.148	0.204
eFRI	I_BWT	White birch, 10-49 years*			
eFRI	I_MCL	Lowland conifers, 30-69 years*			
eFRI	I_MCU	Upland conifers, 30-69 years*	0.058	-0.239	0.144
eFRI	I_MIX	Mixedwoods, 30-69 years*	0.045	-0.156	0.137
eFRI	I_PJK	Jack pine, 30-69 years*			
eFRI	I_POP	Poplar, 10-59 years*	-0.028	0.030	0.273
eFRI	I_PWR	Excluded - data deficient, White pine & red pine, 20-79 years*			
eFRI	I_TOL	Tolerant hardwoods, 10-59 years*	-0.242	0.095	-0.151
eFRI	M_BWT	White birch, >= 50 years*	-0.161	-0.059	-0.028
eFRI	M_MCL	Lowland conifers, >= 70 years*	0.428	-0.129	-0.546
eFRI	M_MCU	Upland conifers, >= 70 years*	0.062	-0.302	0.056
eFRI	M_MIX	Mixedwoods, >= 70 years*	-0.078	-0.331	0.258
eFRI	M_PJK	Jack pine, >= 70 years*			
eFRI	M_POP	Poplar, >= 60 years*	-0.097	-0.219	0.283
eFRI	M_PWR	White pine & red pine, >= 80 years*	-0.231	-0.068	0.121
eFRI	M_TOL	Tolerant hardwoods, >= 60 years*	-0.739	0.263	-0.459
eFRI	SC1	Site class 1	-0.028	-0.041	-0.092
Birds	ALFL	Alder Flycatcher, *Empidonax alnorum*	0.356 / 0.436	0.695 / 0.592	0.367 / 0.149
Birds	AMRE	American Redstart, *Setophaga ruticilla*	-0.32 / -0.207	0.042 / 0.158	0.061 / 0.143
Birds	AMRO	American Robin, *Turdus migratorius*	-0.124 / -0.112	0.537 / 0.388	0.168 / 0.187
Birds	BAWW	Black-and-white Warbler, *Mniotilta varia*	-0.42 / -0.377	0.156 / 0.228	0.308 / 0.294

Group	Code	Description	RDA1	RDA2	RDA3
Birds	BCCH	Black-capped Chickadee, *Poecile atricapillus*	-0.222 / -0.171	-0.371 / -0.31	0.302 / 0.214
Birds	BHVI	Blue-headed Vireo, *Vireo solitarius*	-0.024 / -0.092	-0.151 / -0.214	0.086 / 0.179
Birds	BLBW	Blackburnian Warbler, *Setophaga fusca*	-0.451 / -0.311	-0.178 / -0.236	0.108 / 0.089
Birds	BLJA	Blue Jay, *Cyanocitta cristata*	-0.721 / -0.777	0.164 / 0.235	0.075 / 0.023
Birds	BOCH	Boreal Chickadee, *Poecile hudsonicus*	0.452 / 0.298	-0.281 / -0.188	-0.114 / -0.108
Birds	BRCR	Brown Creeper, *Certhia americana*	-0.15 / -0.114	-0.45 / -0.561	0.029 / 0.011
Birds	BTBW	Black-throated Blue Warbler, *Setophaga caerulescens*	-0.977 / -0.947	0.128 / 0.103	-0.096 / -0.214
Birds	BTNW	Black-throated Green Warbler, *Setophaga virens*	-1.092 / -1.035	-0.023 / 0.05	-0.274 / -0.359
Birds	CAWA	Canada Warbler, *Cardellina canadensis*	-0.3 / -0.222	-0.069 / -0.129	0.141 / 0.23
Birds	CONI	Common Nighthawk, *Chordeiles minor*	0.398 / 0.383	-0.138 / -0.043	-0.181 / -0.403
Birds	CORA	Common Raven, *Corvus corax*	-0.224 / -0.195	0.119 / 0.002	0.019 / 0.233
Birds	COYE	Common Yellowthroat, *Geothlypis trichas*	0.274 / 0.365	0.683 / 0.367	0.207 / -0.132
Birds	CSWA	Chestnut-sided Warbler, *Setophaga pensylvanica*	-0.218 / -0.135	0.588 / 0.406	0.299 / 0.303
Birds	DEJU	Dark-eyed Junco, *Junco hyemalis*	0.502 / 0.423	0.291 / 0.173	-0.526 / -0.256
Birds	EAWP	Eastern Wood-Pewee, *Contopus virens*	-0.552 / -0.508	0.069 / 0.128	-0.244 / -0.253
Birds	GCKI	Golden-crowned Kinglet, *Regulus satrapa*	0.225 / 0.254	-0.811 / -0.715	0.274 / 0.133

Group	Code	Description	RDA1	RDA2	RDA3
Birds	GRAJ	Gray Jay, *Perisoreus canadensis*	0.514 / 0.432	-0.123 / -0.053	-0.109 / -0.113
Birds	HAWO	Hairy Woodpecker, *Picoides villosus*	-0.391 / -0.327	0.091 / 0.052	0.006 / 0.144
Birds	HETH	Hermit Thrush, *Catharus guttatus*	0.445 / 0.402	0.443 / 0.271	-0.535 / -0.285
Birds	LEFL	Least Flycatcher, *Empidonax minimus*	0.256 / 0.223	-0.148 / 0.018	-0.321 / -0.177
Birds	LISP	Lincoln's Sparrow, *Melospiza lincolnii*	0.291 / 0.392	0.672 / 0.53	0.098 / 0.088
Birds	MAWA	Magnolia Warbler, *Setophaga magnolia*	0.368 / 0.294	-0.019 / 0.161	0.464 / 0.421
Birds	MOWA	Mourning Warbler, *Geothlypis philadelphia*	0.105 / 0.178	0.646 / 0.415	0.278 / 0.418
Birds	NAWA	Nashville Warbler, *Oreothlypis ruficapilla*	0.8 / 0.683	0.033 / 0.032	0.124 / 0.274
Birds	NOFL	Northern Flicker, *Colaptes auratus*	-0.052 / -0.029	0.443 / 0.14	0.093 / 0.169
Birds	NOPA	Northern Parula, *Setophaga americana*	-0.088 / -0.112	-0.285 / -0.364	0.358 / 0.21
Birds	NOWA	Northern Waterthrush, *Parkesia noveboracensis*	0 / -0.048	0.119 / 0.164	0.065 / 0.147
Birds	OVEN	Ovenbird, *Seiurus aurocapilla*	-1.051 / -0.872	-0.123 / -0.254	0.043 / 0.155
Birds	PIWO	Pileated Woodpecker, *Dryocopus pileatus*	-0.298 / -0.334	0.185 / 0.1	0.133 / 0.295
Birds	PUFI	Purple Finch, *Haemorhous purpureus*	0.117 / 0.085	-0.334 / -0.233	0.281 / 0.153
Birds	RBGR	Rose-breasted Grosbeak, *Pheucticus ludovicianus*	-0.527 / -0.412	0.302 / 0.345	0.044 / 0.207
Birds	RBNU	Red-breasted Nuthatch, *Sitta canadensis*	-0.312 / -0.316	-0.369 / -0.431	0.474 / 0.471

Group	Code	Description	RDA1	RDA2	RDA3
Birds	RCKI	Ruby-crowned Kinglet, *Regulus calendula*	0.792 / 0.682	-0.056 / -0.112	-0.367 / -0.219
Birds	REVI	Red-eyed Vireo, *Vireo olivaceus*	-1.236 / -1.06	0.157 / 0.129	-0.09 / 0.044
Birds	RUGR	Ruffed Grouse, *Bonasa umbellus*	0.131 / 0.145	0.107 / 0.088	0.583 / 0.338
Birds	SCTA	Scarlet Tanager, *Piranga olivacea*	-0.733 / -0.874	0.093 / 0.345	-0.205 / -0.397
Birds	SWSP	Swamp Sparrow, *Melospiza georgiana*	0.152 / 0.14	0.256 / 0.226	0.277 / -0.04
Birds	SWTH	Swainson's Thrush, *Catharus ustulatus*	0.465 / 0.37	-0.639 / -0.454	0.376 / 0.119
Birds	TEWA	Tennessee Warbler, *Oreothlypis peregrina*	0.434 / 0.38	0.154 / 0.088	0.203 / 0.021
Birds	VEER	Veery, *Catharus fuscescens*	-0.816 / -0.734	0.286 / 0.402	0.121 / 0.143
Birds	WIWR	Winter Wren, *Troglodytes hiemalis*	-0.054 / -0.021	-0.18 / -0.332	0.138 / -0.11
Birds	WTSP	White-throated Sparrow, *Zonotrichia albicollis*	1.019 / 0.959	0.578 / 0.524	0.138 / 0.098
Birds	YBFL	Yellow-bellied Flycatcher, *Empidonax flaviventris*	0.152 / 0.097	-0.126 / -0.183	-0.035 / 0.171
Birds	YBSA	Yellow-bellied Sapsucker, *Sphyrapicus varius*	-0.892 / -0.938	0.132 / 0.062	0.003 / -0.002
Birds	YRWA	Yellow-rumped Warbler, *Setophaga coronata*	0.169 / 0.151	0.028 / 0.103	0.001 / 0.035

* Tree-based habitat descriptions refer to Provincial Forest Types (PFT) partitioned according to three PFT-specific age classes (young, immature, mature)(OMNR 2003).

Appendix 3. Original habitat variables and PCA scores for categories of understory, canopy, landscape, disturbance, and climate. Only significant axes retained using the Kaiser–Guttman criterion are displayed.

Habitat	Variable	PC1	PC2	PC3	PC4	PC5
Understory	Broadleaf litter (%)	-0.306	0.269	-0.281	0.172	-0.049
Understory	Coarse woody debris (%)	0.047	0.122	-0.411	-0.483	0.059
Understory	Herbs (%)	0.121	0.100	-0.572	-0.262	0.187
Understory	Fruit (%)	0.157	-0.274	-0.269	-0.076	-0.193
Understory	Litter depth (mm)	-0.082	0.469	-0.002	0.148	0.158
Understory	Lichen (%)	0.146	-0.138	0.045	-0.103	-0.710
Understory	Sphagnum moss (%)	0.330	-0.173	0.051	0.424	0.232
Understory	Moss - all species (%)	0.412	-0.058	0.081	0.102	0.228
Understory	Shrub species diversity (count)	0.366	-0.070	-0.259	0.202	0.187
Understory	Woody conifer 2-10 m above ground (%)	0.160	0.277	0.363	-0.335	0.267
Understory	Woody conifer 0.5-2 m above ground (%)	0.316	0.396	0.174	-0.133	-0.150
Understory	Woody conifer 0-0.5 m above ground (%)	0.296	0.290	0.043	-0.101	-0.091
Understory	Woody deciduous 2-10 m above ground (%)	-0.322	0.250	-0.136	0.337	-0.005
Understory	Woody deciduous 0.5-2 m above ground (%)	0.171	0.398	-0.011	0.214	-0.358
Understory	Woody deciduous 0-0.5 m above ground (%)	0.281	0.104	-0.302	0.315	-0.148
Canopy	Canopy height (m)	-0.326	-0.174	0.121	-0.161	
Canopy	Age of canopy (years)	-0.243	-0.214	0.278	-0.312	
Canopy	White birch, <= 9 years*	0.044	0.083	-0.046	0.090	
Canopy	Lowland conifers, <= 29 years*	0.181	0.104	-0.013	-0.012	
Canopy	Upland conifers, <= 29 years*	0.150	0.053	0.089	0.032	
Canopy	Mixedwoods, <= 29 years*	0.061	0.063	0.014	0.108	
Canopy	Jack pine, <= 29 years*	0.164	0.076	0.023	-0.057	
Canopy	Poplar, <= 9 years*	0.025	0.208	-0.144	-0.004	
Canopy	White pine & red pine, <= 19 years*	-0.005	0.023	0.043	0.032	
Canopy	Tolerant hardwoods, <= 9 years*	-0.006	0.061	-0.047	-0.015	
Canopy	White birch, 10-49 years*	-0.034	-0.071	-0.196	0.030	
Canopy	Lowland conifers, 30-69 years*	0.028	-0.109	-0.088	0.170	
Canopy	Upland conifers, 30-69 years*	0.020	-0.036	0.040	0.280	
Canopy	Mixedwoods, 30-69 years*	-0.014	-0.039	-0.055	0.248	
Canopy	Jack pine, 30-69 years*	0.042	-0.160	-0.201	0.056	
Canopy	Poplar, 10-59 years*	0.001	0.045	-0.178	0.241	

Habitat	Variable	PC1	PC2	PC3	PC4	PC5
Canopy	White pine & red pine, 20-79 years*	-0.055	0.039	0.019	0.116	
Canopy	Tolerant hardwoods, 10-59 years*	-0.064	0.099	0.053	0.047	
Canopy	White birch, >= 50 years*	-0.082	0.007	-0.260	-0.079	
Canopy	Lowland conifers, >= 70 years*	0.095	-0.226	0.252	-0.222	
Canopy	Upland conifers, >= 70 years*	-0.027	-0.213	-0.030	-0.247	
Canopy	Mixedwoods, >= 70 years*	-0.061	-0.074	0.016	-0.025	
Canopy	Jack pine, >= 70 years*	-0.011	-0.086	0.025	-0.095	
Canopy	Poplar, >= 60 years*	-0.107	0.041	-0.124	-0.028	
Canopy	White pine & red pine, >= 80 years*	-0.089	-0.100	0.092	0.035	
Canopy	Tolerant hardwoods, >= 60 years*	-0.232	0.229	0.190	-0.130	
Canopy	No. of trees per hectare for trees > 8.0 cm d.b.h.	-0.071	-0.422	-0.087	0.269	
Canopy	Mean d.b.h. (diameter at breast height) of trees	-0.291	0.103	0.063	-0.163	
Canopy	Mean height (m) of trees for trees > 8.0 cm d.b.h.	-0.312	-0.098	0.128	0.085	
Canopy	Proportion of dead trees in 11.28 m radius circular tree plots	0.009	0.022	-0.455	-0.397	
Canopy	No. dead trees per hectare	-0.118	-0.283	-0.472	-0.157	
Canopy	No. cavity trees per hectare	-0.158	-0.046	-0.211	-0.085	
Canopy	Conifer % cover in canopy (>10 m above ground) in 1 m radius circular plots	-0.046	-0.313	0.107	0.085	
Canopy	Deciduous % cover in canopy (>10 m above ground) in 1 m radius circular plots	-0.285	0.181	0.083	0.020	
Canopy	Conifer % of species composition in 11.28 m radius circular tree plots	0.291	-0.296	0.106	0.013	
Canopy	No. of tree species in 11.28 m radius circular tree plots	-0.280	-0.008	-0.064	0.262	
Disturbance	Proportion of area <= 10 years post-harvest in 150 m buffer	0.495	-0.076			
Disturbance	Proportion of area <= 10 years post-harvest in 500 m buffer	0.497	-0.072			
Disturbance	Proportion of area <= 20 years post-harvest in 150 m buffer	0.492	-0.037			
Disturbance	Proportion of area <= 20 years post-harvest in 500 m buffer	0.492	-0.040			

Habitat	Variable	PC1	PC2	PC3	PC4	PC5
Disturbance	Mean distance to roads (m) within 150 m buffer of bird and small mammal stations, and within 500 m of camera plots	0.141	0.351			
Landscape	Total edge (conifer, mixed, deciduous) within 500 m buffer	-0.393	0.094			
Landscape	Ratio of total edge to patch area (conifer, mixed, deciduous) within 500 m buffers	-0.359	-0.578			
Landscape	Patch contiguity (conifer, mixed, deciduous) within 500 m buffers	0.371	0.560			
Landscape	Total edge (young, immature, mature) within 500 m buffers	-0.378	0.369			
Landscape	Ratio of total edge to patch area (young, immature, mature) within 500 m buffers	-0.411	0.332			
Landscape	Patch contiguity (young, immature, mature) within 500 m buffers	0.421	-0.301			
Landscape	Mean stand age within 500 m buffers	0.299	0.080			
Climate	Snow accumulation index (unitless)	0.378	-0.370			
Climate	Snow accumulation index (unitless), averaged 1994-2015	0.422	-0.191			
Climate	Mean temperature of the warmest quarter of the year	-0.326	0.330			
Climate	Mean temperature of the coldest quarter of the year	-0.421	-0.185			
Climate	Precipitation of the warmest quarter of the year	0.090	0.567			
Climate	Precipitation of the coldest quarter of the year	-0.268	-0.474			
Climate	Temperature seasonality	0.353	0.352			

Habitat	Variable	PC1	PC2	PC3	PC4	PC5
Climate	Start of the growing season day of year	0.437	-0.119			

* Tree-based habitat descriptions refer to Provincial Forest Types (PFT) partitioned according to three PFT-specific age classes (young, immature, mature) (OMNR 2003).

Appendix 4. Species common names, codes, and scientific names.

Species code	Common name	Scientific name
Birds		
ALFL	Alder Flycatcher	Empidonax alnorum
AMBI	American Bittern	Botaurus lentiginosus
AMCR	American Crow	Corvus brachyrhynchos
AMGO	American Goldfinch	Spinus tristis
AMRE	American Redstart	Setophaga ruticilla
AMRO	American Robin	Turdus migratorius
ATTW	American Three-toed Woodpecker	Picoides dorsalis
BAWW	Black-and-white Warbler	Mniotilta varia
BBCU	Black-billed Cuckoo	Coccyzus erythropthalmus
BBWA	Bay-breasted Warbler	Setophaga castanea
BBWO	Black-backed Woodpecker	Picoides arcticus
BCCH	Black-capped Chickadee	Poecile atricapillus
BHVI	Blue-headed Vireo	Vireo solitarius
BLBW	Blackburnian Warbler	Setophaga fusca
BLJA	Blue Jay	Cyanocitta cristata
BLPW	Blackpoll Warbler	Setophaga striata
BOCH	Boreal Chickadee	Poecile hudsonicus
BRCR	Brown Creeper	Certhia americana
BTBW	Black-throated Blue Warbler	Setophaga caerulescens
BTNW	Black-throated Green Warbler	Setophaga virens
CAWA	Canada Warbler	Cardellina canadensis
CCSP	Clay-colored Sparrow	Spizella pallida
CEDW	Cedar Waxwing	Bombycilla cedrorum
CHSP	Chipping Sparrow	Spizella passeri
CHSP	Chipping Sparrow	Spizella passerina
CMWA	Cape May Warbler	Setophaga tigrina
COGR	Common Grackle	Quiscalus quiscula
CONI	Common Nighthawk	Chordeiles minor
CONW	Connecticut Warbler	Geothlypis agilis
CORA	Common Raven	Corvus corax
COYE	Common Yellowthroat	Geothlypis trichas
CSWA	Chestnut-sided Warbler	Setophaga pensylvanica
DEJU	Dark-eyed Junco	Junco hyemalis
DOWO	Downy Woodpecker	Picoides pubescens
EAPH	Eastern Phoebe	Sayornis phoebe
EAWP	Eastern Wood-Pewee	Contopus virens
EVGR	Evening Grosbeak	Coccothraustes vespertinus
EWPW	Eastern Whip-poor-will	Antrostomus carolinensis
GCFL	Great Crested Flycatcher	Myiarchus crinitus

Species code	Common name	Scientific name
GCKI	Golden-crowned Kinglet	Regulus satrapa
GRAJ	Gray Jay	Perisoreus canadensis
GRYE	Greater Yellowlegs	Tringa melanoleuca
HAWO	Hairy Woodpecker	Picoides villosus
HETH	Hermit Thrush	Catharus guttatus
INBU	Indigo Bunting	Passeri cyanea
KILL	Killdeer	Charadrius vociferus
LEFL	Least Flycatcher	Empidonax minimus
LISP	Lincoln's Sparrow	Melospiza lincolnii
MAWA	Magnolia Warbler	Setophaga magnolia
MOWA	Mourning Warbler	Geothlypis philadelphia
NAWA	Nashville Warbler	Oreothlypis ruficapilla
NOFL	Northern Flicker	Colaptes auratus
NOPA	Northern Parula	Setophaga americana
NOWA	Northern Waterthrush	Parkesia noveboracensis
OCWA	Orange-crowned Warbler	Oreothlypis celata
OSFL	Olive-sided Flycatcher	Contopus cooperi
OVEN	Ovenbird	Seiurus aurocapilla
PAWA	Palm Warbler	Setophaga palmarum
PHVI	Philadelphia Vireo	Vireo philadelphicus
PIGR	Pine Grosbeak	Pinicola enucleator
PISI	Pine Siskin	Spinus pinus
PIWA	Pine Warbler	Setophaga pinus
PIWO	Pileated Woodpecker	Dryocopus pileatus
PUFI	Purple Finch	Haemorhous purpureus
RBGR	Rose-breasted Grosbeak	Pheucticus ludovicianus
RBNU	Red-breasted Nuthatch	Sitta canadensis
RCKI	Ruby-crowned Kinglet	Regulus calendula
REVI	Red-eyed Vireo	Vireo olivaceus
RUBL	Rusty Blackbird	Euphagus carolinus
RUGR	Ruffed Grouse	Bonasa umbellus
RWBL	Red-winged Blackbird	Agelaius phoeniceus
SCTA	Scarlet Tanager	Piranga olivacea
SORA	Sora	Porzana carolina
SOSP	Song Sparrow	Melospiza melodia
SPGR	Spruce Grouse	Falcipennis canadensis
SPSA	Spotted Sandpiper	Actitis macularius
STGR	Sharp-tailed Grouse	Tympanuchus phasianellus
SWSP	Swamp Sparrow	Melospiza georgiana
SWTH	Swainson's Thrush	Catharus ustulatus
TEWA	Tennessee Warbler	Oreothlypis peregrina
TRSW	Tree Swallow	Tachycineta bicolor

Species code	Common name	Scientific name
VEER	Veery	Catharus fuscescens
VESP	Vesper Sparrow	Pooecetes gramineus
WBNU	White-breasted Nuthatch	Sitta carolinensis
WISN	Wilson's Snipe	Gallinago gallinago
WIWA	Wilson's Warbler	Cardellina pusilla
WIWR	Winter Wren	Troglodytes hiemalis
WOOD	Woodpecker drumming	Woodpecker drumming
WOTH	Wood Thrush	Hylocichia mustelina
WTSP	White-throated Sparrow	Zonotrichia albicollis
WWCR	White-winged Crossbill	Loxia leucoptera
YBFL	Yellow-bellied Flycatcher	Empidonax flaviventris
YBSA	Yellow-bellied Sapsucker	Sphyrapicus varius
YRWA	Yellow-rumped Warbler	Setophaga coronata
YWAR	Yellow Warbler	Setophaga petechia
<u>Mammals</u>		
BLBE	American Black Bear	Ursus americanus
FISH	Fisher	Pekania pennanti
LYNX	Canada Lynx	Lynx canadensis
MRTN	American Marten	Martes americana
MOSE	Moose	Alces alces
REFX	Red Fox	Vulpes vulpes
SNHA	Snowshoe Hare	Lepus americanus
WHTD	White-tailed Deer	Odocoileus virginianus
WOLF	Wolf	Canis lupus
DEMO	Deer Mouse	Peromyscus maniculatus
EACH	Eastern Chipmunk	Tamias striatus
FLSQ	Northern \ Southern Flying Squirrel	Glaucomys sabrinus\G. volans
MASH	Masked Shrew	Sorex cinereus
MEVO	Meadow Vole	Microtus pennsylvanicus
RBVO	Red-backed Vole	Myodes gapperi
RESQ	Red Squirrel	Tamiasciurus hudsonicus
SMSH	Smoky Shrew	Sorex fumeus
STSH	Northern short-tailed shrew	Blarina brevicauda
WJMO	Woodland Jumping Mouse	*Napaeozapus insignis*
<u>Amphibian</u>		
RESA	Red-backed Salamander	Plethodon cinereus