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Responses of terrestrial animals to forest characteristics and climate reveals ecological indicators for sustaining wildlife in managed forests

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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 species-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 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.

1. Introduction

Governments and the forest industry are under increasing pressure to address multiple conservation and sustainable resource management objectives, such as maintaining diverse wildlife in forests. Because forest communities are often too complex to assess conservation goals directly, managers must often use indicator species that reflect key ecological processes or management objectives (Wiens et al., 2008). Identifying the best suite of species and forest conditions to serve as indicators remains a challenge. Timber harvest is typically a stand level process yet wildlife may respond to forest conditions at a range of scales (Moraga et al., 2019). Further, climate may have cumulative or interacting effects on wildlife populations. Understanding the relative importance of different forest attributes (e.g., understory, canopy, landscape), and their commonalities and differences among wildlife species, can help identify useful indicators of sustainable forest management.

Vegetation composition and structure are dynamic ecosystem components that can be managed to assist in meeting wildlife population objectives. Forest management can affect wildlife distribution and abundance through direct habitat alteration, or indirectly by altering habitat conditions that influence trophic interactions and predator-prey relationships. Landscape level effects are widely recognized and inherently variable among species (Brown et al., 2007; Venier and Pearce, 2007; Houle et al., 2010); however, forest management also influences local forest features, including understory, that can affect wildlife. Local vegetation simultaneously provides animals with food, shelter, reproductive opportunities, and protection from predators. For example, salamanders are sensitive to soil conditions (Frisbie and Wyman, 1991) that are affected by the structure and composition of the shrub and forest canopy (Shear and Stewart, 1934; Finzi et al., 1998). The density or biomass of understory foliage can be positively correlated with food for birds and small mammals (Greene and Johnson, 1994).

Despite the ecological importance of understory features to wildlife, managers are often limited to assessing habitat using canopy-level information available in forest inventories designed to support tree

Abbreviations: AIC, Akaike Information Criteria; AICw, Akaike Information Criteria weight; FRI, Forest Resources Inventory; GAM, Generalized Additive Model; MNRF, Ministry of Natural Resources and Forestry; MSIM, Multiple Species Inventory and Monitoring; PFT, Provincial Forest Type

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harvesting (McDermid et al., 2009; Government of British Columbia, 2013; OMNR, 2014). Collecting understory and ground-level habitat information over large geographic extents typical of forest management planning is cost-prohibitive. Although fine scale habitat features may not be explicitly managed during forestry activities (exceptions include cavity trees, Gutzat and Dormann, 2018), understanding the influence of habitat alteration on fine scale features will clarify the ecological relationships between forest management and wildlife populations. Quantifying these relationships can aid in setting targets and evaluating the effectiveness of forest policy and management at sustaining wildlife.

We employ a species-based modelling approach to characterize wildlife-habitat associations using data that spans the entire area of forest management on Crown land in Ontario, including temperate hardwood and northern boreal forest. Although multi-scale habitat analyses are used for a range of forest dependent species (Rempel, 2007; Venier and Pearce, 2007), we are unaware of studies that assess the importance of understory forest attributes compared to canopy and landscape attributes for a wide range of taxa. In addition, our dataset spans a broad bioclimatic gradient, allowing us to quantify the effects of climate in shaping wildlife responses.

Our objective was to assess the relative importance of habitat characteristics that can affect wildlife abundance, including disturbance, climate and forest structural attributes (understory, overstory, landscape). In doing so, we sought to quantify the importance of seldom-measured understory attributes and assess what wildlife species are more sensitive to disturbance features than the forest conditions they select. We show that monitoring a range of wildlife and habitat indicators at multiple scales, including understory features, may be needed to adequately assess biodiversity in sustainable forests.

2. Methods

2.1. Study area

Our study area spanned six degrees of latitude (44°N to 50°N) in Ontario, Canada. Mean annual temperatures within this area range from 2 to 6 °C, and moist conditions are more prevalent in the south and east due to the moderating effects of the Great Lakes (MacKey et al., 1996). The study area (Fig. 1) encompassed diverse forest communities, including temperate deciduous forest in the south and boreal forest in the north.

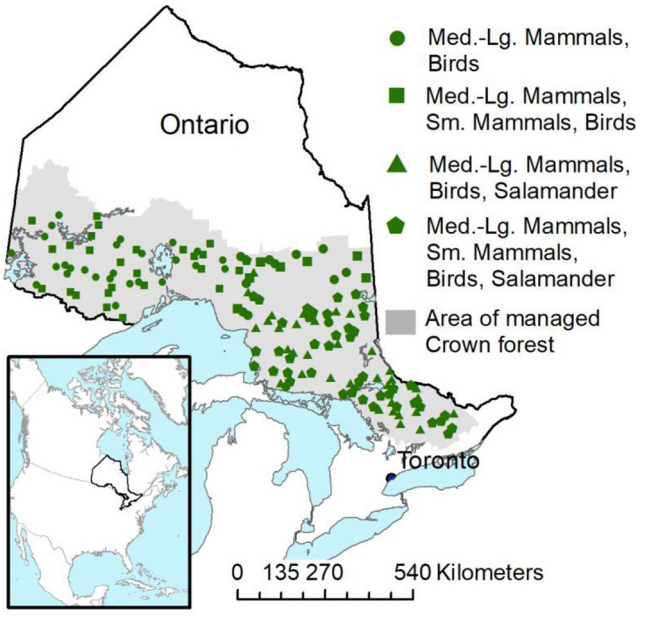

Fig. 1. Study area in Ontario, Canada, showing the distribution of wildlife and habitat sampling sites.

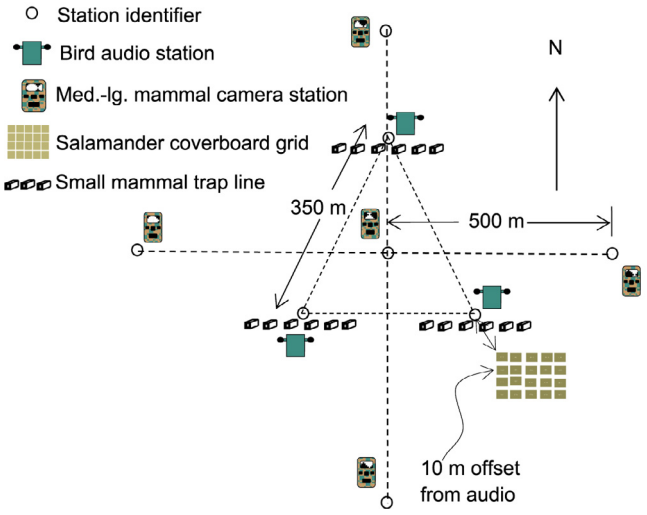

Fig. 2. Wildlife monitoring station layout.

2.2. Wildlife inventories

We used wildlife inventories collected by the Ministry of Natural Resources and Forestry (MNRF) in the province of Ontario. Wildlife data were collected at 141 sites distributed randomly across the study area (Fig. 1). Each site included 5 camera stations designed to detect medium-large sized mammals and 3 acoustic recorder stations primarily designed to detect birds. Some sites included 3 small mammal trap lines (n = 74 sites) and a rectangular grid of cover boards designed to detect terrestrial salamanders (n = 71 sites) (Fig. 2). Details of the sample design are described in Brown et al. (2015). A single season of survey data were collected at each site from 2013 to 2015.

At each site, motion-sensing cameras were placed at the site center and 500 m away in each of the four cardinal directions (Fig. 2). We deployed one PC85 or PC900 camera (Reconyx, WI, USA) at each station. These camera models use an infrared motion sensor to detect animals that cross in front of the camera, and an infrared flash that allows images to be captured during daylight, dusk and night. We programmed cameras to record one image every second for 5 s when triggered by animal movements. Each camera was secured to a tree roughly 0.5 m above the ground and aimed at a second tree 4.5–6 m away and baited with a single can of sardines on the tree and moist dog food at the base of the tree. Cameras were deployed from May to August for a minimum of 100 days and were rebaited at roughly 1-month intervals. The total deployment period for each camera was partitioned into a maximum of seven 15-day sessions. For each species and site, we divided the number of days with a detection by the number of active camera days. The mammal species that we considered in this study could have moved among all cameras at a site during a given day. We calculated the mean detection rate using the 5 replicate stations at each site as an index of abundance for use in statistical analysis (n = 140).

Acoustic stations were placed at the vertices of an equilateral triangle with approximately 350 m between stations, with the goal of increasing independence (Fig. 2). Audio point counts (10-minute duration) were recorded daily, 30 min before to 30 min after sunrise (local time), using a Song Meter SM2 or SM2 + (Wildlife Acoustics Inc., Concord, MA.). A single recording was then selected from 6 equal duration sessions between May 20 and July 7. An experienced biologist listened to each audio recording and examined the associated spectrograms to identify individual birds detected at the monitoring station. For the purposes of this study, we used the mean number of individuals among sessions as an index of abundance for each species and station (n = 387). Stations were treated as independent samples for

subsequent analysis.

Small mammal trap lines were co-located with acoustic stations (Fig. 2). Each trap line consisted of 11 trapping stations spaced 10 m apart. Each station contained one large trap (XLF15, 10.16 cm × 11.43 cm × 38.1 cm, H.B. Sherman Traps Inc.) and one small trap (XLK, 7.62 cm × 9.525 cm × 30.48 cm, H.B. Sherman Traps Inc.). Trapping was conducted for three consecutive nights between mid-July and the end of August. Traps were baited and left open overnight. The following morning captured individuals were identified, measured, marked, and released following the small-mammal live trapping protocol approved by the Ontario Ministry of Natural Resources and Forestry Wildlife Animal Care Committee (Protocol Approvals #13-164, #14-164, #15-164). We calculated and used the number of unique individuals per 1000 trap nights as an index of abundance for each trap line.

Salamander coverboard grids were co-located with one of the acoustic stations (Sugar et al., 2001; Brown et al., 2015) (Fig. 2). Most salamander grids consisted of 20 coverboards placed 8 m apart in a 4 × 5 grid; however, 30 boards were deployed in the northern portion of range where densities were expected to be lower. Biologists counted the number of red-backed salamanders (*Plethodon cinereus*) between and under each board during three surveys from May to July. We calculated the average number of salamanders per board during each survey and used the maximum value as an index of salamander abundance.

2.3. Habitat inventories and bioclimatic conditions

Habitat inventories were centered on the wildlife inventory sites. We characterized habitat conditions using five different datasets: forest understory, forest overstory, forest landscape pattern, anthropogenic disturbance, and climate. Each dataset was characterized within circular buffers of an area appropriate for each wildlife survey and habitat component.

We measured understory characteristics using 1 m radius circular plots. Individual understory plots were associated with salamander coverboards (1 each) and individual acoustic stations (one centered on the station and four offset by 30 m and 50 m to the east and west; 5 per station). Field crews measured litter depth (mm), shrub species diversity, and percentage cover of major vegetation (moss, lichen, herbs, graminoids, ferns), leaf litter, coarse woody debris, and vertical vegetation structure between 0 m and 10 m above ground in six ordinal classes.

We measured overstory characteristics using a combination of ground sampling and an aerial photography-based forest resources inventory (FRI) commonly used to determine wood supply and wildlife habitat supply for forest management planning (OMNR, 2009). Ground sampling was conducted in circular tree plots (11.28 m radius) located at each acoustic station and offset 50 m to the east and west (3 per station). Field crews measured the species and diameter at breast height (d.b.h.) (1.3 m above base of tree) of all trees that were > = 8 cm d.b.h., whether dead or alive, and whether there were one or more cavities present. FRI data include interpreted values of stand age, tree canopy composition, tree canopy height, and canopy cover. The FRI-derived overstory characteristics were extracted in a geographic information system (GIS) using 150 m radius buffers centered on each wildlife station. We used the resulting GIS data to characterize the proportion of young, immature, and mature Provincial Forest Types (PFT); (OMNR, 2003) within the buffered area.

We calculated forest disturbances using mapped road and year-specific forest harvest block data obtained from the MNRF. We pooled all highway, primary and secondary road features, which are mapped consistently across the study area. Disturbance characteristics included the mean distance to roads (m), percentage forest harvest ≤10 years, and percentage harvest ≤20 years within 150 m and 500 m buffers of each wildlife station. A GIS was used to determine the mean distance within buffered station polygons (rasterized) to the nearest road segment.

We calculated landscape metrics describing patterns in forest patches using the FRI data. Metrics included average total edge, ratio of total edge to patch area, and forest patch contiguity using 500 m (78.5 ha) circular buffers centered on the wildlife stations. The patch metrics included total edge, ratio of total edge to patch area, and patch continuity. These 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 Fragstats (Version 4.0, McGarigal, 2015).

We compiled climate characteristics including long-term averages (1984–2010) for mean daily temperature and mean total precipitation of the warmest and coldest quarters of the year, Julian day of the start of the growing season, and temperature seasonality (standard deviation of monthly mean temperature). Spatial grids of historical climate data were obtained from Natural Resources Canada (McKenney et al., 2006, 2007) at a resolution of approximately 4.5 km. We also calculated an index of site cumulative snow depth for the winter prior to the wildlife survey year, as well as an 18-year average (1994–2015). 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 and Webster, 2014). Given the resolution of the source data, mean values for each climate variable were generated within 8 km buffers for each site. All spatial analyses were conducted using ArcGIS desktop 10.3 (ESRI Inc., Redlands, California, USA).

2.4. Statistical analysis

Due to the large number of habitat characteristics, 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. We performed separate PCA for each of the habitat categories (understory, overstory, disturbance, landscape, climate) and used the Kaiser–Guttman criterion to select ordination axes whose eigenvalues were greater than the mean over all axes (Borcard et al., 2011). PCA scores were applied to individual stations for birds, small mammals, and the red-backed salamander. Station-level PCA scores were averaged within sites for analysis of the camera-derived mammal abundance indices.

We constructed generalized additive models (GAMs) to assess how relative abundance of each wildlife species was related to the PCA scores for understory, overstory, landscape, disturbance, and climate. GAMs allow nonlinear response shapes (Guisan et al., 2002) that reflect the underlying ecological relationships and loading of influential raw variables along different ends of PCA axes. To avoid over-fitting and to retain more easily interpretable relationships in the GAM smoothing functions, we set an upper limit of 3 degrees of freedom for each explanatory variable. Data exploration revealed that many species' abundances were skewed towards zero. We used the Tweedie family of error distributions to account for this skewness (Dunn and Smyth, 2005; Bonat and Kokonendji, 2017), as its mean-variance relationship allows them to describe a wide range of functional relationships that can arise from differing species' ecology.

To assess the relative importance of habitat variables, we developed a set of models containing all possible PCA variable combinations, with individual models limited to a maximum of 5 to avoid overfitting. This approach was necessary to ensure a balance in the number of models that contained each variable (Burnham and Anderson, 2002). We calculated the relative importance of each variable by summing the Akaike Information Criteria weights (AICw) across all models in the set that contained that variable (Burnham and Anderson, 2002). We accounted

for spatial autocorrelation among stations by including a residuals autocovariate (RAC) term in each model (Crase et al., 2012). The autocovariate term represents the residual spatial autocorrelation of an environment-only global model that included all explanatory variables. We used the Wilcoxon rank sum test to compare AICw scores between two taxonomic groups and used the Kruskal-Wallace rank sum test and Dunn's multiple comparison test to compare AICw scores among multiple taxonomic groups. Given the low sample sizes within taxonomic groups, we generally interpreted species level results qualitatively rather than conducting a means test or rank-sum test.

We interpreted species habitat associations by inspecting GAM response shapes for PCA-derived explanatory variables and the correlations of the original explanatory habitat variables with each PCA axis (Table S1). A detailed example is provided in Suppl. 1. Species habitat associations for key original explanatory variables were further assessed by estimating standardized coefficients using univariate generalized linear models with a binomial distribution (response = presence/non-detection). 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 (Oksanen et al., 2018), GAMs were constructed using the mgcv package (Wood, 2018), AICw values for each model set were compiled using the MuMIn package (Barton, 2018), and multiple comparison tests of AICw were performed using the DescTools package (Signorell, 2019).

3. Results and discussion

3.1. Habitat

The Kaiser–Guttman criterion identified five understory PCA axes, which captured 68% of the total variation explained for 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 (Table S1). Four overstory axes described 36% of total variation explained in tree age, conifer, deciduous, and abundance of standing dead trees. Two disturbance axes described 83% of total variation explained in forest harvest and roads, and two landscape axes captured 89% of total variation explained in the amount of edge and contiguity of forest patches. Two climate axes captured 90% of total variation explained in the primary gradients in summer precipitation and seasonal phenology, including snow and start of the summer growing season.

3.2. Wildlife habitat associations

Sufficient data were available to develop GAMs for 61 species, including 44 birds, 7 small mammals, 9 medium-large mammals, and 1 salamander. Species codes are defined in Table S2. AICw scores demonstrated the strongest support for models including understory, canopy and climate covariates (Fig. 3). Pooling all species, Dunn's test of multiple comparisons using rank sums indicated significantly greater AICw scores for understory, canopy and climate than for disturbance and landscape (Kruskal-Wallis $X^2 = 45.3$, $p < 0.001$; Dunn: understory-disturbance $Z = -3.2$, $p = 0.004$, understory- landscape $Z = -4.9$, $p < 0.001$, canopy-disturbance $Z = -2.8$, $p = 0.01$, canopy-landscape $Z = -4.6$, $p < 0.001$, and climate-disturbance $Z = -3.8$, $p < 0.001$, climate-landscape $Z = -5.5$, $p < 0.001$). Cavity-nesting birds generally showed greater support for canopy features than understory (4 of 7 species), while the reverse was evident for ground-nesting birds (10 of 16 species) (Table 1). Tree-nesting bird species showed a range of support for canopy and understory variables (Fig. 3). The salamander showed the greatest support for understory. Small mammals generally showed greater support for understory and climate than other variables (5 of 7 species), while medium-large mammals appeared more strongly influenced by the broad scale effects of climate (7 of 9 species). Disturbance received slightly higher support among some birds than other taxonomic groups and landscape had the strongest support for medium-large mammals and the salamander (Fig. 3, Table 1); however, statistical tests did not indicate significant differences in AICw among groups ($p > 0.05$).

3.2.1. Understory and canopy

Our results illustrate the importance of understory to the wildlife community, including vertical vegetation structure and ground cover (e.g. leaf litter, moss, shrub species diversity). Our findings are consistent with Venier and Pearce (2007) who found strong support for the importance of understory structure, in addition to overstory, for boreal land birds. In our study, AICw for Canopy.pc1 was marginally higher for birds than mammals (Wilcoxon, $W = 432$, $p = 0.066$); however, when pooling all species or grouping by species guilds, there was no significant difference in AICw support between understory and canopy variables. Betts et al. (2006) suggested that detailed ground vegetation information may not be needed to predict bird species occupancy; however, they did not explicitly consider vertical vegetation structure beneath the canopy.

Notably, we found that the importance of understory vegetation appears to vary with breeding and foraging guild. For example, if we regress species presence against understory characteristics using a binomial model, the standardized coefficients (Fig. 4) reveal that that ground and shrub-nesting birds showed mixed response to shrub understory. Birds that both nest and forage on the ground tended to show negative relationships to shrubby understories (e.g. OVEN, NOWA (Whitaker and Eaton, 2014)), VEER (Heckscher, 2017)) whereas birds that nest on the ground under low dense vegetation or in bushes, had positive relationships to shrub cover (e.g., NAWA, WTSP, and ALFL). 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 (Holmes et al., 1986; Smith and Shugart, 1987; Touihri et al., 2015; Krikun et al., 2018). Our findings are consistent with Zhang et al. (2013) in suggesting there is an important functional component to community structure that affects the response (positive/negative) of different guilds to forest characteristics.

As noted by Venier and Pearce (2007), 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 relations into planning processes and to assess outcomes of potential harvesting scenarios (Venier and Pearce, 2007). Considering both fine scale ground and remotely sensed information, Betts et al. (2006) concluded that remotely sensed vegetation and topography data was sufficient to predict the site occupancy of forest birds. 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 et al., 2006). However, there is likely independent variation in understory that cannot be inferred from available FRI 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 FRI will be of considerable value when evaluating biodiversity objectives in forest management planning. Notably, Charchuk and Bayne (2018) found that understory protection harvest can benefit mature forest species. 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).

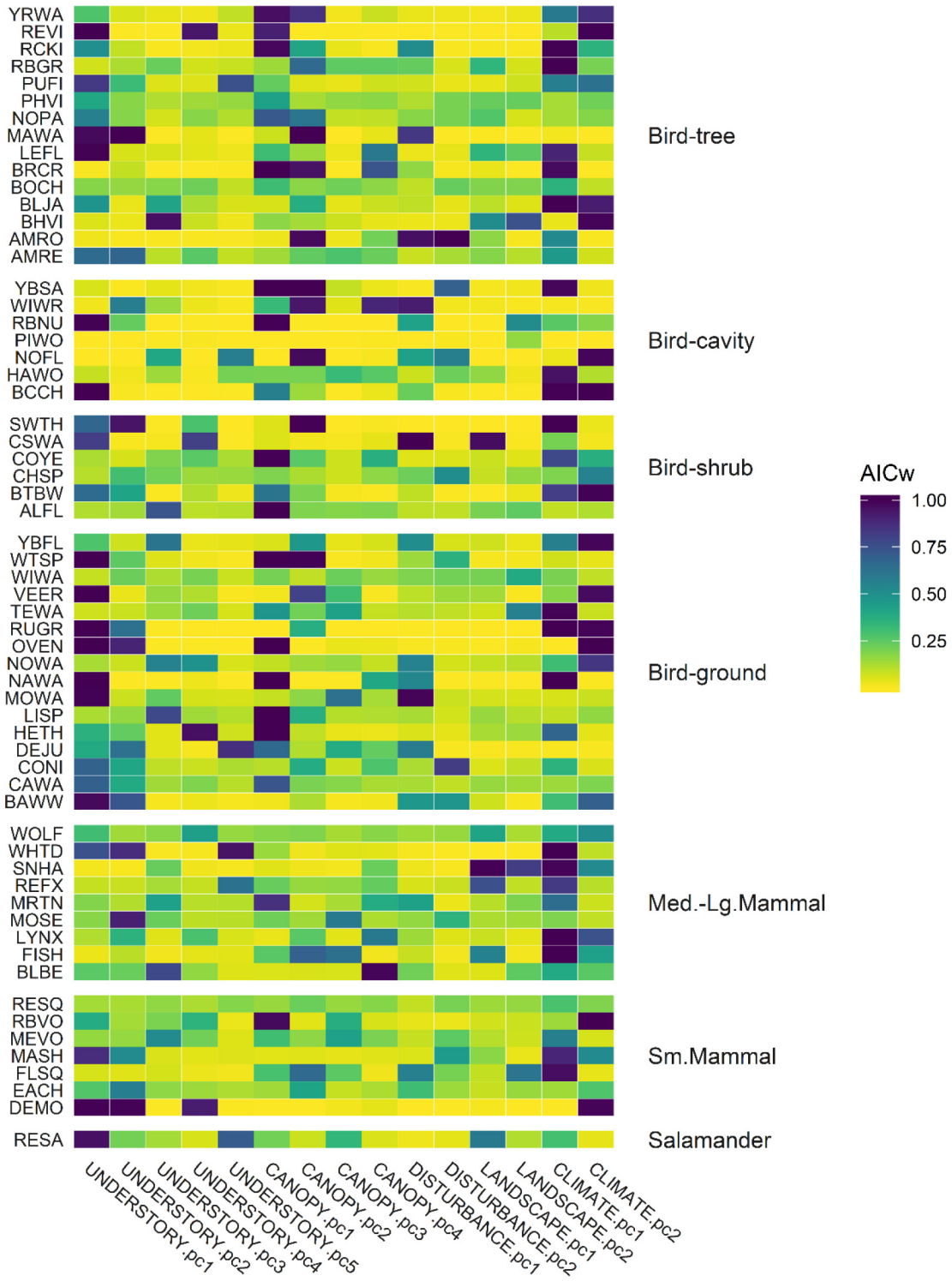

Fig. 3. AIC weights characterizing the strength of support for each of the PCA-derived habitat variables for each wildlife species. Birds are grouped according to their nesting strategy and species codes are defined in Table S2.

3.2.2. *Disturbance*

Positive or negative relationships to forest harvest disturbance were more evident among birds (19 of 44 species) than mammals (1 of 16 species); however, there was no significant difference in AICw among the two groups ($W = 404$, $p = 0.24$) (Fig. 5, Table 1). More shrub- and ground-nesting bird species showed positive than negative relationships to Disturbance.pc1, consistent with greater amounts of forest harvest (Fig. 5, Table S1) and selection for young open stands with an abundant shrub understory (e.g. MOWA, LISP, CSWA). Ground- and shrub-nesting birds that benefit from mature forest habitat or dense vegetation (e.g. YBFL, SWTH) (Gross and Lowther, 2011; Zlonis et al., 2017) had negative relationships to forest harvest. The species responses to forest harvest we observed are similar to patterns reported elsewhere demonstrating positive effects on early successional/edge species and negative effects on mature forest species (Holmes et al., 2017; Zlonis et al., 2017).

Among mammals, only WHTD had a statistically significant response (positive) to forest harvest based on a univariate binomial model

Table 1
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 summarized in Table S1.

Variable	Bird-tree	Bird-cavity	Bird-shrub	Bird-ground	Med.-Lg. Mammal	Sm. Mammal	Salamander
understory.pc1	0.469 (0.094)	0.432 (0.232)	0.416 (0.136)	0.613 (0.098)	0.214 (0.075)	0.377 (0.128)	0.961
understory.pc2	0.2 (0.072)	0.17 (0.112)	0.312 (0.142)	0.307 (0.07)	0.313 (0.115)	0.336 (0.117)	0.210
understory.pc3	0.149 (0.065)	0.083 (0.037)	0.193 (0.116)	0.188 (0.061)	0.228 (0.082)	0.168 (0.057)	0.134
understory.pc4	0.146 (0.06)	0.012 (0.005)	0.284 (0.109)	0.172 (0.065)	0.139 (0.047)	0.244 (0.104)	0.059
understory.pc5	0.104 (0.048)	0.161 (0.112)	0.082 (0.029)	0.113 (0.059)	0.235 (0.109)	0.08 (0.025)	0.715
canopy.pc1	0.433 (0.097)	0.619 (0.166)	0.485 (0.183)	0.498 (0.111)	0.225 (0.084)	0.294 (0.119)	0.212
canopy.pc2	0.449 (0.094)	0.545 (0.193)	0.297 (0.144)	0.284 (0.07)	0.178 (0.07)	0.223 (0.078)	0.077
canopy.pc3	0.084 (0.025)	0.114 (0.072)	0.058 (0.028)	0.175 (0.048)	0.201 (0.08)	0.189 (0.054)	0.341
canopy.pc4	0.185 (0.055)	0.204 (0.144)	0.129 (0.058)	0.119 (0.029)	0.31 (0.103)	0.106 (0.026)	0.056
disturbance.pc1	0.229 (0.078)	0.348 (0.135)	0.243 (0.154)	0.31 (0.072)	0.141 (0.042)	0.175 (0.074)	0.025
disturbance.pc2	0.143 (0.069)	0.252 (0.126)	0.111 (0.081)	0.168 (0.058)	0.092 (0.041)	0.187 (0.05)	0.039
landscape.pc1	0.164 (0.041)	0.04 (0.032)	0.223 (0.153)	0.076 (0.016)	0.344 (0.12)	0.103 (0.018)	0.595
landscape.pc2	0.122 (0.05)	0.146 (0.097)	0.097 (0.045)	0.122 (0.044)	0.186 (0.084)	0.181 (0.074)	0.118
climate.pc1	0.52 (0.099)	0.54 (0.2)	0.515 (0.161)	0.373 (0.091)	0.718 (0.106)	0.413 (0.128)	0.299
climate.pc2	0.374 (0.101)	0.386 (0.194)	0.348 (0.156)	0.391 (0.107)	0.316 (0.082)	0.407 (0.139)	0.037

(Fig. 5). GAM AICw scores indicated that disturbance ranked the lowest among characteristics considered for medium to large mammals (Table 1). Although we did not find a significant effect of Disturbance on MEVO, Verme and Ozoga (1981) found that clearcutting of conifer lowlands increased abundance of meadow voles, likely due to their preference for open grasslands with dense ground-level vegetation cover, and consistent with their positive response to understory cover in our study (Fig. 4).

Mammals that benefit from availability of closed canopy forest conditions (such as SNHA, LYNX and MRTN) were negatively associated with Disturbance.pc1. Our findings for LYNX are consistent with Squires et al. (2010) who observed an avoidance of clear cuts and related open areas in Montana, but contrast with evidence in the Yukon of a preference for regenerating forest over mature forests (Mowat and

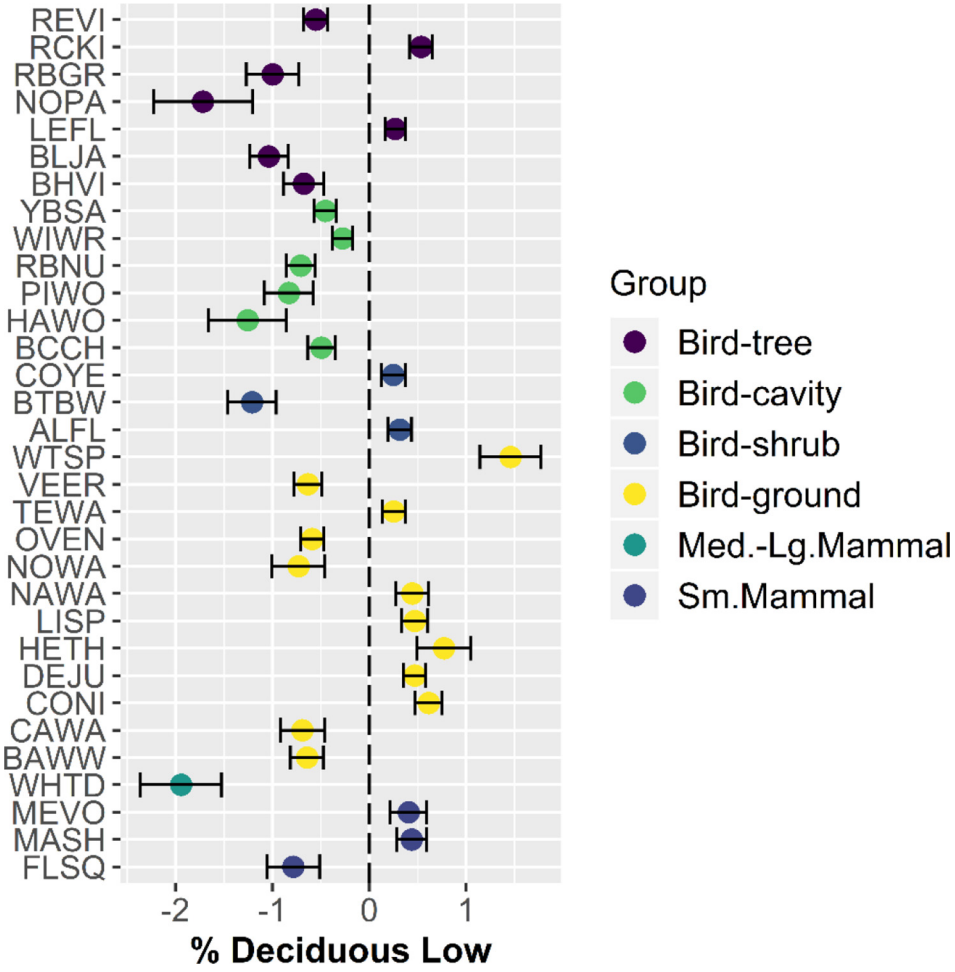

Fig. 4. Effect size of the mean percentage cover of deciduous shrub cover between 0 and 0.5 m above ground. Values are standardized coefficients with standard errors from univariate generalized linear models with binomial distribution for wildlife presence/non-detection. Only species with significant coefficients ($p < 0.05$) are shown. Species codes are defined in Table S2.

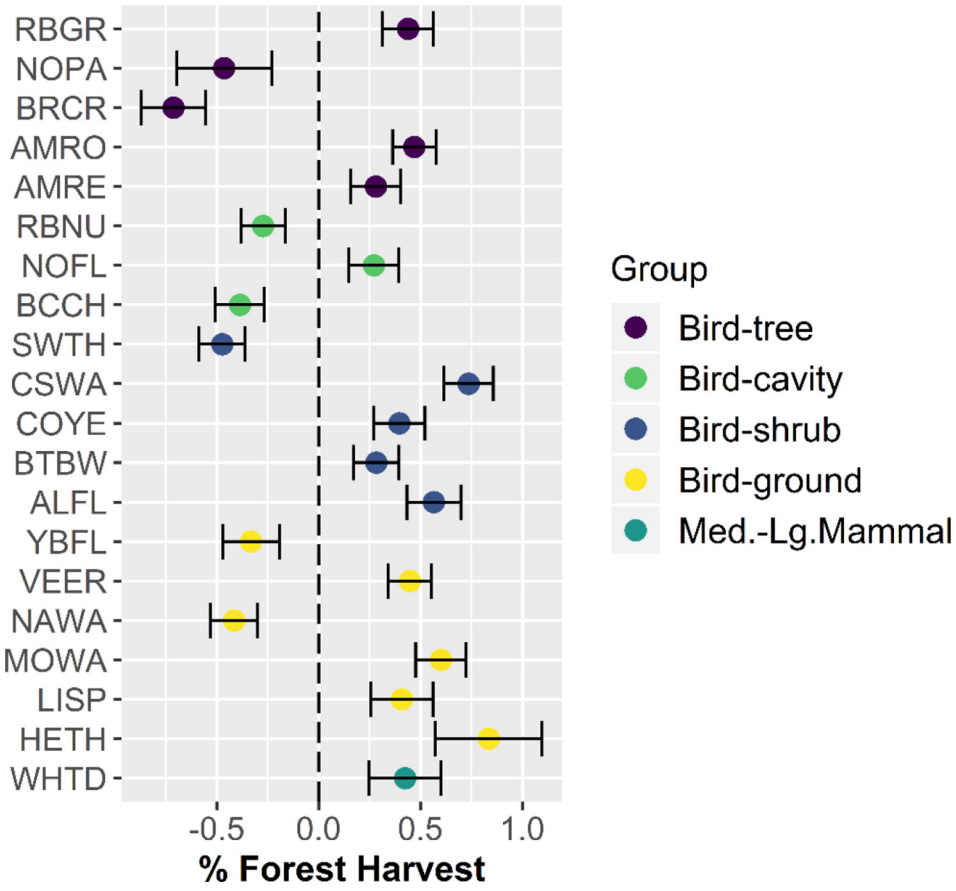

Fig. 5. Effect size of percentage of forest harvest within 500 m of wildlife stations. Values are standardized coefficients with standard errors from univariate generalized linear models with a binomial distribution for wildlife presence/non-detection. Only species with significant coefficients ($p < 0.05$) are shown. Species codes are defined in Table S2.

Slough, 2011). Differences among studies may relate to seasonal variation in habitat selection, prey availability and habitat selection, and the timing of observational studies that can affect inferences about apparent habitat selection (Ferron and Ouellet, 1992; Keim et al., 2011; Mowat and Slough, 2011).

Conservation targets may focus on anthropogenic disturbance related conditions, such as the amount of cut forest and roads (Donovan et al., 2017; Stewart and Komers, 2017). Such effects might operate through the absence of a needed resource or increased mortality risk (Carroll and 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 abundances/occupancies are positively associated with specific desired or suitable habitat conditions. These two aspects - direct effects of disturbance and supply of suitable habitat - are inherently related and may vary among species in importance, creating uncertainty about how managers might best optimize habitat management approaches for diverse wildlife communities. Here, we assessed the relative contributions of apparently negative (disturbance) and positive (resource-providing) habitat conditions. We found that resource-providing habitat conditions (e.g. understory and canopy variables) received greater support in models than the direct characterization of disturbance-related land cover features (Table 1). Zhang et al. (2013) also found that local forest structure, in addition to human disturbance, was an important determinant of bird species richness in boreal forest. In our study, 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 bird species showed negative response to forest harvest (Fig. 5, NOPA, BRCR, BCCH, RBNU, SWTH, YBFL, NAWA), which may support their value as indicators of sustainable 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 BBWA lacked sufficient detections within our dataset to develop statistical models in our study.

3.2.3. Landscape

Landscape features had relatively high support among medium to large mammals and the RESA. For example, SNHA exhibited a positive association with forest edge; whereas, FISH and REFX were associated with more contiguous patches of forest with less edge (Fig. S2). The WOLF GAM for Landscape.pc1 (Fig. S2), indicated a positive effect of forest edge and contiguous patches, perhaps because wolves can 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 et al., 2012). The importance of landscape features likely reflects a combination of mammalian ecology and the scale that we measured forest habitat metrics (e.g. 500 m buffer width). The ecological response of medium to large mammals is consistent with previous studies (Jędrzejewski et al., 2004; Holbrook et al., 2016); however we acknowledge that large mammals were likely responding to habitat conditions inside and outside the spatial extent of our habitat buffers. 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 (Fisher et al., 2011).

3.2.4. Climate

Climate received high support among all taxa considered but ranked more highly in importance than the other habitat groups for medium to large mammals (Table 1, 6 of 9 medium to large mammals had climate

ranked among the highest AICw). Our dataset spanned a broad bioclimatic gradient and relationships were generally consistent with known climatic niche spaces of species. For example, inspection of the Climate.pc1 variable in GAMs and factor loadings of raw variables indicates the relative abundances of WHTD, REFX, and FISH were associated with lower temperature seasonality and snow accumulation, and an earlier start to the summer growing season (Table S1). These species have a more southern distribution in Canada, with northern ranges generally limited by cold climate, severe winters, and low productivity (Smith, 1991; Raine, 2011; Gallant et al., 2012). Conversely, northern adapted species such as LYNX and SNHA had the opposite response (Tumlison, 1987; Sultaire et al., 2016). The importance of climate in our managed forest system and widespread evidence that climate warming affects changes in habitat and species distributions (Thomas et al., 2006; Stralberg et al., 2015; Sultaire et al., 2016) points to the need for additional studies to clarify the role of climate in relation to forest characteristics affecting populations. Understanding the interactions among climate and habitat for managed populations that span a range of bioclimatic conditions can help identify effective management strategies (Brown, 2011).

3.3. Conclusions and recommendations

In many cases, managers use wildlife habitat models to support forest management planning. Our study illustrates how forest managers can identify indicators using wildlife-habitat models built from empirical data collected at scales relevant to policy and management. Given wildlife-habitat associations may vary in relation to resource availability (Van Moorter et al., 2013; Holbrook et al., 2019) that varies geographically, we contend that models should be derived from empirical data consistent with the scales of forest management and species' ecology within a given geography of interest. Our modelling approach provides quantitative measures of species' responses to different habitat characteristics that can support forest management planning and operations. Explicitly integrating habitat and wildlife monitoring into forest management can also facilitate the direct evaluation of management effectiveness (Kimmins et al., 2007; Lindenmayer and Likens, 2009). Habitat monitoring parameters should reflect the conditions that affect wildlife populations, consistent with the adaptive management paradigm. Aligning management, monitoring, and model parameterization in this way has the potential to improve efficiency in effectiveness evaluation and updating of management tools used in forest planning. Field-based sampling that compliments forest inventories can augment the ability to infer wildlife-habitat relationships and track changes in response to management.

Our findings indicate that a range of wildlife and habitat indicators may be needed to assess forest sustainability. Forest managers and industry organizations often focus on stand or landscape level objectives for the maintenance of wildlife habitat (OMNR, 2010a,b, 2014; Sustainable Forestry Initiative, 2015). Our results support the expectation that stand and landscape management can benefit many wildlife species; however, our work also emphasizes the importance of considering understory vegetation and climate to sustain wildlife populations. We found that the relative importance of understory and overstory forest habitat conditions, disturbance, landscape patterns, and climate vary among taxonomic groups. The fact that species' responses varied by taxa and life-history strategy further indicates that stand or landscape scale management may disproportionately impact wildlife guilds that play an important role in forest pest control (Crawford and Jennings, 1989) and supporting socially valued species through trophic interactions (Boutin et al., 1995). Our research shows that considering forest understory characteristics within forest management may be needed to monitor, and ultimately sustain, forest wildlife.

CRediT authorship contribution statement

Glen S. Brown: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data curation, Writing - original draft, Visualization, Supervision, Project administration, Funding acquisition. **Lisa Pollock:** Data curation, Formal analysis. **Philip D. DeWitt:** Writing - review & editing. **Neil Dawson:** Writing - review & editing, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.117854.

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