



RESEARCH ARTICLE

## Influence of landscape, habitat, and species co-occurrence on occupancy dynamics of Canada Warblers

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### ABSTRACT

The Canada Warbler (*Cardellina canadensis*) is a species of high conservation importance because of its low overall density and long-term widespread population declines on the breeding grounds. Results of previous research on the species suggest that its breeding habitat preferences vary across its range. However, the underlying processes associated with habitat use are unknown. Using a 20 yr dataset, we developed occupancy models for Canada Warblers to determine the influence of habitat characteristics (e.g., understory vegetation, canopy cover), landscape context (e.g., edge, forest patch size), and species co-occurrence on occupancy, colonization, and local extinction parameters. Our results show that multiple habitats are used by Canada Warblers on the breeding grounds; common variables associated with large-scale, long-term occupancy dynamics are forest age, landscape composition at the 100 m and 500 m scales, and mean patch size. Overall, Canada Warblers were nearly twice as persistent in mature forest stands (>80 yr) and large, mixed forest stands. Further, models indicated that species co-occurrence was an important predictor of Canada Warbler occupancy in some cover types. The results of this study increase our understanding of population processes over large, dynamic landscapes and provide essential conservation information to improve habitat and landscape management for the Canada Warbler.

**Keywords:** avian conservation, Canada Warbler, competition, forest management mechanisms, habitat use, landscape, occupancy

### Influencia del paisaje, del hábitat y de la presencia simultánea de especies en la dinámica de ocupación de *Cardellina canadensis*

### RESUMEN

*Cardellina canadensis* es una especie de alta importancia de conservación debido a su baja densidad global y a la disminución poblacional generalizada de largo plazo en los sitios reproductivos. Investigaciones previas sobre la especie sugieren que las preferencias de hábitat reproductivo varían a lo largo de su rango. Sin embargo, los procesos subyacentes asociados con el uso de hábitat son desconocidos. Usando una base de datos de 20 años, desarrollamos modelos de ocupación para *C. canadensis* para determinar la influencia de las características del hábitat (e.g., vegetación del sotobosque, cobertura del dosel), el contexto del paisaje (e.g., borde, tamaño del parche de bosque) y la presencia simultánea de especies en la ocupación, colonización y parámetros locales de extinción. Nuestros resultados muestran que *C. canadensis* usa múltiples hábitats en los sitios reproductivos; las variables usuales asociadas con la dinámica de ocupación de gran escala y largo plazo son la edad del bosque, la composición del paisaje a la escala de 100 m y 500 m, y el tamaño promedio del parche. En general, los individuos de *C. canadensis* fueron casi el doble de persistentes en las masas de bosque maduro (>80 años) y en las grandes masas boscosas mixtas. Más aún, los modelos indicaron que la presencia simultánea de especies fue un predictor importante de la ocupación de *C. canadensis* en algunos tipos de cobertura. Los resultados de este estudio aumentan nuestro entendimiento de los procesos poblacionales a lo largo de grandes paisajes dinámicos y brindan información esencial de conservación para mejorar el manejo del hábitat y del paisaje para *C. canadensis*.

**Palabras clave:** *Cardellina canadensis*, competencia, conservación de aves, mecanismos de manejo del bosque, ocupación, paisaje, uso de hábitat

### INTRODUCTION

The Canada Warbler (*Cardellina canadensis*) is a Neotropical migratory songbird that breeds in forests of boreal

Canada, the northeastern United States, and south along the Appalachian Mountains to Tennessee (Reitsma et al. 2010). Canada Warblers winter in northern South America, with the greatest numbers observed in and east of the

Andes (Reitsma et al. 2010). The species' breeding habitat has been suggested to vary across its range (Reitsma et al. 2010). Canada Warblers inhabit a wide range of deciduous and coniferous forests but are most common in mixed coniferous–deciduous forests that are moist and have well-developed understory shrub layers (Reitsma et al. 2010). In the eastern portion of its range the species breeds both in early-successional forest stands and in deciduous and mixed-species understories of mature forests (DeGraaf et al. 1998, Reitsma et al. 2008). It appears to be disturbance dependent at higher elevations, especially in the southern portion of its range (Lambert and Faccio 2005, Becker et al. 2012). Quaking aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*) stands are favored in the central portion of the range, while mixed forests and forested wetlands and swamps seem to be preferred in the northern part (Schmiegelow et al. 2014, Niemi et al. 2016).

Several fine-scale habitat factors are associated with Canada Warbler abundance during the breeding season. The species inhabits many forest-cover types but is most abundant in moist mixed forests with a dense understory and complex ground cover (Conway 1999, Becker et al. 2012). Hallworth et al. (2008a) showed shrub stem density to be critical to breeding Canada Warblers and suggested that a dense understory enhances Canada Warbler breeding habitat. Similarly, Goodnow and Reitsma (2011) found that forests with complex ground structure and thickets of small-stemmed woody plants increase Canada Warbler nesting success. Although Canada Warblers are considered sensitive to forest fragmentation (Enser 1992, Freemark and Collins 1992), populations are known to occupy young, disturbed forests in Wisconsin (Sodhi and Paszkowski 1995); areas that were heavily logged 5–15 yr previously in northern hardwood forests of New York (Webb et al. 1977); and areas heavily logged 15–25 yr before in mixed forests of New Hampshire (Hallworth et al. 2008a). The most important features in recently harvested stands appear to be high understory shrub density (Schmiegelow et al. 1997, Hallworth et al. 2008b) and retention of residual trees (Hagan et al. 1997, Lambert and Faccio 2005, Hallworth et al. 2008b).

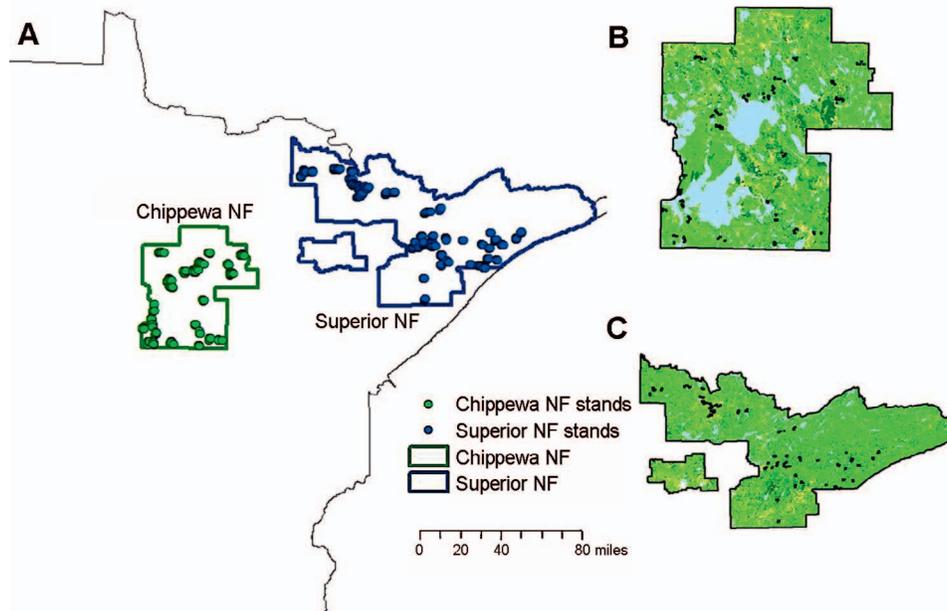
Results from the North American Breeding Bird Survey (BBS) indicate 4 decades of Canada Warbler decline throughout the northeastern breeding range, with annual population changes between  $-3.8\%$  and  $-7.3\%$  since 1980 (Sauer et al. 2014). The reasons for the declines are unknown, but factors may include loss of wintering habitat in South America, loss and degradation of habitat on the breeding grounds (Lambert and Faccio 2005), and collisions with man-made structures (Loss et al. 2014, Machtans and Thogmartin 2014). The species was designated as “threatened” by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 2008, and since 2010 has been listed as “threatened” under the

Species at Risk Act (COSEWIC 2012, Environment Canada 2015). In the United States, it is included on the list of species of conservation concern at the national level (U.S. Fish and Wildlife Service 2008) and is considered a “Yellow Watch List” species (Butcher et al. 2007). Population trend estimates for Canada Warblers in the boreal hardwood transition zone (Bird Conservation Region 12) have declined  $-2.85\%$  since 1966. However, BBS population trends have been relatively stable in Minnesota, USA (Sauer et al. 2014).

Long-term and wide-ranging declines in Canada Warbler populations suggest the need for additional information on long-term occupancy dynamics. The Minnesota National Forest Breeding Bird Monitoring Program (hereafter “Minnesota monitoring program”) was established in 1995, in response to concerns about biodiversity and population declines of migratory passerines, including the Canada Warbler (Hanowski and Niemi 1995, Hanowski et al. 2005, Niemi et al. 2016). The program was designed to provide an estimate of population change for forest bird species in national forests in Minnesota (Figure 1). Results from the Minnesota monitoring program indicate stable population trends for Canada Warblers (1995–2014: annual change =  $0.53\%$ ,  $P = 0.33$ ) in Superior National Forest and significantly increasing trends (1995–2014: annual change =  $4.87\%$ ,  $P = 0.02$ ) in Chippewa National Forest. Data from this monitoring program provide an opportunity to assess habitat and landscape factors that support stable or increasing Canada Warbler populations, using a long-term (20 yr) occupancy dataset.

In addition to habitat factors, species interactions have long been thought to influence avian population dynamics (MacArthur 1958, Lovette and Hochachka 2006, Niven et al. 2009). Behavioral decisions based on both positive and negative interspecific interactions can influence important aspects of a species' ecology such as habitat selection, foraging, spatial distribution, and dispersal, and thus can influence occupancy dynamics. The results of recent studies (Gotelli et al. 2010, Ricklefs 2013) have shown that both aggregated and segregated distribution patterns among ecologically similar species result from a combination of competitive and positive interactions, independent of habitat characteristics, at local and broad spatial scales. We also used null models to investigate potential patterns of co-occurrence in bird community assemblages (Gotelli 2001), in order to assess the influence of species co-occurrence on Canada Warbler occupancy in Minnesota's national forests.

Our objective was to better understand factors associated with long-term Canada Warbler occupancy dynamics over large, dynamic landscapes. We identified potential variables important to Canada Warbler population dynamics from the existing literature (e.g., Webb et al. 1977, Freemark and Collins 1992, Sodhi and Paszkowski 1995,



**FIGURE 1.** Stand locations of Minnesota National Forest Breeding Bird Monitoring Program point counts. Each point represents 3–5 forest stands (A) in northern Minnesota’s Chippewa (B) and Superior (C) National Forests (NF).

Schmiegelow et al. 1997, Conway 1999, Lambert and Faccio 2005, Hallworth et al. 2008a, 2008b, Becker et al. 2012). We used habitat and landscape variables from the literature along with species co-occurrence variables to create candidate model sets to assess the influence of stand, landscape, and species co-occurrence on Canada Warbler occupancy dynamics in 2 national forests. Specific objectives of this study were to identify (1) land-cover and stand-level characteristics associated with colonization and local extinction probabilities in each national forest and (2) the influence of stand-level characteristics and species co-occurrence on occupancy and local extinction probabilities in different cover types in each national forest.

## METHODS

### Study Area

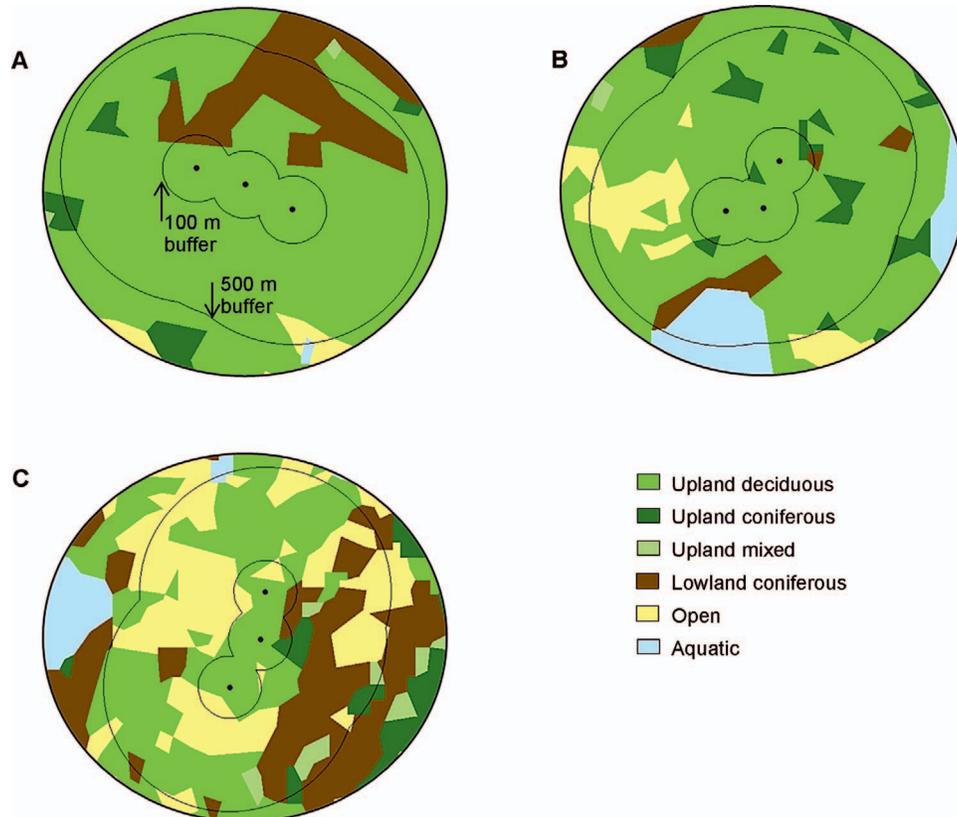
The study was conducted from 1995 to 2014 in 2 national forests in Minnesota. Chippewa National Forest (hereafter “Chippewa”) encompasses >269,000 ha in north-central Minnesota (Figure 1) and includes approximately 1,300 lakes and ponds, 1,500 km of running water, and 178,000 ha of wetlands. Superior National Forest (hereafter “Superior”) comprises >1,580,000 ha (Figure 1), a significant portion of the northeastern “arrowhead” region of Minnesota, and includes >180,000 ha of open water with >2,000 lakes and >3,500 km of streams.

Superior and Chippewa are located near the ecotone of boreal and northern temperate forests and contain a mix of forest-cover types. The most representative forest-cover

types in Superior and Chippewa are aspen (*Populus* spp.), paper birch (*Betula papyrifera*), spruce (*Picea* spp.), balsam fir (*Abies balsamea*), tamarack (*Larix laricina*), and pine (*Pinus* spp.) forests. Superior and Chippewa have relatively similar proportions of upland deciduous (~35%) and lowland conifer (~25%) cover types. However, Chippewa has more upland coniferous forest (~35%), primarily pine and spruce plantations, than Superior (~20%), while Superior has more upland mixed forest (i.e. aspen–fir; 17%) than Chippewa (~2%). Both national forests have relatively low proportions of lowland hardwood cover. The mosaic of habitats found in this region supports ~155 breeding species of forest-dwelling birds (Green 1995). The breeding bird communities of these hemiboreal forests are among the most diverse in North America (Niemi et al. 1998).

### Sampling

At the onset of the Minnesota monitoring program, avian point-count sampling locations were distributed across the forest mosaic in a stratified random manner (Figure 1; Hanowski and Niemi 1995). For each national forest, stands were selected so that the final proportion of stands of each forest-cover type was equal to the proportion of forested land available. The sample of stands is therefore representative of the percent forest cover found in each national forest. Selected stands were large enough to accommodate 3 replicate sampling points separated by a minimum of 220 m (Figure 2). Point-count sampling in the Minnesota monitoring program followed national and



**FIGURE 2.** Land cover and patch configuration of 3 aspen stands, each consisting of 3 point counts. Stands represent examples of (A) high, (B) medium, and (C) low mean patch size and (A) low, (B) medium, and (C) high percent open cover in the 100 m and 500 m buffers around the stand.

regional standards (Ralph et al. 1995, Howe et al. 1997). Ten-minute point counts were conducted at each point between June and early July (Hanowski et al. 2005, Etersson et al. 2009, Niemi et al. 2016). Point counts were conducted by trained observers from  $\sim 0.5$  hr before to 4 hr after sunrise on days with little wind ( $< 15$  km hr $^{-1}$ ) and little or no precipitation. All birds heard or seen from the point were recorded, and distance was estimated as  $< 50$  m, 50–100 m, or  $> 100$  m (Howe et al. 1997). We excluded from analyses birds that were  $> 100$  m from the point.

#### Stand Characteristics and Land-Cover Variables

A total of 308 stands (924 points) were included in the analysis: 183 stands (549 points) in Superior and 125 stands (375 points) in Chippewa. From existing literature on the Canada Warbler (Sodhi and Paszkowski 1995, Schmiegelow et al. 1997, Conway 1999, Lambert and Faccio 2005, Hallworth et al. 2008a, 2008b, Reitsma et al. 2010, Becker et al. 2012), we established a set of candidate variables that we thought would influence occupancy. Covariates were calculated over the 20 yr study period, using a variety of data sources. Percent canopy cover (estimated visually at 10% intervals), percent ground cover

(estimated visually at 10% intervals), and shrub (diameter at breast height  $< 2.5$  cm) density (on a scale of 1–5; Pattison et al. 2011) were recorded in the field at intervals of 3–5 yr. Although the study area is extensively forested, we included distance to the nearest road for each stand; the average distance from a point in a stand to the road was used as the “distance to road” covariate value for the stand (Lapin et al. 2013). Ages of forest stands were obtained from the Interagency Information Cooperative, which has integrated forest inventory data measured in the field by foresters from several forest-management groups within Minnesota, including county, state, and federal agencies (Skally 2000, Niemi et al. 2016). All variables were averaged across the 3 sample points in each stand to calculate annual average stand values for the study period.

Canada Warblers are territorial during the breeding season, with reported territory size averaging 1 ha but ranging up to 3.3 ha or larger (Hallworth et al. 2008a, Environment Canada 2015). However, results from recent studies have shown that landscape factors at larger spatial scales were important drivers for warbler species (Streby et al. 2012, Lapin et al. 2013). On the basis of this information and available land-cover data, we chose to calculate cover-

type and landscape variables at scales of 100 m (3.14 ha) and 500 m (78.5 ha), using ArcGIS 10.1 (ESRI, Redlands, California, USA). Stands were analyzed by placing a 100 m and 500 m buffer around each point-count location and taking the union to form one asymmetrical buffer (Figure 2; Lapin et al. 2013). Percent land-cover type in each buffer was calculated using National GAP Land Cover data, which uses Landsat 1999–2001 imagery as the base for its models and provides land-cover data at a  $30 \times 30$  m resolution (U.S. Geological Survey 2011). A combination of field observation data, Forest Inventory Analysis data, and Global Forest Change data (Hansen et al. 2013) was used to assess changes in land cover over the duration of the study, including the occurrence of logging within the buffers during the study. We classified land-cover types into 6 broad categories, including 4 forest-cover types: lowland coniferous forest, upland coniferous forest, upland deciduous forest, and upland mixed forest. “Open” and “aquatic” were also included as land-cover categories. Land-cover types classified as aquatic are those that are open water year round, such as lakes, open wetlands, ponds, and streams. Open cover types were considered habitats with <10% canopy cover, generally clear-cut areas, wetlands, agricultural land, pastures, and shrublands. The Patch Analyst 5 application for ArcGIS (Rempel et al. 2012) was used to calculate mean patch size (ha) and total edge (m) for the 100 m and 500 m buffers around the 3 sample points of each stand in 5 yr intervals, to track changes in patch size and edge density over the course of the study (McGarigal and Marks 1995). Because of the duration of the study and inconsistencies between datasets, we were not able to develop a precise, reliable measure for extent of logging or logging type (clear-cut, partial harvest) that occurred in 100 m and 500 m buffers around the stands. For this reason, we included logging as a binary variable. We recognize that this is not an ideal method for including logging disturbance in the models. However, logging disturbance was also indirectly incorporated at the stand level as a function of stand age and at the landscape level as a function of average percent open habitat over time.

### Co-occurrence Analysis

To generate a list of species that may influence Canada Warbler occupancy, EcoSimR's co-occurrence module (Gotelli and Ellison 2013) was used to assess patterns of species co-occurrence. The co-occurrence module tests for nonrandom patterns of co-occurrence in a presence–absence matrix by using Monte Carlo randomizations that create “pseudo-communities” (Pianka 1986), then statistically compares the patterns in these randomized communities with those in the real data matrix (Diamond 1975). Species richness for each stand was analyzed for each national forest and by cover type to minimize the

possibility of “habitat checkerboards.” These can occur when species are associated with different abiotic features of the sites and lead to more or less co-occurrence than expected by chance (Gotelli 2001). Data were organized in a matrix of presence (1) and absence (0), in which each species represents a row and each stand a column. The C-score index (Stone and Roberts 1990) was used as a quantitative co-occurrence index; the C-score is the number of checkerboard units for all unique pairs of species. We used fixed-sum row and column constraints and a “sequential swap” algorithm for randomizing matrices and ran 10,000 simulations (Ulrich and Gotelli 2007a, 2007b, and Ulrich et al. 2009). Using fixed-sum row and column constraints produces null matrices with the same number of site co-occurrences per species (row totals) and the same number of species per site (column total) as observed in the original dataset. The sequential swap algorithm reshuffles the original matrix by repeatedly swapping submatrices that preserve row and column totals, and it is not prone to Type I or Type II errors (Gainsbury and Colli 2003, Gotelli and Entsminger 2005).

### Occupancy Analyses

We used a single-species, multiseason occupancy modeling framework (MacKenzie et al. 2002) to evaluate the influence of stand characteristics, landscape, and species co-occurrence on Canada Warbler occupancy dynamics. Multiseason occupancy modeling allows spatial and temporal dynamics of populations to be modeled and analyzed and accounts for errors in detection during sampling. These models use information (detection or nondetection) from repeated observations (multiple points per stand), which are used to estimate probabilities of occupancy and detectability (MacKenzie et al. 2006). Our occupancy analysis utilized spatial replicates (3 points stand<sup>-1</sup>) associated with the monitoring program's experimental design to estimate detection probabilities. Multiple studies (e.g., Kendall and White 2009, Guillera-Aroita 2011) have examined potential estimation bias associated with spatial replication. We recognize the potential for bias when using spatial replicates, but we consider that the value of inference gained from applying occupancy models to this long-term dataset outweighed the issues associated with biased estimations.

Multiseason occupancy models assume that the population is open between seasons or that stands that were previously occupied can become unoccupied, and stands that were previously unoccupied can become occupied, between seasons. In the occupancy modeling framework, estimates associated with these processes are referred to as probability of local extinction (i.e. site abandonment) and probability of colonization. Multiseason occupancy modeling considers the dynamic changes in occupancy as a first-order Markov process (MacKenzie et al. 2006) where

the probability of a site being occupied in season  $t + 1$  depends only on the occupancy state of the site in the previous season,  $t$ . Modeling changes in occupancy as a Markov process accounts for temporal autocorrelation (MacKenzie et al. 2006) when observations on the same sampling unit are positively correlated. Parameter estimates were related to covariates using the logistic equation or logit-link function. This general framework was used to develop a set of candidate models that address competing hypotheses of occupancy dynamics. We ranked models on the basis of  $AIC_c$  (Akaike's Information Criterion corrected for sample size), and the strength of evidence for each model was determined using  $\Delta AIC_c$  (Burnham and Anderson 2002). All analyses were implemented in PRESENCE 6.9 (Hines 2006) to obtain maximum-likelihood parameter estimates. Preliminary analyses indicated that Canada Warbler occupancy dynamics differed between Chippewa and Superior; moreover, the dynamics differed between cover types within each forest. Therefore, we used 2 approaches to model Canada Warbler occupancy dynamics.

**Forest dynamics.** Candidate models for the first modeling approach were built to determine the land-cover and stand-level characteristics influencing occupancy dynamics in each national forest. For this analysis, national forests were analyzed separately and all stands within each forest were included in the analysis. Models were built using stand-level and land-cover covariates that were calculated at the 100 m and 500 m buffer scales. At each scale, we subset the variables into "stand-characteristic variables" (age, ground cover, shrub density, distance to road, logging disturbance, mean patch size within the buffer, and total edge within the buffer) and "land-cover variables" (percent upland conifer, upland deciduous, upland mixed, lowland conifer, open, and aquatic cover within the buffer; Appendix Table 1).

Occupancy models estimated the probabilities of initial site occupancy ( $\psi$ ), colonization ( $\gamma$ ), local extinction ( $\epsilon$ ), and detection ( $p$ ) (Appendix Table 1; MacKenzie et al. 2006). Here, colonization was defined as the event of a site being occupied during survey  $t$  when it had not been during survey  $t - 1$ . By contrast, local extinction was the event of a site being unoccupied during survey  $t$  when it had been occupied at survey  $t - 1$ . This type of model consists of a probability of occupancy estimated for the first survey's  $\psi_0$ , whereas subsequent occupancy states depend on the probability of colonization and local extinction between consecutive survey years (MacKenzie et al. 2006). We chose to model initial occupancy without covariates to focus investigation on rate parameters for this portion of the analysis (after Ferraz et al. 2007).

**Cover-type dynamics.** This portion of the analysis considered stands by cover type, in order to determine similarities and differences in drivers of occupancy

dynamics in each cover type. For example, the importance of ground cover may be similar in upland deciduous and upland conifer stands but may not have the same influence in lowland conifer stands. Models were subset into "stand-characteristic variables" (age, ground cover, shrub density, distance to road, logging disturbance, mean patch size within the buffer, total edge within the buffer, percent open habitat in 500 m buffer, and percent aquatic habitat in 500 m buffer) and "species co-occurrence variables" (abundance of potentially competing or positively interacting species, based on co-occurrence results; Appendix Table 2). Occupancy models for this analysis estimated the influence of covariates on  $\psi$  and  $\epsilon$  and also estimated  $p$  (Appendix Table 2; MacKenzie et al. 2006).

We used the same model-building approach for both analyses. First, we evaluated single predictor models and determined predictors with the highest model weight(s) based on  $AIC_c$  from each variable subset. The best predictors ( $w_i > 5\%$ ) were added to build a "full model"; predictors that were nonsignificant in the full model were removed to produce final occupancy models. If the final models included more than one predictor, we evaluated variables for collinearity and interactions. This procedure allowed us to minimize the number of models examined and avoid collinearity issues. Initial modeling of observer effects and habitat on  $p$  resulted in model convergence issues. For this reason, we chose to model detection probability as a function of year to represent differences in observers and habitats between seasons. We modeled  $p$  as a constant (without a covariate relationship) and as a function of year (Appendix Table 1); and, using the most general model structure for occupancy dynamics, we selected the covariance structure on  $p$  with the lowest  $AIC_c$  value. We then fit the remaining occupancy models separately for each candidate model subset (Appendix Tables 1 and 2). We used the parametric bootstrap procedure for assessing the goodness-of-fit of our best model (MacKenzie and Bailey 2004). Results are presented as means  $\pm$  SE.

## RESULTS

### Observation Summary

A total of 2,163 Canada Warblers were observed within a 100 m radius during 1995–2014 in a total of 243 stands. The majority of these detections (1,844) occurred in Superior in a total of 168 stands; another 319 were recorded in a total of 75 stands in Chippewa. Over the 20 yr of the study the average naive stand occupancy rates were 0.28 (range: 0.15–0.37) and 0.08 (range: 0.05–0.14) in Superior and Chippewa, respectively. Average observed frequency of stand occupancy (i.e. how frequently a stand was occupied) over 20 yr was 6.12 (range: 1–17) in Superior and 5.10 (range: 1–17) in Chippewa. Observed

mean abundance of Canada Warblers in occupied stands was 2.22 birds stand<sup>-1</sup> (range: 1.5–2.10) in Superior and 1.65 birds stand<sup>-1</sup> (range: 1.1–2.29) in Chippewa. Detections varied by forest-cover type in both forests. In Superior, detections were highest in mixed forest (0.78 detections stand<sup>-1</sup>), lowland conifer (0.70 detections stand<sup>-1</sup>), and upland deciduous (0.63 detections stand<sup>-1</sup>) cover types. In Chippewa, detections were highest in lowland conifer (0.44 detections stand<sup>-1</sup>) and upland conifer (0.12 detections stand<sup>-1</sup>).

### Co-occurrence Models

Co-occurrence analysis was conducted for each cover type in both national forests. Species that had high (ranked in top 5) checkerboard-unit values with Canada Warblers in  $\geq 3$  forest-cover types were used as covariates in occupancy models; these values can represent positive or negative associations with Canada Warblers. Six species fit these criteria: Black-and-white Warbler ( $n = 3,983$ ), Mourning Warbler ( $n = 3,342$ ), Magnolia Warbler ( $n = 2,611$ ), Black-throated Green Warbler ( $n = 3,644$ ), Blackburnian Warbler ( $n = 4,142$ ), and Hermit Thrush ( $n = 2,720$ ) (see Appendix Table 3).

### Occupancy Models

**Forest dynamics.** The final model for Chippewa showed that age, percent upland conifer in the 100 m buffer, and percent lowland conifer in the 500 m buffer were significant predictors of local extinction or site abandonment. The Chippewa final model indicated that the estimated extinction coefficient was lower in older stands, indicating a greater rate of habitat abandonment in younger stands over time ( $\beta_{\text{age}} = -0.22 \pm 0.13$ ; Figure 3A). Stands with greater percent lowland conifer cover in the 500 m buffer ( $\beta_{\text{lowlandcon500}} = -0.64 \pm 0.17$ ; Figure 3B) and stands with greater percent upland conifer cover in the 100 m buffer ( $\beta_{\text{uplandcon100}} = -0.28 \pm 0.11$ ; Figure 3C) also had lower probabilities of local extinction. The final model indicated that detection probability in Chippewa was constant over time.

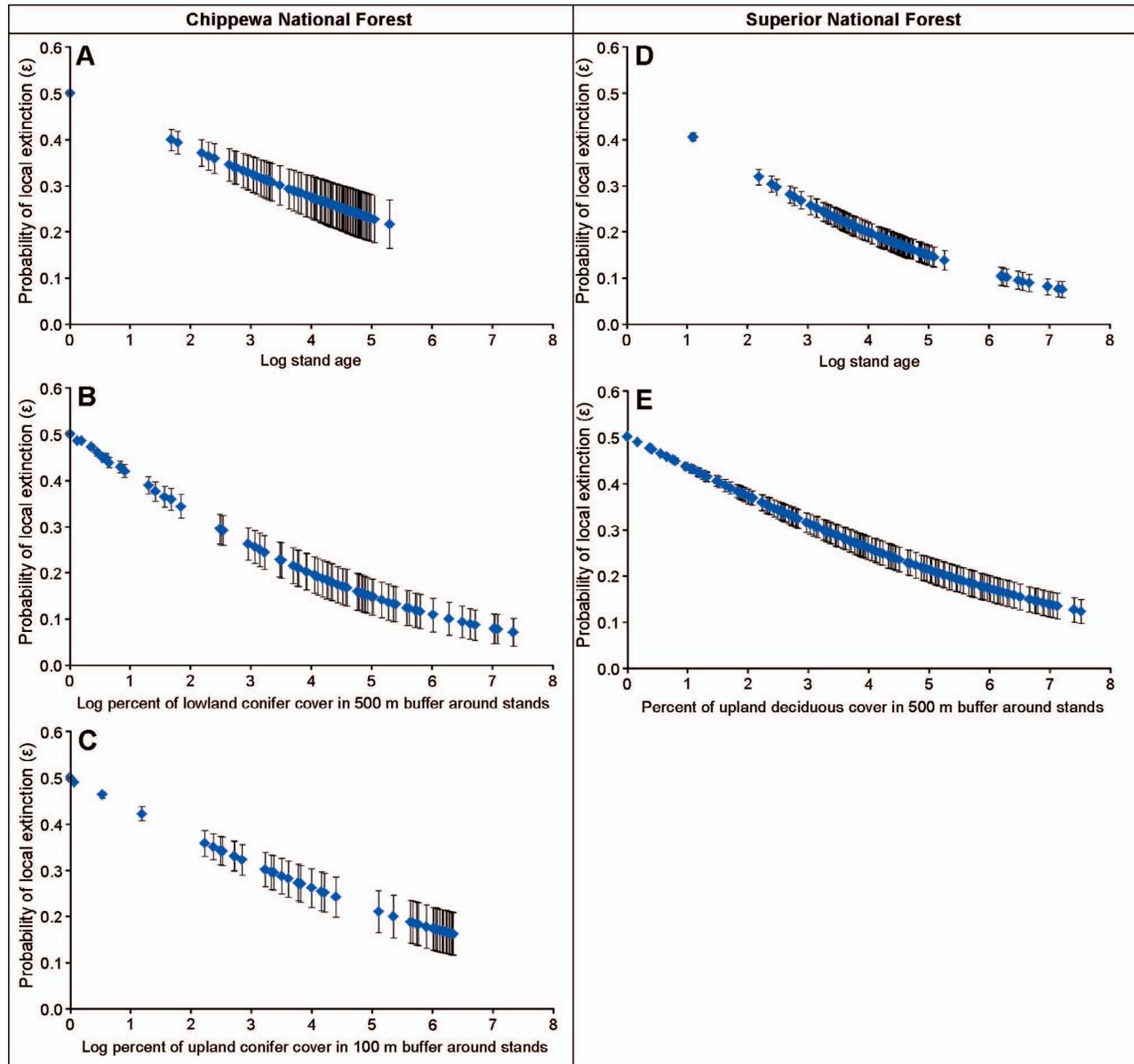
In Superior, stand age and percent upland deciduous forest in the 500 m buffer around the stands were included in the final model as predictors of local extinction. Similar to the final model for Chippewa, the results of the final model showed that local extinction was less common in older stands ( $\beta_{\text{age}} = -0.13 \pm 0.003$ ; Figure 3D) and that the probability of local extinction was lower in stands with a greater amount of upland deciduous habitat in the 500 m buffer around the stand ( $\beta_{\text{uplanddec500}} = -0.08 \pm 0.002$ ; Figure 3E). The top model in Superior indicated that detection probability for Canada Warblers varied by year. We used estimates from best models for each forest to derive average probability-of-occupancy estimates and standard deviations for each cover type (Figure 4).

**Cover-type dynamics.** Three land-cover types were analyzed in Chippewa: upland deciduous, upland conifer, and lowland conifer. An additional habitat type, mixed forest, was analyzed in Superior but excluded from Chippewa because of low representation. The best models for Chippewa indicate that age, percent open habitat in the 500 m buffer, and abundance of Black-and-white Warblers were significant covariates for occupancy and local extinction probabilities. In upland deciduous stands, probability of occupancy was higher in younger stands (average age = 41 yr; range: 5–89 yr). Probability of extinction decreased in stands with a greater percent open habitat in the 500 m buffer in upland deciduous stands ( $\beta_{\text{age}} = -0.59 \pm 0.09$ ;  $\beta_{\text{open500}} = -0.48 \pm 0.19$ ; Figure 5A, 5B). However, in lowland conifer stands, probability of occupancy decreased as the amount of open habitat in the 500 m buffer increased ( $\beta_{\text{open500}} = -0.34 \pm 0.19$ ; Figure 5C). Black-and-white Warbler abundance was negatively associated with Canada Warbler occupancy in upland conifer stands ( $\beta_{\text{BAWW}} = -1.60 \pm 0.32$ ; Figure 5D) in Chippewa; no habitat covariates were included in this cover type.

The best models in Superior indicated that age and mean patch size were important variables for local extinction. Hermit Thrush and Magnolia Warbler abundances also influenced occupancy. Specifically, younger stands had a higher probability of local extinction in upland deciduous ( $\beta_{\text{age}} = -0.31 \pm 0.15$ ; Figure 5E), lowland conifer ( $\beta_{\text{age}} = -0.14 \pm 0.04$ ; Figure 5G), and upland conifer ( $\beta_{\text{age}} = -0.34 \pm 0.16$ ; Figure 5I) stands in Superior. Hermit Thrush abundance negatively affected the probability of Canada Warbler occupancy in upland deciduous ( $\beta_{\text{HETH}} = -0.34 \pm 0.16$ ; Figure 5F) and upland conifer stands ( $\beta_{\text{HETH}} = -0.68 \pm 0.33$ ; Figure 5J). In lowland conifer stands, Magnolia Warbler abundance was positively associated with the probability of occupancy ( $\beta_{\text{MAWA}} = 0.45 \pm 0.16$ ; Figure 5H). In mixed forest stands, local extinction probabilities were lower in stands with larger patches of mixed forest habitat at the 100 m scale ( $\beta_{\text{mps100}} = -1.96$ , SE = 0.28; Figure 5K).

## DISCUSSION

Our results indicate that Canada Warblers utilize a variety of cover types. Canada Warbler occupancy was highest in mixed forest and lowland conifer stands (Figure 6A, 6B). These findings are consistent with the results of several studies that reported the species to be associated with a variety of forest types, but to be most common in wet, mixed deciduous–coniferous forest with a well-developed shrub layer (Conway 1999, Reitsma et al. 2008, 2010, Schmiegelow et al. 2014, Niemi et al. 2016). However, our results provide inference about processes associated with differential habitat use that extends our understanding of long-term habitat use over a large, dynamic landscape.

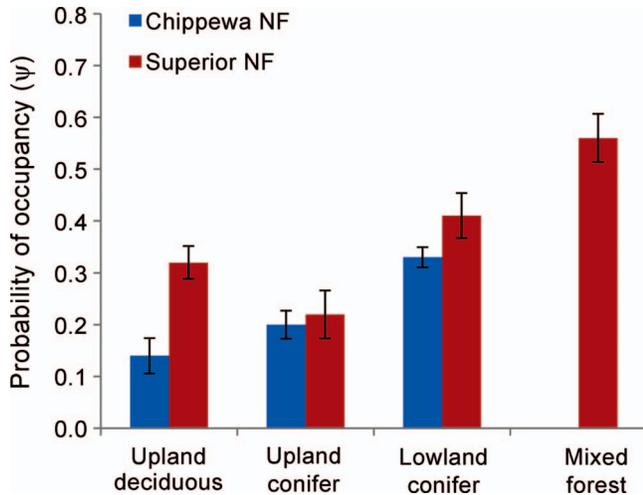


**FIGURE 3.** Predicted probabilities ( $\pm$  SE) of local extinction for Canada Warblers, based on final models for forest dynamics in Chippewa (A–C) and Superior (D–E) National Forests, in relation to (A) natural log of stand age in Chippewa; (B) natural log of percent lowland cover in 500 m buffer in Chippewa; (C) natural log of upland conifer cover in 100 m in Chippewa; (D) natural log of stand age in Superior; and (E) percent upland deciduous cover in 500 m buffer around stands in Superior.

### Forest Dynamics

Forest age significantly affected the probability of site abandonment (local extinction) in both national forests, indicating that the probability of local extinction is higher in younger forests or that persistence is greater in mature forest stands over time. These results were consistent across both national forests, even though the average age of surveyed stands differed—the average age of forests in Chippewa is 74 yr, compared to 112 yr in Superior. Throughout their range, Canada Warblers breed in mature

(>80 yr) forests with canopy gaps that promote a dense, well-developed shrub layer (Schieck et al. 1995, Enns and Siddle 1996, Cooper et al. 1997, Hobson and Bayne 2000b, Hobson et al. 2000, Schieck and Hobson 2000, Schieck et al. 2000, Cumming and Machtans 2001, Machtans and Latour 2003, Hannon et al. 2004, Lambert and Faccio 2005). Further, this species is positively associated with natural disturbances such as wind or tree-fall gaps (Hagan and Grove 1999, Mitchell 1999, Faccio 2003) and outbreaks of invasive insects such as the eastern spruce budworm



**FIGURE 4.** Predicted probabilities ( $\pm$  SE) of occupancy by cover type for Canada Warblers, based on estimates from final models for Chippewa and Superior National Forests (NF).

(*Choristoneura fumiferana*; Crawford and Jennings 1989), dynamics generally associated with mature forest stands. Our models suggest that older stands (>80 yr) provide stable long-term suitable habitat and thus have lower local extinction probabilities. Zlonis and Niemi (2014) reported that Canada Warblers were more abundant in unmanaged forests of the Boundary Waters Canoe Area Wilderness (BWCAW) compared with managed stands in Superior. Importantly, unmanaged stands in the BWCAW were, on average, older and more mixed; they had a greater variety in shrub density and tree size classes than stands in Superior, due to natural disturbances and gap dynamic processes (Frelich and Reich 1995, Zlonis and Niemi 2014).

Throughout its range, increases in local abundance of Canada Warblers in regenerating forests (i.e. 5–30 yr postdisturbance) following natural and anthropogenic disturbances have been reported (Titterton et al. 1979, Christian et al. 1996, Hobson and Schieck 1999, Drapeau et al. 2000, Hobson and Bayne 2000a, Schieck and Hobson 2000, Becker et al. 2012). Young forest stands likely provide temporary open and shrub-like habitats with complex ground cover that can increase Canada Warbler abundance and nesting success (Figure 6C; Schmiegelow et al. 1997, Goodnow and Reitsma 2011). However, extent of harvest, harvest type, and number of residual trees that remain postharvest likely influence the suitability, and the duration of suitability, of postharvest stands for Canada Warblers. For example, Becker et al. (2012) found that Canada Warblers showed positive selection for 3 types of timber harvest (clear-cut, heavy partial, and light partial harvests), yet response was greatest in sites with light partial harvest, owing to the combination of a well-developed shrub story and residual trees associated with this harvest type. Several studies have shown that the probability of local extinction

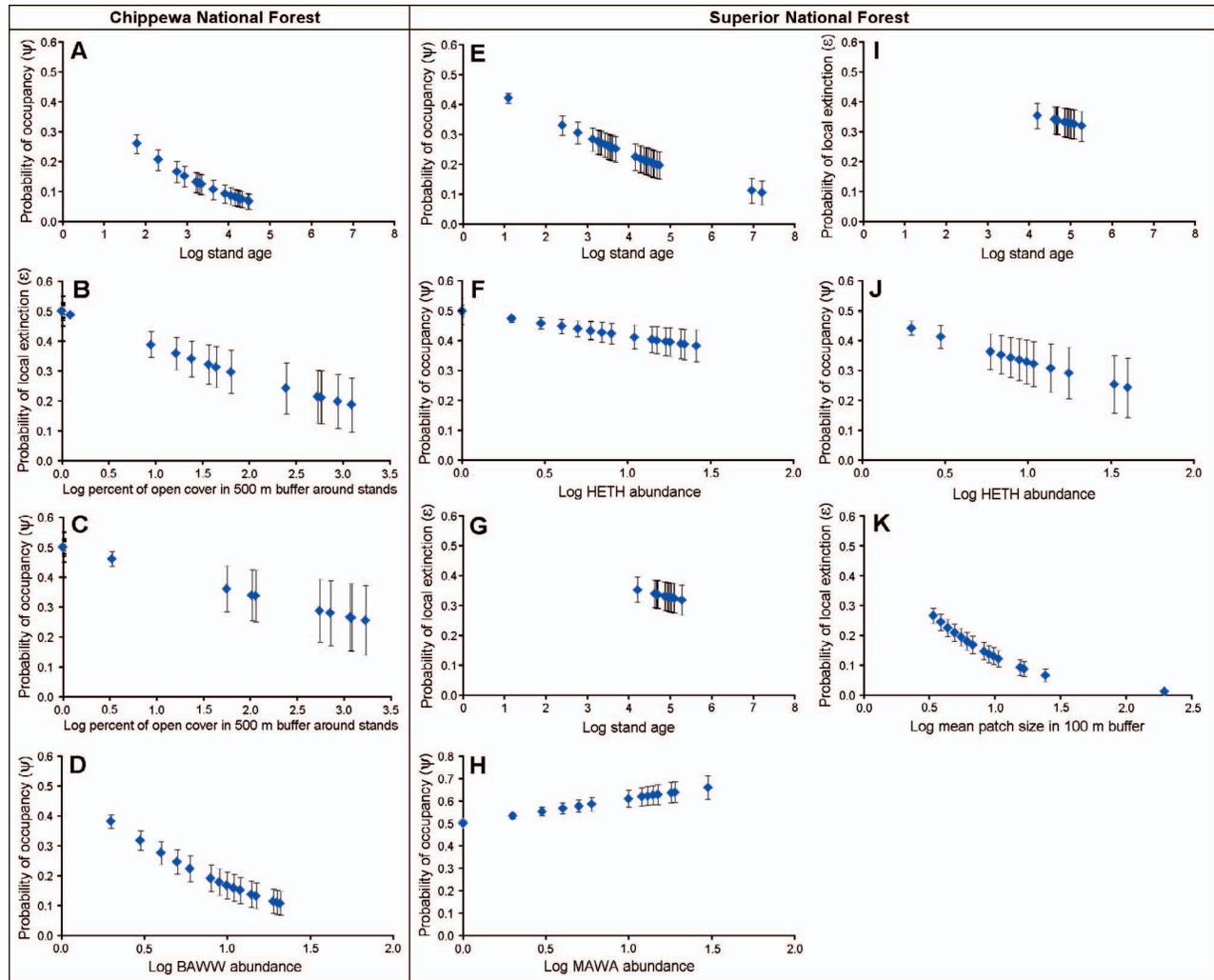
increases as habitat suitability decreases (Gates and Donald 2000, Broughton et al. 2013, Porter and Jarzyna 2013, Yntze et al. 2015); thus, the increased extinction estimates in early-successional stands suggest decreased habitat suitability for Canada Warblers, compared to mature stands. The increased probability of site abandonment in early-successional stands may be associated with postharvest stand characteristics (i.e. number of residual trees) or changes in stand characteristics that are associated with forest succession (i.e. shrub density).

The results of several previous studies show the importance of shrub density and complexity of ground cover for Canada Warblers (Schmiegelow et al. 1997, Hallworth et al. 2008b, Becker et al. 2012). However, because of the spatial extent and duration of our study, detailed vegetation data were not consistently available for all stands. The importance of age in our models likely illustrates the interaction between stand age, succession, and associated changes to shrub canopy and ground cover. Long-term experimental studies that include detailed hydrological and vegetation assessments of early-successional and mature stands will be beneficial for determining the factors associated with stand abandonment that occurs as a result of the stand aging, compared with abandonment when stand characteristics remain unchanged.

The type of land cover important to Canada Warbler occupancy dynamics differed between forests, but land-cover variables at the 500 m scale were included as covariates in the best models in both forests. This indicates the importance of the larger landscape matrix to Canada Warbler dynamics. In Superior a greater amount of upland deciduous habitat at the 500 m scale positively affected persistence, and in Chippewa a greater amount of lowland conifer at the 500 m scale and upland conifer at the 100 m scale had positive effects on species persistence. Results from Superior are consistent with the finding of Schmiegelow et al. (2014) that landscapes with a higher proportion of mixed wood and deciduous stands were more suitable for Canada Warblers. However, Schmiegelow et al.'s (2014) results also indicated that conifer stands were not selected by Canada Warblers across 3 bird conservation regions in Canada. This difference in reported habitat preference may be associated with the broader habitat classifications used by Schmiegelow et al. (2014) or may be a reflection of differences in habitat availability between the hemiboreal forests of Minnesota and the boreal forests in the northern region of the species' range.

### Cover-type Dynamics

Age, percent open (nonforest) cover type at the 500 m scale, mean patch size at the 100 m scale, Black-and-white Warbler abundance, Hermit Thrush abundance, and Magnolia Warbler abundance were the variables associated with the best occupancy models in this portion of the



**FIGURE 5.** Predicted probabilities ( $\pm$  SE) of occupancy and local extinction for Canada Warblers, based on final models for cover-type dynamics in Chippewa (A–D) and Superior (E–K) National Forests, in relation to (A) natural log of stand age in upland deciduous stands; (B) natural log of percent lowland cover in 500 m buffer around upland deciduous stands; (C) natural log of percent open cover in 500 m buffer around lowland conifer stands; (D) natural log of Black-and-white Warbler (BAWW) abundance in upland conifer stands; (E) natural log of stand age in upland deciduous stands; (F) natural log of Hermit Thrush (HETH) abundance in upland deciduous stands; (G) natural log of stand age in lowland conifer stands; (H) natural log of Magnolia Warbler (MAWA) abundance in lowland conifer stands; (I) natural log of HETH abundance in upland deciduous stands; (J) natural log of HETH abundance in upland conifer stands; and (K) natural log of mean patch size in mixed forest stands. Abundance was measured as the number of birds heard or observed in 100 m buffer around stands.



**FIGURE 6.** Representative (A) mixed forest, (B) lowland conifer, and (C) early-successional cover types occupied by Canada Warblers.

analysis. The relationship between age and the probability of local extinction was similar to results of the forest-level occupancy model in lowland conifer stands in Chippewa (average age = 129 yr) and upland conifer stands in Superior (average age = 89 yr); local extinction was lower in older stands.

In upland deciduous stands in Chippewa and Superior, stand age was negatively associated with Canada Warbler occupancy. The relationship between occupancy and stand age in upland deciduous stands seemingly contradicts the results reported above; however, these results speak to the differential dynamics that occurred between cover types. The average ages of upland deciduous stands surveyed in Chippewa (41 yr) and Superior (72 yr) were considerably less than the average ages of all stands surveyed in the two forests (74 yr and 112 yr, respectively). A large proportion of upland deciduous stands in both forests represents a “middle age class” with high canopy cover that does not allow for the development of complex subcanopy vegetation. In deciduous stands, this age class appears to be less suitable for Canada Warblers than younger age classes that are associated with a well-developed understory. It is likely that occupancy has a quadratic relationship with stand age in deciduous forest stands. The probability of local extinction is lowest (and habitat suitability is highest) in early-successional stands (0–30 yr) because of increased ground cover and shrub layers from harvest, and in mature stands (>80 yr) because of gap processes that increase subcanopy complexity; local extinction is highest (and habitat suitability lowest) in middle-aged (30–80 yr) deciduous stands. We included age as a quadratic term in preliminary modeling efforts, but these models had extensive convergence issues. Survey locations for the Minnesota monitoring program were distributed in a stratified random manner, so our study included relatively fewer early-successional and mature deciduous forest stands than middle-aged stands (Minnesota Forest Resource Council 2014). Conducting additional surveys that focus on early-successional and mature deciduous forest stands will be beneficial for assessing long-term dynamics in mature stands in Minnesota.

Probability of Canada Warbler occupancy was highest in mixed forest stands. The results reported here suggest that small patches of mixed forest stands had negative effects on species persistence. Area sensitivity in this species has been well documented in many studies, especially in the context of fragmentation of forests in an agricultural or urbanized landscape (Ambuel and Temple 1983, Robbins et al. 1989). However, the species has been reported to be relatively tolerant of habitat fragmentation that results from forest harvesting (Schmiegelow et al. 1997). Management plans that aim to create or maintain large extents of mixed forest stands will likely benefit Canada Warblers.

### Species Co-occurrence

Species co-occurrence may influence Canada Warbler occupancy. Our results indicated that in Superior, Magnolia Warbler abundance was positively associated with Canada Warbler occupancy in lowland conifer stands, and Hermit Thrush abundance was negatively associated with occupancy in upland conifer and upland deciduous stands. In Chippewa, Black-and-white Warbler abundance was negatively associated with occupancy of Canada Warblers in upland conifer stands. Several recent studies have shown that behavioral decisions based on species co-occurrence influence habitat selection and persistence in many species and are a result of a combination of competitive and positive interactions, often independent of habitat characteristics, at multiple spatial scales (Mönkkönen et al. 2004, Gotelli et al. 2010, Ricklefs 2013).

The relationship between Canada Warbler occupancy and species co-occurrence may reflect interspecific (positive and negative) interactions or preferences in habitat characteristics or may be spurious. The positive association between Magnolia Warbler abundance and Canada Warbler occupancy in lowland conifer stands is likely associated with commonalities in habitat use between the 2 species. Magnolia Warblers are often associated with regenerating clear-cuts (Titterton et al. 1979) and disturbed conifer stands with increased shrub layers (Burris and Haney 2006), similar to the preferences of Canada Warblers. Hermit Thrush and Black-and-white Warbler abundances were negatively associated with Canada Warbler occupancy. The mechanisms of these influences are unknown; they do not necessarily imply interspecific competition. Interestingly, in upland conifer stands of Chippewa, Black-and-white Warbler abundance was the only significant predictor of occupancy. Our models showed that Canada Warblers and Black-and-white Warblers occupied the same stands when Black-and-white Warbler abundance was low (<1.3 observations) but were less likely to occupy a stand in years with high (>1.9 observations) Black-and-white Warbler abundance. Both of these species nest on or near the ground and exhibit similar habitat preferences in Chippewa. Although there are no documented interactions between Canada Warblers and Black-and-white Warblers, several sources cite aggressive behavior by Black-and-white Warblers. For example, Morse (1970, 1989) reported that “on territory, [Black-and-white Warblers are] inclined to become aggressive toward other wood-warblers.” Similarly, the Hermit Thrush is a ground-nesting species and may limit available nest-site locations in certain habitats. The Hermit Thrush is not known to be an aggressive species (Dellinger et al. 2012); however, aggressive interactions among thrush species have been documented (Able and Noon 1976, Freeman and Montgomery 2016). Canada Warblers are among the last species to arrive on the breeding grounds, which may make them more vulnerable to exclusion by other ground-nesting

species that have already established territories and begun nesting. Alternatively, Hermit Thrush and Black-and-white Warbler abundance may be associated with untested biotic or abiotic factors, such as ground-cover substrate, which in turn influence Canada Warbler occupancy.

We caution that co-occurrence analysis was conducted using raw (unadjusted) species counts; potentially, differences in detectability among species could have biased the results. However, Etersson et al. (2009) reported that trends calculated from raw counts and detectability-adjusted counts did not differ, given large within-year sample sizes and standardized data-gathering methods, as were used in the present study. The detection results of Canada Warbler occupancy models may also support an argument for constant detectability. Continued research in this area will provide important information for assessing the relative influence of positive, negative, and neutral species co-occurrence on long-term population dynamics.

### Conclusions

Our results identify underlying processes associated with long-term habitat use across large, dynamic landscapes. This information provides insight for conservation and management efforts to restore Canada Warbler populations and highlights the importance of including multiple habitat types and scales in the conservation of species. Occupancy of Canada Warblers was highest in mixed forest stands and lowland conifer stands. Habitat management plans that maximize patch size of mixed aspen stands and minimize open areas in the matrix surrounding lowland conifer stands will likely increase the persistence of this species over time. The relationship between consistent occupancy and high survival and reproductive success has been reported in other species (Lee and Bond 2015, Dugger et al. 2016); however, these types of data were not collected as part of the current monitoring program. Future research focused on nesting success and survival in this study area will aid in understanding the relationship between occupancy and long-term demography of Canada Warblers and will improve future conservation efforts.

Our results also show that young forests can provide habitat for Canada Warblers on a short-term basis but that, as deciduous forest stands mature to the midsuccessional age class (31–80 yr old), the stands become less suitable for Canada Warblers. As deciduous stands age beyond conventional harvest periods (>75 yr old), stand heterogeneity increases through gap dynamic processes that provide suitable long-term Canada Warbler habitat. Our results suggest that forest management practices or natural disturbances that increase the density of understory vegetation and adequately retain canopy cover are beneficial to the species. Reitsma et al. (2010) suggested that Canada Warbler population declines likely occur in response to forest succession. Our results agree with this,

but the long-term population changes may also be linked with forest management practices and alterations to natural disturbance regimes. For example, short rotations of logging (40–70 yr) in relation to historical fire disturbances (Heinselman 1996) may prevent a high proportion of deciduous stands from reaching mature, mixed status. Those natural disturbance regimes likely provided habitats that contributed to the long-term persistence of Canada Warblers across the landscape.

Additional information on the species' breeding ecology (e.g., nesting success, postfledging activity, site fidelity) in relation to habitat and landscape context are also needed. Information on nesting success and food availability in different habitat types across large spatial scales would be an important addition to understanding mechanisms associated with occupancy dynamics. Importantly, logging disturbance was not included in final occupancy models, likely because of limitations in the availability of precise, consistent disturbance data throughout the duration of the study. However, in the eastern part of the species' range, recent studies found that certain logging disturbances positively influenced Canada Warblers. Given the important effects that forest age, percent open cover, and mean patch size had on Canada Warbler dynamics in the present study, we suggest that a large-scale, long-term experimental approach be used to assess the direct effects of harvest on Canada Warblers.

Extensive changes in habitats and landscapes are occurring in the central and northern portions of the Canada Warbler's breeding range, due to climate change, forest management, and agricultural and residential development (Mladenoff et al. 1997, Wolter and White 2002, Frelich and Reich 2009, Galatowitsch et al. 2009, Wells 2011, Sturtevant et al. 2014). These widespread changes signal the need for urgent conservation action for this species. The present study used data from a long-term, large-scale, forest-bird monitoring program to increase our understanding of Canada Warbler population dynamics in relation to habitat and landscape context. Our results describe the complexity of the spatial and temporal responses that drive Canada Warbler habitat occupancy, information that can help us make better forest management decisions and ultimately improve conservation of the species.

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**APPENDIX TABLE 1.** Candidate models in forest dynamics analysis used to build final models to assess Canada Warbler occupancy dynamics in Chippewa and Superior National Forests from 1995 to 2014. Models were built using stand-characteristic covariates and land-cover covariates that were calculated at the 100 m and 500 m buffer scales. Based on the results of the preliminary analysis, detectability ( $p$ ) was modeled as constant in Chippewa and was modeled with annual variation in Superior.

Candidate model	Colonization	Local extinction	$K_{\text{Chippewa}}$	$K_{\text{Superior}}$	Predicted effect
Null	$\gamma(\cdot)$	$\varepsilon(\cdot)$	4	4	.
	$\gamma(\cdot)$	$\varepsilon(\cdot)$	23	23	.
Annual variation	$\gamma(\text{year})$	$\varepsilon(\text{year})$	40	59	.
<b>100 m buffer</b>					
Stand-characteristic variables					
Age <sup>a</sup>	$\gamma(\text{age})$	$\varepsilon(\cdot)$	4	23	+
	$\gamma(\cdot)$	$\varepsilon(\text{age})$	4	23	-
Ground cover <sup>a</sup>	$\gamma(\text{grcov})$	$\varepsilon(\cdot)$	4	23	+
	$\gamma(\cdot)$	$\varepsilon(\text{grcov})$	4	23	-
Shrub density <sup>a</sup>	$\gamma(\text{shrub})$	$\varepsilon(\cdot)$	4	23	+
	$\gamma(\cdot)$	$\varepsilon(\text{shrub})$	4	23	-
Distance to road	$\gamma(\text{disrd})$	$\varepsilon(\cdot)$	4	23	+
	$\gamma(\cdot)$	$\varepsilon(\text{disrd})$	4	23	-
Logging disturbance (500 m)	$\gamma(\text{logdist100})$	$\varepsilon(\cdot)$	4	23	+
	$\gamma(\cdot)$	$\varepsilon(\text{logdist100})$	4	23	-
Mean patch size (100 m) <sup>a</sup>	$\gamma(\text{mps100})$	$\varepsilon(\cdot)$	4	23	+
	$\gamma(\cdot)$	$\varepsilon(\text{mps100})$	4	23	-
Total edge (100 m)	$\gamma(\text{te100})$	$\varepsilon(\cdot)$	4	23	-
	$\gamma(\cdot)$	$\varepsilon(\text{te100})$	4	23	+
Land-cover variables					
Upland conifer (100 m) <sup>a</sup>	$\gamma(\text{upcon100})$	$\varepsilon(\cdot)$	4	23	.
	$\gamma(\cdot)$	$\varepsilon(\text{upcon100})$	4	23	.
Upland deciduous (100 m)	$\gamma(\text{upcon100})$	$\varepsilon(\cdot)$	4	23	.
	$\gamma(\cdot)$	$\varepsilon(\text{upcon100})$	4	23	.
Upland mixed forest (100 m) <sup>a</sup>	$\gamma(\text{upmix100})$	$\varepsilon(\cdot)$	4	23	.
	$\gamma(\cdot)$	$\varepsilon(\text{upmix100})$	4	23	.
Lowland conifer (100 m) <sup>a</sup>	$\gamma(\text{llcon100})$	$\varepsilon(\cdot)$	4	23	.
	$\gamma(\cdot)$	$\varepsilon(\text{llcon100})$	4	23	.
Aquatic (%) (100 m) <sup>a</sup>	$\gamma(\text{wet100})$	$\varepsilon(\cdot)$	4	23	+
	$\gamma(\cdot)$	$\varepsilon(\text{wet100})$	4	23	-
Open (%) (100 m) <sup>a</sup>	$\gamma(\text{open100})$	$\varepsilon(\cdot)$	4	23	-
	$\gamma(\cdot)$	$\varepsilon(\text{open100})$	4	23	+
<b>500 m buffer</b>					
Stand-characteristic variables					
Logging disturbance (500 m)	$\gamma(\text{logdist500})$	$\varepsilon(\cdot)$	4	23	+
	$\gamma(\cdot)$	$\varepsilon(\text{logdist500})$	4	23	-
Mean patch size (500 m) <sup>a</sup>	$\gamma(\text{mps500})$	$\varepsilon(\cdot)$	4	23	+
	$\gamma(\cdot)$	$\varepsilon(\text{mps500})$	4	23	-
Total edge (500 m)	$\gamma(\text{te500})$	$\varepsilon(\cdot)$	4	23	-
	$\gamma(\cdot)$	$\varepsilon(\text{te500})$	4	23	+
Land-cover variables					
Upland conifer (500 m) <sup>a</sup>	$\gamma(\text{upcon500})$	$\varepsilon(\cdot)$	4	23	.
	$\gamma(\cdot)$	$\varepsilon(\text{upcon500})$	4	23	.
Upland deciduous (500 m)	$\gamma(\text{upcon500})$	$\varepsilon(\cdot)$	4	23	.
	$\gamma(\cdot)$	$\varepsilon(\text{upcon500})$	4	23	.
Upland mixed forest (500 m) <sup>a</sup>	$\gamma(\text{upmix500})$	$\varepsilon(\cdot)$	4	23	.
	$\gamma(\cdot)$	$\varepsilon(\text{upmix500})$	4	23	.
Lowland conifer (500 m) <sup>a</sup>	$\gamma(\text{llcon500})$	$\varepsilon(\cdot)$	4	23	.
	$\gamma(\cdot)$	$\varepsilon(\text{llcon500})$	4	23	.
Aquatic (%) (500 m) <sup>a</sup>	$\gamma(\text{wet})$	$\varepsilon(\cdot)$	4	23	+
	$\gamma(\cdot)$	$\varepsilon(\text{wet})$	4	23	-
Open (%) (500 m) <sup>a</sup>	$\gamma(\text{open500})$	$\varepsilon(\cdot)$	4	23	-
	$\gamma(\cdot)$	$\varepsilon(\text{open500})$	4	23	+

<sup>a</sup> Natural log transformation was used prior to analysis.

**APPENDIX TABLE 2.** Candidate models in cover-type dynamics analysis used to build final models to assess Canada Warbler occupancy dynamics in Chippewa and Superior National Forests from 1995 to 2014. Models were built using stand characteristics and species co-occurrence covariates. Species co-occurrence covariates were included on the basis of co-occurrence analysis. Based on the results of the preliminary analysis, detectability ( $p$ ) was modeled as constant in both forests and in all forest-cover types. Upland deciduous, upland conifer, and lowland conifer cover types were modeled in both forests; mixed forest-cover type was modeled in Superior only. Scientific names of species are given in Appendix Table 3.

Candidate model	Occupancy	Local extinction	Detection	$K$	Predicted effect
Null	$\psi(.)$	$\varepsilon(.)$	$p(.)$	3	.
Annual variation	$\psi(.)$	$\varepsilon(\text{year})$	$p(.)$	21	.
	$\psi(\text{year})$	$\varepsilon(.)$	$p(.)$	22	.
Stand-characteristic variables					
Age <sup>a</sup>	$\psi(\text{age})$	$\varepsilon(.)$	$p(.)$	3	+
	$\psi(.)$	$\varepsilon(\text{age})$	$p(.)$	3	-
Ground cover <sup>a</sup>	$\psi(\text{grcov})$	$\varepsilon(.)$	$p(.)$	3	+
	$\psi(.)$	$\varepsilon(\text{grcov})$	$p(.)$	3	-
Shrub density <sup>a</sup>	$\psi(\text{shrub})$	$\varepsilon(.)$	$p(.)$	3	+
	$\psi(.)$	$\varepsilon(\text{shrub})$	$p(.)$	3	-
Distance to road	$\psi(\text{disrd})$	$\varepsilon(.)$	$p(.)$	3	+
	$\psi(.)$	$\varepsilon(\text{disrd})$	$p(.)$	3	-
Aquatic (%) (500 m) <sup>a</sup>	$\psi(\text{wet})$	$\varepsilon(.)$	$p(.)$	3	+
	$\psi(.)$	$\varepsilon(\text{wet})$	$p(.)$	3	-
Open (%) (500 m) <sup>a</sup>	$\psi(\text{open500})$	$\varepsilon(.)$	$p(.)$	3	-
	$\psi(.)$	$\varepsilon(\text{open500})$	$p(.)$	3	+
Mean patch size (100 m) <sup>a</sup>	$\psi(\text{mps100})$	$\varepsilon(.)$	$p(.)$	3	+
	$\psi(.)$	$\varepsilon(\text{mps100})$	$p(.)$	3	-
Mean patch size (500 m) <sup>a</sup>	$\psi(\text{mps500})$	$\varepsilon(.)$	$p(.)$	3	+
	$\psi(.)$	$\varepsilon(\text{mps500})$	$p(.)$	3	-
Total edge (100 m)	$\psi(\text{te100})$	$\varepsilon(.)$	$p(.)$	3	-
	$\psi(.)$	$\varepsilon(\text{te100})$	$p(.)$	3	+
Total edge (500 m)	$\psi(\text{te500})$	$\varepsilon(.)$	$p(.)$	3	-
	$\psi(.)$	$\varepsilon(\text{te500})$	$p(.)$	3	+
Species co-occurrence variables					
Black-and-white Warbler <sup>a</sup>	$\psi(\text{BAWW})$	$\varepsilon(.)$	$p(.)$	3	.
Blackburnian Warbler <sup>a</sup>	$\psi(\text{BLBW})$	$\varepsilon(.)$	$p(.)$	3	.
Black-throated Green Warbler <sup>a</sup>	$\psi(\text{BTNW})$	$\varepsilon(.)$	$p(.)$	3	.
Hermit Thrush <sup>a</sup>	$\psi(\text{HETH})$	$\varepsilon(.)$	$p(.)$	3	.
Magnolia Warbler <sup>a</sup>	$\psi(\text{MAWA})$	$\varepsilon(.)$	$p(.)$	3	.
Mourning Warbler <sup>a</sup>	$\psi(\text{MOWA})$	$\varepsilon(.)$	$p(.)$	3	.

<sup>a</sup> Natural log transformation was used prior to analysis.

**APPENDIX TABLE 3.** Bird species and C-scores (see text) from tests for nonrandom patterns of co-occurrence with Canada Warblers in Chippewa and Superior National Forests. The C-score index was used as a quantitative co-occurrence index to determine the probability of all species' co-occurrence with Canada Warblers. C-scores were standardized using the mean of simulated indices for comparison between forest-cover types. Species in bold are those that had high (ranked in top 5) checkerboard-unit values with Canada Warblers in  $\geq 3$  cover types and were used as covariates in occupancy models.

Forest-cover type	Bird species	C-score
<b>Chippewa</b>		
Upland deciduous	<b>Black-and-white Warbler (<i>Mniotilta varia</i>)</b>	3.21
	<b>Mourning Warbler (<i>Geothlypis philadelphia</i>)</b>	2.75
	Red-breasted Nuthatch ( <i>Sitta canadensis</i> )	2.75
	Swamp Sparrow ( <i>Melospiza georgiana</i> )	2.48
	<b>Magnolia Warbler (<i>Setophaga magnolia</i>)</b>	2.06
Upland mixed	Ovenbird ( <i>Seiurus aurocapilla</i> )	6.67
	<b>Black-and-white Warbler</b>	4.00
	<b>Mourning Warbler</b>	4.00
	<b>Hermit Thrush (<i>Catharus guttatus</i>)</b>	3.33
	<b>Blackburnian Warbler (<i>Setophaga fusca</i>)</b>	2.67
Upland conifer	<b>Black-throated Green Warbler (<i>Setophaga virens</i>)</b>	5.07
	<b>Blackburnian Warbler</b>	3.16
	Brown Creeper ( <i>Certhia americana</i> )	2.63
	<b>Hermit Thrush</b>	2.37
	<b>Magnolia Warbler</b>	2.30
Lowland conifer	<b>Black-and-white Warbler</b>	5.88
	Black-capped Chickadee ( <i>Poecile atricapillus</i> )	3.78
	Ruby-throated Hummingbird ( <i>Archilochus colubris</i> )	3.78
	Brown Creeper	3.78
	Song Sparrow ( <i>Melospiza melodia</i> )	2.94
<b>Superior</b>		
Upland deciduous	<b>Black-throated Green Warbler</b>	2.13
	<b>Blackburnian Warbler</b>	1.93
	American Robin ( <i>Turdus migratorius</i> )	1.82
	<b>Mourning Warbler</b>	1.64
	<b>Hermit Thrush</b>	1.47
Upland mixed	Chestnut-sided Warbler ( <i>Setophaga pensylvanica</i> )	2.63
	Winter Wren ( <i>Troglodytes hiemalis</i> )	2.26
	<b>Blackburnian Warbler</b>	1.64
	Chipping Sparrow ( <i>Spizella passerina</i> )	1.50
	<b>Hermit Thrush</b>	1.50
Upland conifer	<b>Magnolia Warbler</b>	3.16
	Nashville Warbler ( <i>Oreothlypis ruficapilla</i> )	3.16
	Least Flycatcher ( <i>Empidonax minimus</i> )	2.84
	Chestnut-sided Warbler	2.53
	Pileated Woodpecker ( <i>Dryocopus pileatus</i> )	2.53
Lowland conifer	Ruffed Grouse ( <i>Bonasa umbellus</i> )	4.74
	Song Sparrow	4.15
	Eastern Wood-Pewee ( <i>Contopus virens</i> )	3.16
	Winter Wren	2.17
	<b>Black-throated Green Warbler</b>	1.98