Research Paper

Understory structure and heterospecifics influence the occupancy of a ground-nesting species of conservation concern, the Canada Warbler

Gordon W. Dimmig[1], *Christopher Rota*[1], *Petra Wood*[2] *and Christopher M. Lituma*[1]

[1]Division of Forestry and Natural Resources, West Virginia University, Morgantown, West Virginia, USA, [2]U.S. Geological Survey, West Virginia Cooperative Fish and Wildlife Research Unit, West Virginia University, Morgantown, WV, USA

ABSTRACT. Forest structure and composition in eastern U.S. forests are changing because of forest regeneration after farmland abandonment, less frequent occurrence of severe disturbances, and climate change. Some of these changes may disproportionally affect birds that rely on gap dynamics or other forest canopy disturbances to create understory habitat. The Canada Warbler (*Cardellina canadensis*) is one such understory specialist that has undergone consistent declines. We assessed environmental and interspecific factors associated with Canada Warbler space use in its southern breeding distribution to understand potential causes of population declines and inform conservation efforts. We evaluated Canada Warbler occupancy from 840 point count surveys conducted in 2017 and 2018 at 470 unique locations (79% of locations surveyed in both years) throughout Monongahela National Forest, West Virginia, USA. We modeled Canada Warbler occupancy probability as a function of environmental variables and included Black-throated Blue Warbler (*Setophaga caerulescens*) and Hermit Thrush (*Catharus guttatus*) as interacting species because all three species exhibit similar habitat preferences. Canada Warblers were most likely to occur in areas with rhododendron (*Rhododendron maximum*) density > 0.27 stems/ m² and within 3 m of riparian areas (streams and wetlands). They were also more likely to occur in mid-elevation (highest occupancy at 930 m) northern hardwood forests when Black-throated Blue Warblers were also present. Black-throated Blue Warblers were most likely to occupy mid-elevation sites with high shrub density, whereas Hermit Thrushes were more likely to occupy high-elevation, old-age forests. Potential management actions could focus on conserving riparian areas in northern hardwood forests, especially those with dense rhododendron thickets. Such potential actions could also be beneficial across the entire elevation range we explored within the region (500–1300 m). Canada Warblers may be benefiting from the recent spread of rhododendron habitats and northern hardwood forest types within West Virginia.

Influence de la structure du sous-étage et des hétérospécifiques sur la présence d'une espèce nichant au sol et dont la conservation est préoccupante, la Paruline du Canada

RÉSUMÉ. La structure et la composition des forêts de l'Est des États-Unis changent en raison de la régénération des forêts à la suite de l'abandon des terres agricoles, de l'avènement moins fréquent de perturbations graves et des changements climatiques. Certains de ces changements peuvent affecter de manière disproportionnée les oiseaux qui dépendent de la dynamique des trouées ou d'autres perturbations du couvert forestier pour qu'un habitat de sous-bois se crée. La Paruline du Canada (*Cardellina canadensis*) est l'une de ces spécialistes de sous-bois dont les populations ont subi des baisses constantes. Nous avons évalué les facteurs environnementaux et interspécifiques associés à l'utilisation de l'espace par la Paruline du Canada dans la partie méridionale de son aire de reproduction afin de comprendre les causes potentielles des baisses de population et d'orienter les mesures de conservation. Nous avons évalué la présence de la Paruline du Canada à partir de 840 dénombrements par points d'écoute menés en 2017 et 2018 à 470 sites (79 % des sites étudiés les deux années) dans la Monongahela National Forest, en Virginie-Occidentale, aux États-Unis. Nous avons modélisé la probabilité de présence de la Paruline du Canada en fonction de variables environnementales et avons ajouté la Paruline bleue (Setophaga caerulescens) et la Grive solitaire (*Catharus guttatus*) en tant qu'espèces en interaction, car les trois espèces présentent des préférences d'habitat similaires. Les Parulines du Canada étaient plus susceptibles de se trouver dans des secteurs où la densité de rhododendrons (*Rhododendron maximum*) était > 0,27 tiges/m² et à moins de 3 m de zones riveraines (cours d'eau et milieux humides). Elles étaient également plus susceptibles d'être présentes dans les forêts de feuillus du nord d'altitude moyenne (présence jusqu'à 930 m) lorsque les Parulines bleues étaient également présentes. La Paruline bleue était plus susceptible d'occuper des sites d'altitude moyenne avec une forte densité d'arbustes, tandis que la Grive solitaire était plus susceptible d'occuper des forêts anciennes d'altitude élevée. Les mesures de gestion potentielles devraient porter sur la conservation de zones riveraines dans les forêts de feuillus du nord, en particulier celles qui présentent des fourrés denses de rhododendrons. Ces mesures potentielles pourraient également être bénéfiques dans toute la gamme d'altitudes que nous avons explorée dans la région (500-1300 m). Les Parulines du Canada bénéficient sans doute de l'expansion récente des milieux de rhododendrons et des types de forêts de feuillus du nord en Virginie-Occidentale.

Correspondent author: Christopher Rota, PO Box 6125, Morgantown, WV 26506, christopher.rota@mail.wvu.edu

INTRODUCTION

Forest structure and composition are critical determinants of habitat use by birds (Sherry and Holmes 1985). Forests are dynamic ecosystems, and several land-use and disturbance trends have been changing the structure and composition of forested environments within eastern USA for several decades. Many forested habitats within the eastern United States are subject to fragmentation or conversion, for example, because of oil and gas development (Farwell et al. 2019) or urbanization (Lepczyk and Warren 2012). Simultaneously, there is a general trend within eastern U.S. forests toward less frequent occurrence of severe disturbances such as wildfire and flooding (DeGraaf and Yamasaki 2003). This decline in naturally occurring disturbances parallels increasing forest area and age in the northeastern United States, which is, in part, due to farm abandonment and declining regional hardwood timber production (Trani et al. 2001, Morin and Widmann 2015, Oswalt et al. 2019). In addition to the changing structure of eastern forests, the composition is changing in favor of mesophytic species such as American Beech (*Fagus grandifolia*), perhaps as a consequence of climate change (Bose et al. 2017). Against this backdrop of changing forest structure and composition is the decline of many eastern forest bird species, some of which are associated with gap dynamics (e.g., Cerulean Warbler *Setophaga cerulea;* Perkins and Wood 2014) or other forest disturbances such as fire or flooding (DeGraaf and Yamasaki 2003). Understanding how species may be affected by changing forest conditions will be critical for understanding causes of declines in many forest-associated birds.

The Canada Warbler (*Cardellina canadensis*) is one such species that may be affected by structural and compositional changes in eastern U.S. forests. Canada Warblers are understory specialists, and forest maturation may contribute to population declines because forests that reach mid-successional stages often have limited understory structure necessary for this species (Franzreb and Rosenberg 1997, USDA 2011, Oswalt and Smith 2014). Indeed, this species has experienced average range-wide declines of 2% annually since 1966, amounting to a 63% total decline over the 50-yr period (Sauer et al. 2017). Wilson et al. (2018) report that the steepest declines are occurring in the southeastern portion of the species' range, which includes provinces adjacent to the Great Lakes within Canada, and the Appalachian mountains within the United States. As a result, it is listed as a species of management concern by the U.S. Fish and Wildlife Service (USFWS 2008) and threatened in Canada (COSEWIC 2008), and is a species of conservation concern in states across the northern United States (e.g., a Priority 1 species within West Virginia, meaning it is a primary focus for conservation activities; WVDNR 2015).

As understory specialists, Canada Warblers consistently occupy forested areas with high densities of shrubs and small stems (Sodhi and Paszkowski 1995, Chace et al. 2009, Ball et al. 2016). Because Canada Warblers are ground nesters, a dense understory is important for nesting habitat (Goodnow and Reitsma 2011), supports high Canada Warbler densities (Hobson and Bayne 2000), and is selected by the first males arriving on the breeding grounds (Hallworth et al. 2008b). The well-developed understory layer preferred by this species often forms in response to canopy openings created by disturbances that allow sunlight to reach the forest floor, which encourages herbaceous and woody plant regeneration. Given the strong association of this species with dense shrubby understories, timber harvest has often been recommended as a method for creating Canada Warbler habitat (Hagan et al. 1997, Becker et al. 2012). Indeed, Canada Warblers use harvested areas throughout their range to varying degrees depending on the size and intensity of harvest (Hagan et al. 1997, King and DeGraaf 2000, Weakland et al. 2002, Hallworth et al. 2008a, Becker et al. 2012, Harding et al. 2017, Westwood et al. 2020).

In addition to changes associated with aging forests, Canada Warblers may also be at risk from changes in forest composition and structure due to climate change. The Appalachian Mountains of the eastern United States constitute the trailing edge of the breeding distribution of Canada Warblers, and the species is largely limited to high-elevation areas within this region (Reitsma et al. 2009). Forest composition is strongly associated with climate and elevation in this region, with forest types such as spruce-fir only occurring within suitable climates at relatively high elevations (Butler et al. 2015). Within the Appalachian region, climate change is projected to reduce suitability for tree species that occur at high elevations (Butler et al. 2015), leading to potential changes in forest composition and structure, with potentially cascading effects for forest birds. Understanding how the Canada Warbler distribution is related to elevation and forest type will provide critical insight into the species' potential response to changes in forest structure and composition that are expected to occur because of climate change.

Heterospecific interactions can also affect species' spatial distributions (Gotelli et al. 2010, Ricklefs 2013), including Canada Warblers (Grinde and Niemi 2016). When evaluating habitat relationships, therefore, it is important to understand the role of potentially interacting species in influencing distributions, given that Canada Warblers are likely responding to a mix of environmental effects and interspecific interactions. Species interactions can affect bird occurrence both positively (Forsman et al. 2002) and negatively through direct encounters and indirect competition for resources (Gotelli et al. 2010). Within the Appalachian region, some songbird species share similar preferences for a dense shrub layer, including Black-throated Blue Warbler (*Setophaga caerulescens*) in lower elevation deciduous forests (Holway 1991), and Hermit Thrush (*Catharus guttatus*) in high-elevation mixed and coniferous forests (Martin and Roper 1988, Dellinger et al. 2007). Both Canada Warbler and Hermit Thrush are ground-nesting species, and competition for similar resources may have led to previous observations of negative correlations between the two species' occurrences (Grinde and Niemi 2016). Similarly, both Canada Warblers and Black-throated Blue Warblers forage and nest in dense understory shrubs, which led Sabo (1980) to suggest that these two species may compete for resources. Canada Warblers on breeding grounds often exhibit aggression and territoriality toward other birds, and these encounters may limit their use of otherwise suitable habitat (Cody 1981, Grinde and Niemi 2016). Thus, accounting for potential interspecific interactions will be important in more fully understanding factors affecting Canada Warbler space use.

Here, we simultaneously examined environmental and interspecific correlates of Canada Warblers within West Virginia,

Fig. 1. Transect locations for sampling Canada Warbler (*Cardellina canadensis*), Black-throated Blue Warbler (*Setophaga caerulescens*), and Hermit Thrush (*Catharus guttatus*) within Monongahela National Forest, West Virginia, USA during the 2017 and 2018 breeding seasons. Transects were stratified across three elevation zones (< 853 m, 853–1158 m, and > 1158 m).
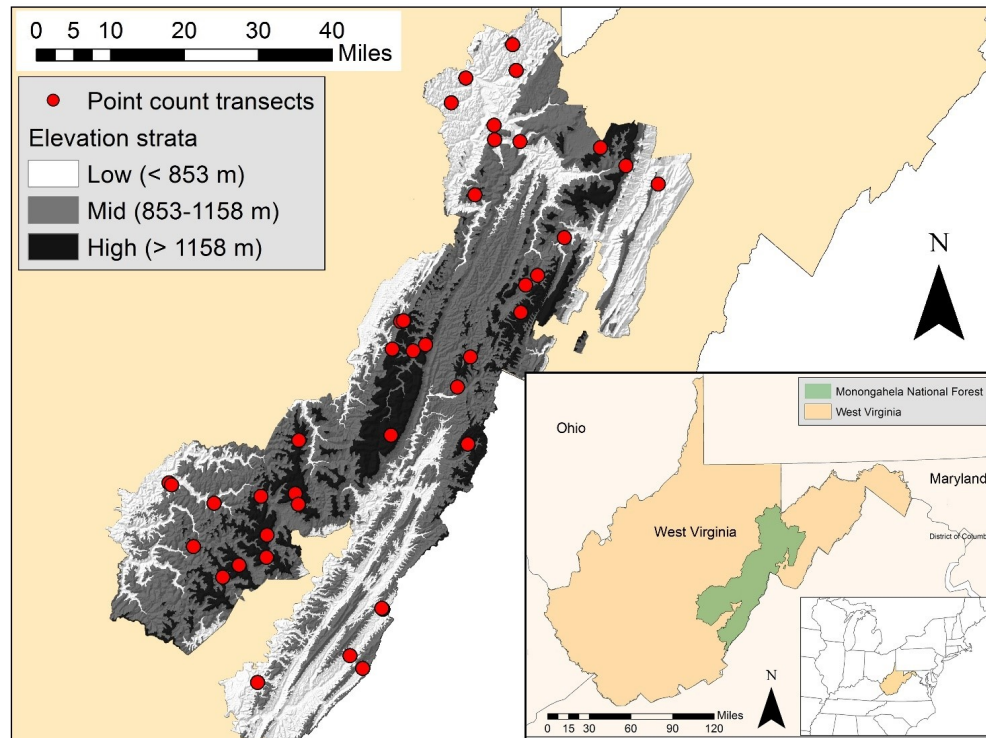
which is the only state with an apparently increasing population of Canada Warblers (Sauer et al. 2017). Assessing Canada Warbler occupancy in the central Appalachian Mountains may shed light on the factors that are driving apparent regional population growth amid range-wide declines. Despite the apparent increase in abundance, only two studies have examined Canada Warblers in the central Appalachians, and both investigated their habitat use primarily in harvested areas (Weakland et al. 2002, Becker et al. 2012). However, the amount of area managed through timber harvesting has been declining within the central Appalachians (Morin and Widmann 2015), and there is a need to assess habitat relationships in unmanaged forest conditions. We hypothesized that Canada Warblers are: (1) more likely to occur in forested areas with high shrub density, including recently harvested areas; (2) most likely to occur at elevations > 850 m (Harding et al. 2017); (3) most likely to occur in forest types that are more common farther north such as northern hardwood forests, which include species such as sugar maple (*Acer saccharum*) and American beech, and red spruce-eastern hemlock (*Picea rubens* and *Tsuga canadensis,* respectively) forests; and (4) negatively associated with potential competitors such as Black-throated Blue Warblers and Hermit Thrushes. Evaluating factors affecting the Canada Warbler distribution in the central Appalachians may give insight into how changing forest composition and structure in northeastern U.S. forests are affecting this and other forest bird species.

METHODS

Study area

The study occurred throughout the Monongahela National Forest (MNF), which is situated in the central Appalachians within West Virginia (Fig. 1). The MNF covers approximately 372,000 ha, with elevation of 300–1482 m (USDA 2011). Vegetation conditions vary longitudinally because of the orographic effect and by elevation. While the western part of the MNF receives > 150 cm of annual rainfall that produces moist forest conditions, the eastern portion receives half as much rainfall, leading to a greater proportion of dry oak-pine forests (USDA 2011). Forests in the MNF are categorized into four major types that are distributed along the elevation gradient: mixed mesophytic forests typically occur below 900 m on the west side of the mountains, oak-pine forests typically occur at low elevations on the east side of the mountains, northern hardwood forests typically occur between 900 and 1150 m, and red spruce forests tend to occur above 1150 m (DeMeo 1999). As elevation increases, forests transition from oak-pine and mixed mesophytic forests to northern hardwood forests (USDA 2011). At the highest elevations, remnant boreal forests are often found, characterized by thick stands of red spruce (Cogbill and White 1991, USDA 2011). Rhododendron (*Rhododendron maximum*) is a common understory shrub, often forming dense thickets. A majority of MNF land comprises 70–100 year-old stands, with high regional

tree diversity (USDA 2011). MNF harvests timber on a small and declining portion of public land, with the amount of land subject to timber harvest making up < 0.2% of the total MNF area.

Point count sampling

We evaluated Canada Warbler, Black-throated Blue Warbler, and Hermit Thrush distributions throughout the MNF by conducting 10-min, unlimited-radius, point count surveys. We conducted 380 point counts between 18 May and 15 July 2017, and 460 point counts during the same date range in 2018. A total of 370 sites were sampled in both years, which translates to 470 unique point count survey locations. One observer, who was highly skilled in bird identification and distance estimation, conducted all surveys from ~0.25 h before sunrise to no later than 4 h after sunrise on days without rain, heavy fog, or high wind, following the general guidelines outlined by Ralph et al. (1995). We recorded all individuals once, only the first time they were seen or heard during the 10-min survey, and classified each survey into one of two time intervals: 0–5 min or > 5–10 min (Ralph et al. 1995). With this removal sampling method, detection probability can be estimated from a single visit per year (Farnsworth et al. 2002, Rota et al. 2009). We used this approach because the closure assumption is more likely to be met when replicate surveys are conducted close in time (Rota et al. 2009), and visiting sites once per year allowed us to survey more locations, which is important when surveying for uncommon species such as the Canada Warbler (MacKenzie and Royle 2005). Additionally, this design follows historic protocols that have consistently been used to sample birds within the MNF for more than two decades.

Selection of point count sites

Given the importance of elevation in shaping Canada Warbler distributions in the central Appalachians, we stratified sampling points into three elevation gradients: < 853 m, 853–1158 m, and > 1158 m (Fig. 1). We chose the 853-m break point because it is the suggested lower limit for Canada Warblers in the Appalachians (Harding et al. 2017). The 1158-m break point represents the general ecotone shift from northern hardwoods to conifers and creates approximately equal elevation ranges for each strata (Cogbill and White 1991). Points selected for sampling included those at historic sites that had been used to monitor birds since 1999 (details in DeMeo 1999) and at newly established sites that ensured sampling was approximately balanced across the elevation gradient (details in Dimmig 2019). All point counts were placed along transects on public land, and each transect comprised 10–12 points separated by at least 250 m.

Given the small amount of area subject to timber harvest within MNF, point counts rarely occurred within harvested stands in 2017. Therefore, in 2018, we sampled 90 additional points (20% of all point counts) within harvested stands to ensure adequate sampling of harvested forest. We included 22 historic points established in 1993–1996 in harvested stands (Duguay et al. 2001) and 68 points selected from harvest sale areas (Dimmig 2019). We stratified the 90 sample points by elevation (< 853 m, 853–1158 m, and > 1158 m) and harvest age (< 10 yr, 11–20 yr, and 20–50 yr). We placed points 250 m apart primarily within even-aged silvicultural treatments that had some seed-trees or residual trees, with an average stand size of 11 ha (3–92 ha). Notably, in 2018, harvested areas were over-represented in our sample relative to their occurrence on the landscape.

Environmental covariates

At each point count, we measured several biotic and abiotic variables thought to affect Canada Warbler occupancy (Table 1). We measured tree density in a variable-radius plot centered on the point count, using a 10 basal area factor angle gauge to determine which trees were in the plot. For each tree > 2.5 cm in diameter at breast height, we recorded the diameter at breast height and the canopy position as one of the following categories (Jennings et al. 1999): suppressed (shortest canopy layer, no direct light), intermediate (crown below canopy level but receiving direct light), codominant (crown at canopy level), dominant (crown above canopy level), legacy (old tree that has survived stand-replacing disturbance, not exhibiting open growth characteristics), or open growth (tree that grew in previously open conditions, with substantial diameter and wood volume). We measured shrub density using a 5 m radius plot centered on the point count and counted all stems < 2.5 cm in diameter at breast height and taller than 0.5 m for each species present (DeMeo 1999). Rhododendron stems were counted regardless of stem diameter or height, and we separately calculated shrub density and rhododendron density. Because none of the sampling points experienced major disturbance between the two sampling years, we only measured vegetation variables in one year, either 2017 or 2018 (McDermott et al. 2011).

We calculated additional biotic and abiotic variables at point count locations from remotely sensed spatial layers in ArcMap 10.3 (ESRI 2018). We classified forest type as mixed mesophytic, oak-pine, northern hardwoods, and red spruce using a spatial layer of forest stands within MNF (MNF 2004). We determined elevation for each location using a 7.5 min 30-m digital elevation model (USGS 2000). We also calculated the minimum distance to streams and wetlands. To determine the minimum distance from each point count to a stream or wetland, we combined streams from the National Hydrography Dataset (USGS 2017) with areas classified as woody wetland and emergent herbaceous wetland from the National Land Cover Database of 2011 (Homer et al. 2015). We then calculated the minimum distance to either a stream or a wetland (hereafter termed distance to riparian area). Finally, we categorized points as young harvest (0–19 yr), old harvest (20–40 yr), mature forest (40–120 yr), or old-age forest (> 120 yr) from the forest stands layer (MNF 2004). We split harvest into 20-yr increments because past studies suggest that Canada Warblers begin to go locally extinct approximately 20 yr following harvest (Lambert and Faccio 2005). None of the predictor variables we evaluated were highly correlated (the absolute value of all correlation coefficients was < 0.49; Table A.1 in Appendix 1).

Detection covariates

We measured several factors thought to influence detection probability at each point count (Table 1). We recorded the ordinal date and time since sunrise at the start of each survey. During the 10-min count, we measured the maximum wind speed (in m/s) using a Kestrel 1000 anemometer, and we recorded sky condition, adapted from the U.S. Weather Bureau and Breeding Bird Survey protocols (USGS 1998).

Statistical analyses

We modeled Canada Warbler, Black-throated Blue Warbler, and Hermit Thrush detection and nondetection data using

Table 1. Detection and occupancy covariates used to model multispecies occupancy of Canada Warbler (*Cardellina canadensis*), Black-throated Blue Warbler (*Setophaga caerulescens*), and Hermit Thrush (*Catharus guttatus*) in Monongahela National Forest, West Virginia, 2017–2018.

Covariate	Occupancy or detection	Values[†]
Ordinal day	Detection	168 (138–196)
Hours after sunrise (h)	Detection	1.49 (−0.37 to 4.57)
Wind speed (km/h)	Detection	1.45 (0–14.49)
Sky condition	Detection	clear, cloudy, or overcast (93%)
		fog or mist (7%)
Elevation (m)	Occupancy	1023 (526–1420)
Distance to riparian area (m)	Occupancy	261 (0.06–1505)
Shrub density (stems/m²)	Occupancy	0.46 (0–3.48)
Rhododendron density (stems/m²)	Occupancy	0.02 (0–1.09)
Suppressed and intermediate tree density (stems/ha)	Occupancy	217 (0–1355)
Dominant and co-dominant tree density (stems/ha)	Occupancy	101 (0–1443)
Percentage of deciduous trees (%)	Occupancy	0.75 (0–1.00)
Forest age class	Occupancy	Young harvest (0–19 yr; 7%)
		Old harvest (20–40 yr; 7%)
		Mature forest (40–120 yr; 81%)
		Old-age forest (> 120 yr; 6%)
Forest type	Occupancy	Mixed mesophytic (43%)
		Oak-pine (23%)
		Northern hardwood (23%)
		Red spruce (9%)
Year	Occupancy	2017 (45%)
		2018 (55%)

[†]Mean (range) for continuous variables; levels (proportion of observations within each level) for categorical variables.

multispecies occupancy models (Rota et al. 2016). Following MacKenzie et al. (2006), we define occupancy as the probability that one of the focal species is present at a randomly selected location within the study area. Multispecies occupancy models can include up to $2^S - 1$ linear models (where S is the number of species) that account for increasingly higher-order species interactions (Rota et al. 2016). For example, S first-order models describe the log odds of each species occurring when all others are absent, $S!/([S - 2]! \times 2!)$ second-order models describe the log odds of two species occurring together, etc.

We fit one multispecies occupancy model using Bayesian methods. For this model, we only estimated first- and second-order interactions, with all higher-order interactions fixed at 0. We assumed all three first-order models were a function of the occupancy variables in Table 1. We assumed quadratic effects of elevation to allow species to obtain greatest occupancy probability at intermediate elevations. We log-transformed distance to riparian area, shrub density, and rhododendron density so that incremental changes in these variables had the strongest effect at small values and weaker effects at large values (e.g., the change in log odds of occurrence was greater when distance to riparian area changed from 10 to 11 m than when the distance to riparian area changed from 100 to 101 m). All other occupancy variables were untransformed. Additionally, to account for multiple surveys at the same sites across years, we added a site-specific random effect to all three first-order models. We assumed intercept-only models for all three second-order models, which permits constant pairwise dependence between species.

We treated each of the two survey intervals (0–5 min, > 5–10 min) as replicate surveys and employed a removal sampling detection

model (Rota et al. 2009). We assumed conditional detection probability was a function of the detection variables in Table 1. We assumed quadratic effects of ordinal day to allow detection probability to peak mid-season. All other detection variables were untransformed.

Finally, we performed model checking for each species using posterior predictive checks (Kéry and Royle 2015). We based posterior predictive checks on the Pearson residual test statistic described by Parsons et al. (2018). We simulated a distribution of test statistics calculated from observed data (T_y) and simulated data (T_{sim}), and calculated a Bayesian *P*-value as $\Pr(T_{sim} > T_y)$. We assumed adequate fit for each species if $0.10 < \Pr(T_{sim} > T_y) < 0.90$ (Gelman et al. 2013).

We fit the multispecies occupancy model using Bayesian methods in JAGS (Plummer 2003) via the jagsUI version 1.5.1 (Kellner 2019) interface to program R version 4.0.2 (R Core Team 2020). We assumed logistic (0, 1) prior distributions for all slope coefficients in first-order occupancy and conditional detection probability models and for all second-order intercept parameters (Rota et al. 2016). We assumed flat prior distributions for the intercept parameters in all conditional detection probability models and for the mean (μ_s) and standard deviation (σ_s) of the random intercepts in first-order models. We then assumed realizations of intercept parameters of first-order models were Gaussian (μ_s, σ_s). We drew 11,000 posterior samples from three chains, discarding the first 1000 samples as burn-in and keeping every 10th sample thereafter. The Brooks-Gelman-Rubin convergence diagnostic (Brooks and Gelman 1998) indicated that all chains converged (i.e., Rhat < 1.1). Data and code used to fit the model are available online at Zenodo (Dimmig et al. 2022).

RESULTS

We detected Canada Warbler, Black-throated Blue Warbler, and Hermit Thrush at 7% (N = 59), 37% (N = 311), and 36% (N = 301) of all surveys, respectively. Our model-checking procedure indicated adequate fit for all species (Bayesian P-values = 0.53, 0.48, and 0.49 for Canada Warbler, Black-throated Blue Warbler, and Hermit Thrush, respectively).

First-order occupancy

Canada Warblers were detected along the entire elevation gradient. Although they were most likely to occur at middle elevations (930 m, 95% credible interval [CI] = 526–1131 m), the 95% CI of elevation slope coefficients overlapped zero, indicating no strong relationship with this variable. They were more likely to occur in areas that had high rhododendron stem density (log odds ratio [LOR] = 1.95, 95% CI = 0.88–3.78, Fig. 2) and that were close to riparian areas (LOR = −1.73, 95% CI = −3.08 to −0.73). Canada Warblers were most likely to occupy northern hardwood forests and were least likely to occupy oak-pine forests (LOR oak-pine = −5.12, 95% CI = −9.06 to −1.97). Year of the study, forest age class, dominant and codominant tree density, suppressed and intermediate tree density, percent deciduous trees, and shrub stem density were not strong predictors of Canada Warbler occupancy (i.e., 95% CI of slope coefficients overlapped zero).

Fig. 2. Marginal occupancy probability of Canada Warbler (*Cardellina canadensis*) in Monongahela National Forest, West Virginia, 2017 and 2018. Black lines and dots = point estimates, gray areas and vertical bars = 95% credible intervals, NH = northern hardwood, MM = mixed mesophytic, OP = oak-pine, and SH = red spruce-eastern hemlock. For each covariate of interest, all other continuous covariates were held at their mean, forest type was northern hardwood, forest age was mature, and study year was 2017.
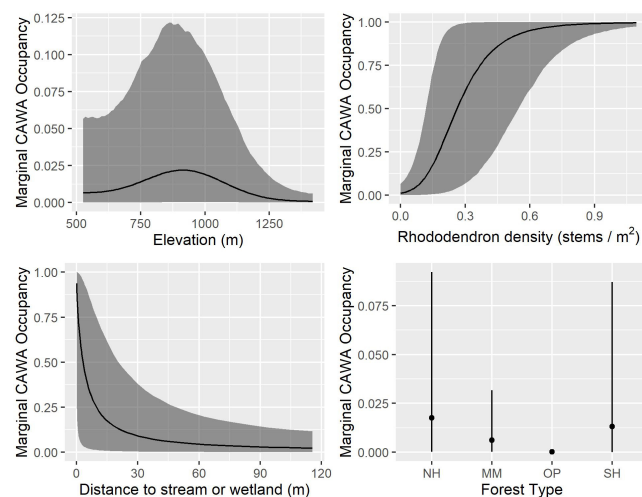
Black-throated Blue Warblers were also more likely to occur at mid-elevation sites, with the greatest estimated occupancy at 1002 m (95% CI = 941–1077 m, Fig. 3). They were more likely to occur in areas with high shrub stem density (LOR = 0.47, 95% CI = 0.05–0.97), and low dominant and codominant tree density (LOR = −0.91, 95% CI = −1.52 to −0.39). Black-throated Blue Warblers were most likely to occur in mixed mesophytic forest types, and were least likely to occur in oak-pine forests (LOR oak-pine = −2.76, 95% CI = −4.37 to −1.40). Finally, Black-throated Blue Warblers were more likely to occupy sites in 2017 than 2018 (LOR = 0.65, 95% CI = 0.11–1.28). Distance to riparian area, rhododendron stem density, percent deciduous trees, suppressed and intermediate tree density, and forest age class were not strong predictors of Black-throated Blue Warbler occupancy (i.e., 95% CI of slope coefficients overlapped zero).

Fig. 3. Marginal occupancy probability of Black-throated Blue Warbler (*Setophaga caerulescens*) in Monongahela National Forest, West Virginia, 2017 and 2018. Black lines and dots = point estimates, gray areas and vertical bars = 95% credible intervals, NH = northern hardwood, MM = mixed mesophytic, OP = oak-pine, and SH = red spruce-eastern hemlock. For each covariate of interest, all other continuous covariates were held at their mean, forest type was northern hardwood, forest age was mature, and study year was 2017.
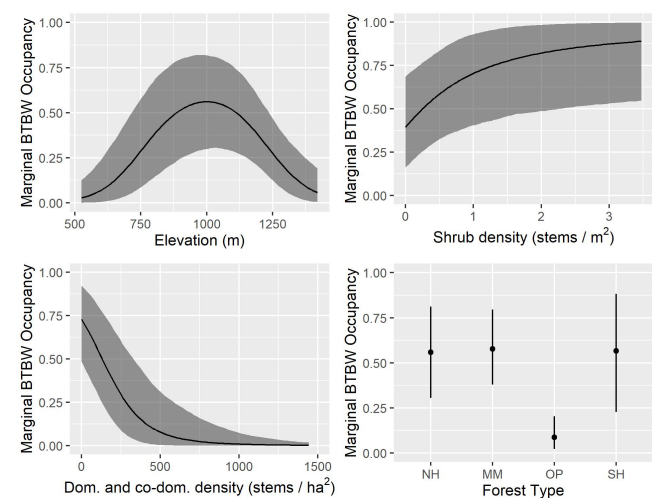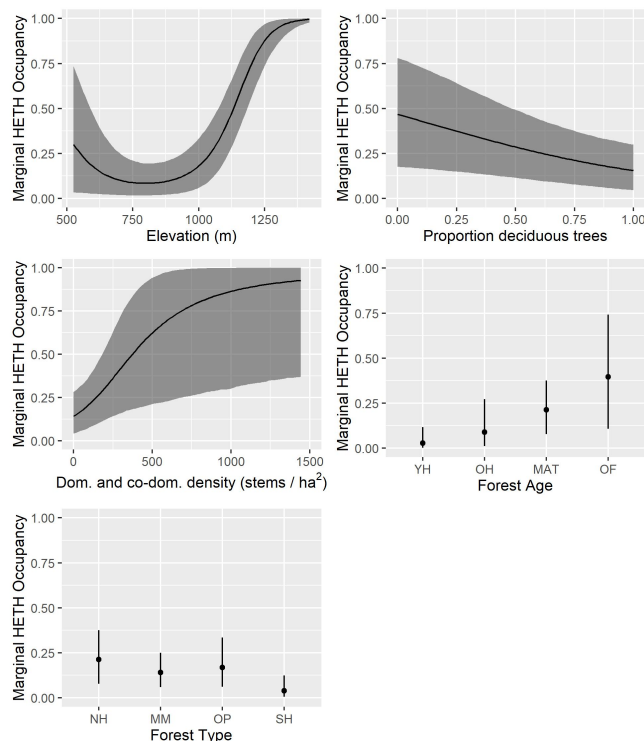

Hermit Thrushes were more likely to be found at sites with high elevation (LOR elevation = 2.21, 95% CI = 1.48–3.13; LOR elevation² = 1.01, 95% CI = 0.48–1.63, Fig. 4), low proportion of deciduous trees (LOR = −0.47, 95% CI = −0.94 to −0.06), and high dominant and codominant tree density (LOR = 0.55, 95% CI = 0.07–1.15). They were most likely to occur in old-age forests (> 120 yr; LOR = 0.89, 95% CI = −0.40 to 2.32) and least likely to occur in young harvests (0–19 yr; LOR = −2.65, 95% CI = −4.76 to −0.91). Hermit Thrushes were most likely to occur within northern hardwood forests and least likely to occur in red spruce-eastern hemlock forests (LOR spruce-hemlock = −2.13, 95% CI = −3.61 to −0.73). Year, distance to riparian area, shrub density, rhododendron density, and suppressed and intermediate tree density were not strong predictors of Hermit Thrush occupancy (i.e., 95% CI of slope coefficients overlapped zero).

Second-order occupancy

After accounting for first-order effects, Canada Warblers and Black-throated Blue Warblers were positively correlated, with Canada Warbler occupancy higher when Black-throated Blue

Warblers were present at a site (LOR = 1.53, 95% CI = 0.40–2.89) than when they were absent (Fig. 5). Canada Warblers were slightly less likely to occupy sites if Hermit Thrushes were present, but the CI of the Canada Warbler-Hermit Thrush second-order coefficient broadly overlapped zero, suggesting no strong interaction between these two species (LOR = −0.03, 95% CI = −1.19 to 1.12). Black-throated Blue Warblers tended to occur in sites less often if Hermit Thrushes were present, but the CI again overlapped zero, suggesting no strong interaction between the two species (LOR = −0.21, 95% CI = −0.81 to 0.39).

Fig. 4. Marginal occupancy probability of Hermit Thrush (Catharus guttatus) in Monongahela National Forest, West Virginia, 2017 and 2018. Black lines and dots = point estimates, gray areas and vertical bars = 95% credible intervals, NH = northern hardwood, MM = mixed mesophytic, OP = oak-pine, SH = red spruce-eastern hemlock, YH = young harvest (< 20 yr), OH = old harvest (20–40 yr), MAT = mature forest (40–120 yr), and OF = old forest (> 120 yr). For each covariate of interest, all other continuous covariates were held at their mean, forest type was northern hardwood, forest age was mature, and study year was 2017.

95% CI = −0.89 to −0.12). Ordinal date and sky condition had no strong effect on Black-throated Blue Warbler detection probability (95% CI of slope coefficients overlapped zero). Hermit Thrush detection probability was greatest close to sunrise (LOR = −0.46, 95% CI = −0.82 to −0.06). Ordinal date, wind speed, and sky condition had no strong effect on Hermit Thrush detection probability (95% CI of slope coefficients overlapped zero).

Fig. 5. Occupancy probability of Canada Warbler (*Cardellina canadensis*) conditional on Black-throated Blue Warbler (*Setophaga caerulescens*) presence and absence in Monongahela National Forest, West Virginia, 2017 and 2018. There is a higher occupancy probability for Canada Warbler at sites where Black-throated Blue Warbler are present, relative to where sites where Black-throated Blue Warbler are absent. Black lines = point estimates, gray areas = 95% credible intervals. All other continuous covariates were held at their mean, forest type was northern hardwood, forest age was mature, and study year was 2017. Choice of rhododendron stem density as the predictor variable was arbitrary; this predicted relationship holds for all variables evaluated.
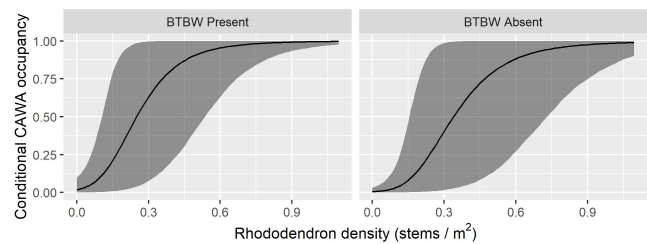

Detection probability

Canada Warblers were most likely to be detected in the middle of the breeding season, with greatest detection probability at approximately 07 June (95% CI = 23 May–17 June). Canada Warbler detection probability was not strongly influenced by time of day, wind speed, or sky condition (i.e., 95% CI of slope coefficients overlapped zero). Black-throated Blue Warblers were more likely to be detected close to sunrise (LOR = −0.47, 95% CI = −0.81 to −0.13) and when wind speed was low (LOR = −0.53,

DISCUSSION

Changing forest composition and structure within the eastern United States is likely contributing to changes in bird communities observed over recent decades (e.g., Millington et al. 2011, Toenies et al. 2018). Less frequent and less severe disturbances may particularly affect species that rely on gap dynamics to create understory structure. As hypothesized, we found that Canada Warbler distribution was associated with areas that had thick understory structure. However, the nature of this relationship was not as expected because the occupancy probability of Canada Warbler was not greatest in recently harvested forest or in areas with high non-rhododendron shrub density. Instead, we found that Canada Warblers were highly associated with rhododendron density. Although rhododendron can take advantage of recent canopy disturbances to establish at a site (Nowacki and Abrams 1994), it is well known to inhibit growth of other plants (Clinton et al. 1994, Rivers et al. 1999), which allows establishment of stable rhododendron habitats through time. A lack of forest disturbance has been credited with spreading rhododendron thickets (Baker and Van Lear 1998). In contrast, shrubby habitat created by naturally occurring gap dynamics or timber harvest is ephemeral. For example, Lambert and Faccio (2005) found that Canada Warblers began to be extirpated by 20 years postharvest. Areas with dense rhododendron growth may therefore be preferred by Canada Warblers because they are structurally more stable through time.

Indeed, rhododendron shrub cover has been expanding regionally in recent decades (1980s to present; Atkins et al. 2018, Dudley et al. 2020), which we hypothesize may be contributing to stabilize or increase the abundance of Canada Warblers within the region, despite changes in forest structure and composition that may be driving declines in other portions of the range.

Both forest age and proximity to riparian areas are forest characteristics that can promote the dense understory preferred by Canada Warblers. Surprisingly, our results showed no difference in Canada Warbler occupancy among forest age categories. In Alberta, Canada, Hunt et al. (2017) found low abundance of Canada Warblers in postharvest stands, and home ranges within postharvest stands were clustered close to adjacent unharvested stands. Similarly, in West Virginia, USA, Becker et al. (2012) found that Canada Warbler abundance in managed areas was low in intense even-aged cuts, which is the primary silvicultural treatment used in MNF (USDA 2011). Canada Warblers would likely benefit more from uneven-aged partial harvest treatments that retain greater canopy cover (Becker et al. 2012, Grinde and Niemi 2016). Although our inference may have been limited by the relatively small sample sizes for young harvest (56 point counts) and old harvest (59 point counts), managed stands were oversampled relative to their availability in MNF (USDA 2011). Ultimately, timber harvest comprises a very small portion of forest area within MNF (< 3000 ha/yr; USDA 2011) and will not likely be an important source of habitat at current harvest levels. Alternatively, we found that Canada Warblers were more likely to occur close to riparian areas, which is consistent with several other studies (Swift et al. 1984, Hallworth et al. 2008*a*, Reitsma et al. 2008, Gross 2009, Ball et al. 2016). Riparian areas provide stable canopy openings that promote the development of rhododendron (Atkins et al. 2018) and other understory shrubs and saplings while creating a moist forest floor required for nesting. In addition to riparian areas directly improving environmental conditions for Canada Warblers, this association may also be acting as a proxy for other measures of understory density we did not obtain.

As expected, we found that Canada Warblers were most likely to use northern hardwood forests, which primarily occur at medium and high elevations within the central Appalachians (Butler et al. 2015). However, contrary to our initial hypothesis, we also found that they were most likely to occur at mid-elevation sites within the study area. Previous guidelines suggest managing for Canada Warbler at elevations > 850 m in the Appalachians (Harding et al. 2017). However, managing solely above this elevation would ignore a substantial portion of the Canada Warbler population in West Virginia. Our observation that Canada Warblers were more likely to occupy mid-elevation northern hardwood forests may be linked to contemporary changes in forest structure within MNF. Since the early 20th century, annual precipitation within the central Appalachians has increased on average (though with high variability), and projections suggest that precipitation will continue to increase (though with substantial uncertainty; Butler et al. 2015). Accompanying this modest increase in precipitation is a concomitant change in forest structure. For example, in 2000, three mesophytic northern hardwood species (yellow birch [*Betula alleghaniensis*], sugar maple, and American beech) were found at the greatest density above 1200 m within MNF (Dimmig 2019). By 2017, however, the density of these three species was greatest

at mid-elevation sites within MNF (900–1200 m; Dimmig 2019). Increased regional precipitation may be allowing northern hardwood species to increase in density at lower elevations, concomitantly expanding the range of available habitat for Canada Warblers. Indeed, Tingley et al. (2012) observed similar patterns of bird species expanding distribution downslope in the Sierra Nevada Mountains, California, USA in response to increased precipitation. Although we have no evidence that Canada Warbler distributions are shifting within the central Appalachians, conditions favorable for expansion of northern hardwood forests may be contributing to regional trends of stable or increasing Canada Warbler abundance.

After accounting for other environmental variables, we found that Canada Warblers exhibited a positive association with Black-throated Blue Warblers. This positive effect is contrary to what was expected, given overlapping habitat preferences that may result in competition for resources (Sabo 1980). Our result suggests that any interactions that occur between Canada Warblers and Black-throated Blue Warblers do not result in one species excluding the other, at least at the scale at which we recorded habitat use. Alternatively, the positive association between these species may be acting as a proxy for other unmodeled environmental variables or could indicate mutualism or commensalism between these two species. Heterospecific attraction has been observed between migrant birds, where later-arriving species use cues from earlier-arriving species to locate suitable breeding habitat (Szymkowiak et al. 2017). Canada Warblers may be using a similar mechanism with Black-throated Blue Warblers given that Canada Warblers arrive on the breeding grounds later than most migrants (e.g., Francis and Cooke 1986 and Wilson et al. 2000 report that the median arrival dates of Canada Warblers lagged ≥ 2 weeks behind the earliest arriving warblers). The use of heterospecific attraction could reduce the costs of finding a high-quality breeding site and improve reproductive success (Mönkkönen and Forsman 2002). The positive relationship between these two species highlights the potential for species interactions to affect the space use of Canada Warbler and warrants further investigation into the possible mechanisms that are driving this relationship.

In addition to heterospecific interactions influencing Canada Warbler occupancy, conspecific attraction may also influence the probability that a site is occupied by this species. Indeed, Hunt et al. (2017) observed a similar process of conspecific attraction by Canada Warblers. Canada Warblers tend to cluster together, likely using conspecific social cues to locate suitable habitat (Hunt et al. 2017). Although we did not test for conspecific attraction, such processes may strongly influence the site selection of Canada Warblers. For example, if conspecific attraction strongly influences occupancy probability, the absence of conspecifics from apparently suitable habitat may preclude colonization. Future studies aimed at understanding the role of conspecific attraction could have practical implications for management and conservation.

Gaining a better understanding of the environmental factors that affect bird distributions can improve the success of conservation and management plans for species of concern. Our findings provide new insight into the factors that affect Canada Warbler habitat selection in their trailing edge distribution of the central

Appalachians in an era of rapid forest change. We found that Canada Warblers tended to occur lower on the elevation gradient than previously described, so regional conservation actions could span a large elevation gradient (500–1250 m) in northern hardwood forests to manage effectively for the species. Continued protection of riparian corridors (Naiman et al. 1993, USDA 2011) could benefit Canada Warblers as forests mature, especially those with well-established rhododendron thickets. The strong correlations we found with the Black-throated Blue Warbler, which is also a Priority 1 species within the central Appalachians (WVDNR 2015), suggests that conservation actions for Canada Warblers could benefit multiple species. Altogether, we expect this research will aid the conservation of Canada Warblers and associated species throughout the Appalachian Mountains.

Responses to this article can be read online at:
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Appendix 1

Covariate summary from 840 point count surveys within the Monongahela National Forest, West Virginia, USA, summarized by surveys where Canada Warblers (*Cardellina canadensis*) were and were not detected.
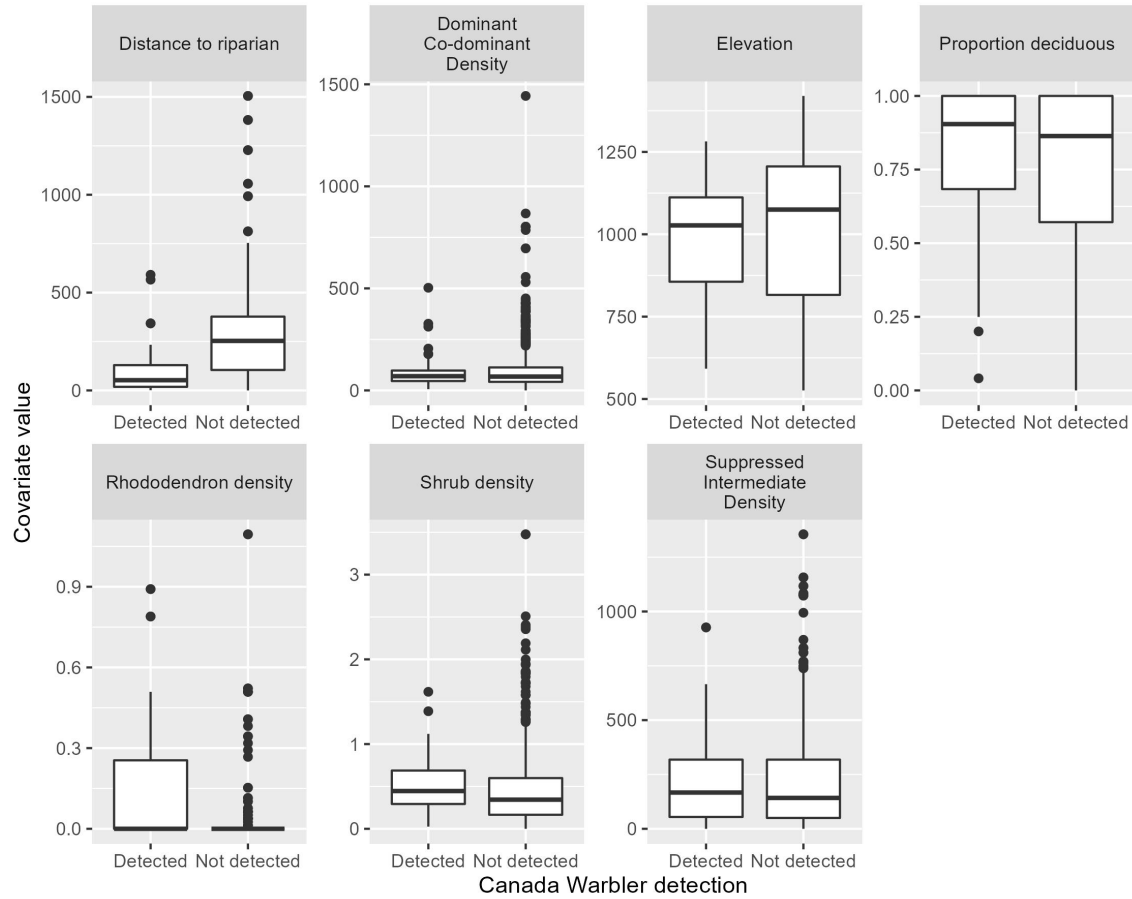

Figure A1: Boxplot of variables at point count surveys where Canada warblers (*Cardellina canadensis*) were and were not detected in the Monongahela National Forest, West Virginia, USA. Horizontal lines represent the median value; lower and upper hinges represent the 25th and 75 percentiles; whiskers extends to the smallest and largest values no further than 1.5 * IQR (interquartile range) from each hinge; and the remaining outlying points are plotted individually. Rhododendron and shrub density are reported in units of stems per square meter; dominant / co-dominant and suppressed / intermediate density are reported in units of stems per hectare.

Table A1: Correlation between predictor variables used to model Canada warbler (*Cardellina canadensis*) detection / non-detection data in the Monongahela National Forest, West Virginia, USA. Complete variable descriptions are presented in the main text.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N
A	1.00	-0.01	0.02	0.09	-0.02	0.17	0.17	-0.02	0.04	0.03	-0.03	0.07	-0.01	0.05
B	-0.01	1.00	0.36	0.15	-0.05	-0.21	-0.05	0.00	-0.19	-0.43	0.35	0.21	0.15	-0.31
C	0.02	0.36	1.00	0.07	-0.08	0.00	0.03	-0.03	-0.01	-0.09	0.12	0.10	0.00	-0.03
D	0.09	0.15	0.07	1.00	0.13	0.37	0.02	-0.05	0.08	-0.16	0.18	0.04	-0.07	-0.10
E	-0.02	-0.05	-0.08	0.13	1.00	-0.03	-0.06	0.02	-0.07	-0.02	-0.07	-0.04	0.07	0.03
F	0.17	-0.21	0.00	0.37	-0.03	1.00	-0.07	-0.07	0.28	-0.11	-0.09	-0.05	-0.12	0.10
G	0.17	-0.05	0.03	0.02	-0.06	-0.07	1.00	-0.07	-0.04	0.27	-0.09	0.27	0.04	0.18
H	-0.02	0.00	-0.03	-0.05	0.02	-0.07	-0.07	1.00	-0.17	0.07	0.21	-0.10	0.03	-0.07
I	0.04	-0.19	-0.01	0.08	-0.07	0.28	-0.04	-0.17	1.00	-0.48	-0.28	-0.09	-0.05	0.23
J	0.03	-0.43	-0.09	-0.16	-0.02	-0.11	0.27	0.07	-0.48	1.00	-0.18	-0.05	-0.05	0.14
K	-0.03	0.35	0.12	0.18	-0.07	-0.09	-0.09	0.21	-0.28	-0.18	1.00	0.26	0.11	-0.37
L	0.07	0.21	0.10	0.04	-0.04	-0.05	0.27	-0.10	-0.09	-0.05	0.26	1.00	0.14	-0.14
M	-0.01	0.15	0.00	-0.07	0.07	-0.12	0.04	0.03	-0.05	-0.05	0.11	0.14	1.00	-0.08
N	0.05	-0.31	-0.03	-0.10	0.03	0.10	0.18	-0.07	0.23	0.14	-0.37	-0.14	-0.08	1.00

A: 2017
B: Elevation
C: Distance to riparian
D: Shrub density
E: Rhododendron density
F: Young harvest
G: Old harvest
H: Old-age forest
I: Mixed mesophytic forest
J: Oak / pine forest
K: Red spruce forest
L: Co-dominant tree density
M: Intermediate / suppressed tree density
N: Proportion deciduous

Table A2: Mean value of each predictor variable from 840 point count surveys summarized by surveys where Canada warbler (*Cardellina canadensis*) were and were not detected in the Monongahela National Forest, West Virginia, USA. Complete variable descriptions are presented in the main text.

Variable	Detected	Not detected
Rhododendron density	0.16	0.01
Distance to riparian	99.04	273.65
Elevation	976.10	1026.29
Shrub density	0.53	0.45
Dominant / Codominant Density	90.62	101.36
Suppressed / Intermediate Density	222.38	217.10
Proportion deciduous	0.79	0.75
2017	0.42	0.45
2018	0.58	0.55
<20 yr old harvest	0.03	0.07
20 - 40 yr old harvest	0.05	0.07
Mature forest	0.85	0.80
Old age forest	0.07	0.06
Mixed mesophytic	0.42	0.43
Oak / pine	0.05	0.25
Red spruce	0.03	0.10
Northern hardwood	0.49	0.22