Refined conservation strategies for Golden-winged Warblers in the West Virginia highlands with implications for the broader avian community

Authors: Aldinger, Kyle R., Wood, Petra B., and Johnson, Catherine M.

RESEARCH ARTICLE

Refined conservation strategies for Golden-winged Warblers in the West Virginia highlands with implications for the broader avian community

Kyle R. Aldinger,[1]* Petra B. Wood,[2] and Catherine M. Johnson[3]

[1] West Virginia Cooperative Fish and Wildlife Research Unit, West Virginia University, Morgantown, West Virginia, USA
[2] U.S. Geological Survey, West Virginia Cooperative Fish and Wildlife Research Unit, West Virginia University, Morgantown, West Virginia, USA
[3] USDA Forest Service, Monongahela National Forest, Elkins, West Virginia, USA
* Corresponding author: kylealdinger@gmail.com

ABSTRACT

Golden-winged Warbler (*Vermivora chrysoptera*) populations in the Appalachian Mountains region of North America are imperiled, warranting species-specific conservation. However, management for Golden-winged Warblers can affect both early-successional and forest species, many of which are also declining in the region. We conducted point counts in sites representing a range of successional stages within the Golden-winged Warbler's breeding range in West Virginia, USA, during 2008–2015. We identified plausible models of Golden-winged Warbler density using covariates at 4 spatial scales representing annual dispersal (5-km radius), extraterritorial movement (1.5-km radius), intraterritorial movement (100-m radius), and local resource utilization (11.3-m radius). Golden-winged Warbler density peaked at an intermediate elevation at the 1.5-km radius scale, but was negatively associated with 100-m radius minimum elevation. Density was positively associated with 100-m radius shrubland cover. Southerly latitudes were associated with higher densities when modeled alone, but there was no association when controlling for other covariates. We then examined the relationship between covariates from these plausible models and avian community structure using canonical correspondence analysis to assess the value of Golden-winged Warbler conservation for the broader avian community. We identified 5 species likely to benefit from management for Golden-winged Warblers and 21 species likely to be affected positively or negatively to varying degrees depending on their affinity for early-successional vegetation communities. Golden-winged Warblers were plotted higher along the 100-m shrubland cover gradient than any other bird species, suggesting that they may be the most shrubland area–sensitive songbird in our study area. However, the species also requires heavily forested landscapes. Therefore, a species-specific conservation strategy that balances shrubland (patches of 9–13 ha in size, comprising 15% of the landscape) and contiguous forest area (≥75% of the landscape) could concurrently meet the needs of Golden-winged Warblers and the 26 other species identified.

Keywords: density, detection probability, early succession, elevation, canonical correspondence analysis, shrubland, *Vermivora chrysoptera*

Estrategias de conservación refinadas para *Vermivora chrysoptera* en las tierras altas de Virginia del Oeste con implicancias para la comunidad de aves en su conjunto

RESUMEN

Las poblaciones de *Vermivora chrysoptera* en la región de las Montañas Apalaches están en peligro, justificando la conservación específica de la especie. Sin embargo, el manejo de *V. chrysoptera* puede afectar tanto especies de la sucesión temprana como especies del bosque, muchas de las cuales también están disminuyendo en la región. Realizamos conteos en puntos en sitios representando un rango de estadios sucesionales adentro del rango reproductivo de *V. chrysoptera* en Virginia del Oeste durante 2008–2015. Identificamos modelos plausibles de densidad de *V. chrysoptera* usando covariables a 4 escalas espaciales, representando la dispersión anual (5 km de radio), el movimiento extra-territorial (1.5 km de radio), el movimiento intra-territorial (100 m de radio) y la utilización de recursos locales (11.3 m de radio). La densidad de *V. chrysoptera* alcanzó su punto más alto a una elevación intermedia a la escala de 1.5 km de radio, pero estuvo negativamente asociada con la mínima elevación a 100 m de radio. La densidad estuvo positivamente asociada con la cobertura de matorral en un radio de 100 m. Las latitudes más al sur estuvieron asociadas con densidades más altas cuando se modelaron solas, pero no hubo una asociación cuando se controló por las covariables. Luego examinamos la relación entre las covariables de aquellos modelos plausibles y la estructura de la comunidad de aves usando análisis de correspondencia canónica para evaluar el valor de la conservación de *V. chrysoptera* para la comunidad de aves en su conjunto. Identificamos 5 especies que se beneficiarían del manejo para *V. chrysoptera* y 21 especies que estarían positiva o negativamente impactadas a distinto nivel dependiendo de su afinidad por las comunidades vegetales de la sucesión temprana. *V. chrysoptera* se ordenó

más alto a lo largo del gradiente de cobertura de matorral de 100 m que cualquier otra especie de ave, sugiriendo que esta sería el ave canora más sensible al área de matorral en nuestra área de estudio. Sin embargo, la especie también necesita paisajes con una alta cobertura de bosque. Por ende, una estrategia de conservación específica para esta especie que balance áreas de matorral (parches de 9–13 ha abarcando 15% del paisaje) y bosque contiguo (≥75% del paisaje) podría alcanzar de modo concurrente las necesidades de *V. chrysoptera* y de las restantes 26 especies.

Palabras clave: análisis de correspondencia canónica, densidad, elevación, matorral, probabilidad de detección, sucesión temprana, *Vermivora chrysoptera*

INTRODUCTION

Golden-winged Warbler (*Vermivora chrysoptera*) populations in West Virginia, USA, have decreased by an average of ∼9% (95% confidence limits [CL]: −10%, −7%) annually since 1966 (data from the North American Breeding Bird Survey [BBS], 1966–2015; Sauer et al. 2017). Contemporary BBS trends are increasingly unreliable (2005–2015: −8% per year [95% CL: −13%, 1%]) because Golden-winged Warblers are so rare in West Virginia and throughout the Appalachians (Rosenberg et al. 2016a). In the face of these declines, the Golden-winged Warbler Working Group aims to double the current Appalachian Mountain population by 2050 (Roth et al. 2012), from 22,000 to 44,000 individuals based on population estimates from Partners in Flight (Rich et al. 2004, Rosenberg and Blancher 2005). Meeting this population objective will require ongoing conservation management into the foreseeable future because of the Golden-winged Warbler's reliance on shrublands and young forests for nesting (Scott et al. 2010, Confer et al. 2011).

Conservation actions such as the formation of the Working Lands for Wildlife partnership and state-level activities through the Golden-winged Warbler Breeding Season Conservation Plan are underway to create and maintain vegetation communities needed to sustain breeding populations of Golden-winged Warblers in the Appalachian Mountains (Roth et al. 2012, U.S. Natural Resources Conservation Service 2012). Region-specific studies of the warbler's nesting ecology and breeding territories are available to guide these conservation efforts (Rossell et al. 2003, Bulluck and Buehler 2008, Patton et al. 2010, Aldinger and Wood 2014, Aldinger et al. 2015, Frantz et al. 2016). However, few region-specific multiscale spatial evaluations of abundance have been completed (Bakermans et al. 2015), despite evidence for geographic variation in breeding habitat use throughout the Appalachian Mountain region (Golden-winged Warbler Working Group 2013). Of particular need are studies using multiple ecologically relevant spatial scales representing different components of the Golden-winged Warbler's hierarchical resource utilization process (Johnson 1980), such as extraterritorial movements to seek extrapair copulations (Frantz et al. 2016), nest-site selection (Terhune et al.

2016), or other scale-dependent behaviors. Such studies would allow stronger inference about abundance patterns because of the link to specific life-history characteristics and the reduction of bias associated with choosing arbitrary scales (i.e. the modifiable areal unit problem; Gehlke and Biehl 1934). Finally, multiscale spatial studies of abundance can more clearly direct managers toward where to work on the landscape and how to manage selected sites.

The Golden-winged Warbler population in West Virginia arguably warrants conservation action, but consideration of other species is justified because 62% of successional or scrub and 27% of forest breeding birds are also declining in the Appalachian Mountains Bird Conservation Region (Sauer et al. 2017). Many of these declining species coexist with Golden-winged Warblers during at least a portion of their breeding cycle because of the broad range of successional stages and vegetation communities used by breeding Golden-winged Warblers (Streby et al. 2016a). Furthermore, species that nest in later stages of succession sometimes use earlier stages of succession during the postbreeding period (McDermott and Wood 2010, King and Schlossberg 2014).

Our overall objectives were to identify conditions favorable for high densities of Golden-winged Warblers, and to evaluate the relationships between these conditions and overall avian community structure. First, we modeled Golden-winged Warbler density using habitat covariates at 4 spatial scales representing annual dispersal (5-km radius), extraterritorial movement (1.5-km radius), intraterritorial movement (100-m radius), and local resource utilization (11.3-m radius). We expected that each scale might be similarly important for density (Thogmartin 2010), so we first analyzed each scale separately and then combined covariates from plausible models into a final multiscale model suite. We developed multiple alternative hypotheses to explain variation in density and followed an information-theoretic approach to evaluate these alternative hypotheses (Burnham and Anderson 2002). Second, we examined the relationships between covariates from those plausible models and avian community structure to evaluate the potential impact of Golden-winged Warbler habitat management on the broader avian community.
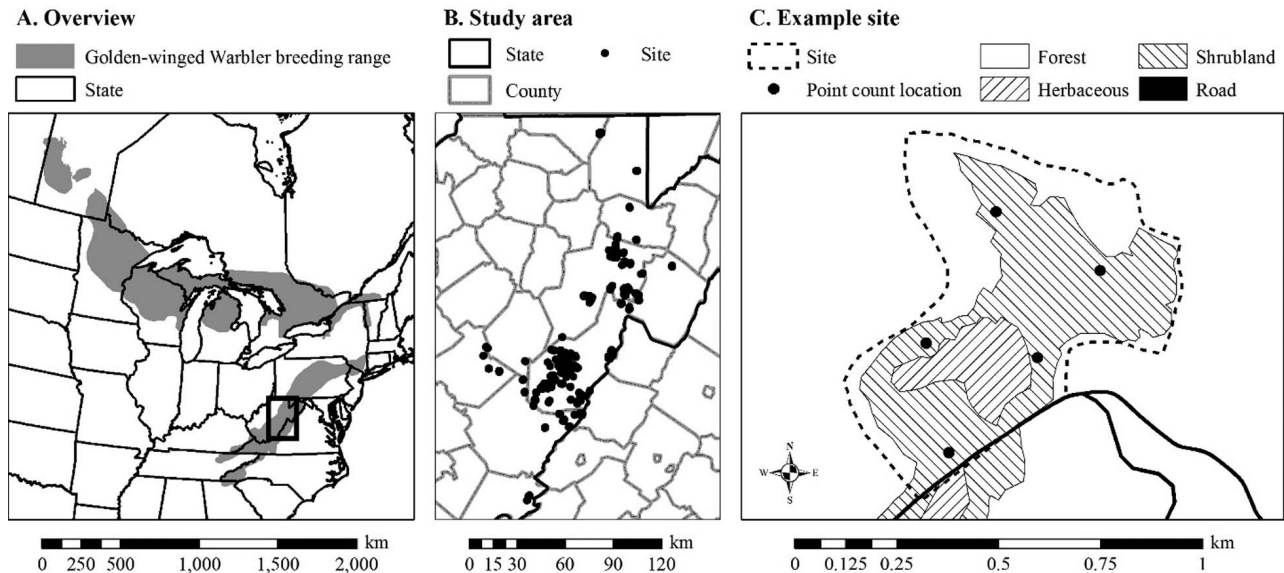
FIGURE 1. Within (**A**) the Golden-winged Warbler's contemporary breeding range in North America (Roth et al. 2012), we surveyed (**B**) sites in West Virginia, USA ($n = 121$) with (**C**) 10-min, 100-m radius avian point counts ($n = 273$ unique point count locations, $n = 1,096$ point counts) during May–June, 2008–2015.

METHODS

Study Area

During 2008–2015, we conducted point counts and measured vegetation characteristics in Greenbrier, Monongalia, Monroe, Nicholas, Pendleton, Pocahontas, Preston, Randolph, Tucker, and Webster counties, West Virginia (39.6188°N–37.5527°N, 80.6729°W–79.3180°W), within the contemporary Appalachian Mountain breeding range of the Golden-winged Warbler (Figure 1; Roth et al. 2012). We selected sites that had existing Golden-winged Warbler nesting cover or the potential to create nesting cover through vegetation management. We defined a site as a discrete area with a single management regime resulting in vegetative structure and composition that were relatively uniform within the site. For example, a fenced pasture with livestock grazing and mowing or a ridgetop network of timber harvests each would be considered a site. Sites ($n = 121$, size: 3–494 ha, elevation: 547–1,343 meters above sea level) were in the Monongahela National Forest ($n = 79$) and State Wildlife Management Areas ($n = 3$) or on private land ($n = 39$). Management regimes primarily responsible for creating or maintaining vegetation communities on our sites included active ($n = 42$) and abandoned ($n = 21$) livestock grazing, forest management ($n = 13$), mowing of herbaceous vegetation ($n = 13$), mechanical brush removal ($n = 22$), mine reclamation ($n = 3$), and prescribed fire ($n = 7$). Vegetative conditions varied widely among point count locations at the 100-m scale due to varied management regimes among sites (Figure 2), but forest cover dominated the 1.5-km (median: 86%) and 5-km (median: 87%) scales (Table 1).

Data Collection

Point counts. Each year before point counts began (April 25–May 19), training of all observers ($n = 9$ total observers, 1–4 observers per year) was conducted by the same trainer. All observers practiced distance estimation by estimating known distances. In the 2–3 days before point counts began, observers concurrently, but independently, conducted 10-min practice point counts as a group at the same point count locations and compared results to help standardize results among observers.

Within sites, we randomly distributed point count locations ≥250 m apart (median: 2 point count locations per site, range: 1–12 locations) to reduce the risk of double counting individual birds (Ralph et al. 1995). We eliminated point count locations with 100% herbaceous or forest cover within a 100-m radius because Golden-winged Warblers do not breed in these types of vegetation communities (Confer et al. 2011). This design reduced the number of point count locations per site and allowed us to sample a larger number of sites, but ultimately limited our inference about bird communities when herbaceous or forest cover was completely homogeneous. Annually during the peak daily (median: 119 min after sunrise, range: 13 min before to 300 min after sunrise) and seasonal (median: June 1, range: May 20–June 25) singing periods for most songbirds, we conducted 10-min fixed-radius point counts ($n = 1,096$ total point counts during 2008–2015, range: 33–323 point counts per year) across 273 point count locations (range: 23–235 point count locations per year) at 121 sites (range: 9–99 sites per year). Observers visited point count locations 1–2 times per
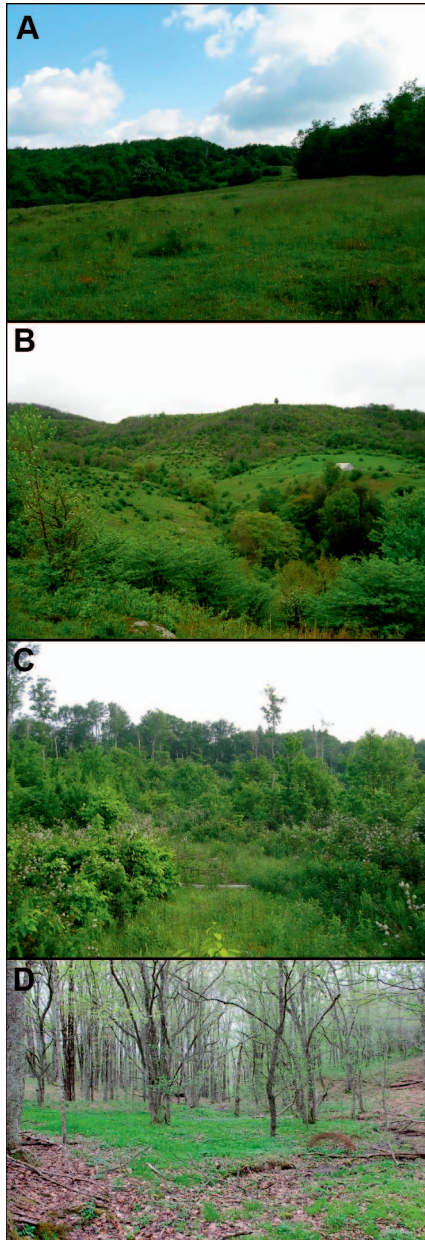
FIGURE 2. We sampled a successional gradient ranging from (**A**) herbaceous to (**B**) shrubland to (**C**) young forest to (**D**) later successional forest vegetation communities to assess Golden-winged Warbler densities across this gradient in West Virginia, USA, in 2008–2015. Vegetative conditions varied widely among point count locations ($n = 273$) at the 100-m scale due to varied management regimes among sites ($n = 121$).

year dependent on time constraints (≥ 12 days apart if visited twice) for 1–7 yr per point (median: 3 visits per point, range: 1–14 visits). We recorded sky and wind conditions using categories from Hamel et al. (1996). We recorded species, distance category (≤ 25 m, >25–50 m, >50–75 m, >75–100 m, or >100 m), time (0–2, >2–3, >3–4, >4–5, >5–6, >6–7, >7–8, or >8–10 min),

detection type (call, flyover, song, visual, or nonvocal sound), and sex (male, female, unknown, or juvenile) for each bird detection. We pooled the first 2 min to allow sufficient time for an observer to record all birds detected instantaneously at the start of the point count. Thus, individuals could not be placed into minute 2, rather than minute 1, based solely on the order in which the individuals were recorded. We also pooled the last 2 min to reduce the sparsity of our count matrices for detection probability analysis.

Geospatial data. We used ArcGIS 10.3 (Environmental Systems Research Institute [ESRI], Redlands, California, USA) for all geospatial analysis. We used a 30-m resolution National Elevation Dataset digital elevation model (West Virginia GIS Technical Center 1999) to derive aspect (°) and slope (°) grids. We used the slope grid to derive a flow direction grid and the flow direction grid to derive a flow accumulation grid. We then used these grids to calculate a topographic wetness index (TWI) as $\ln(A_s/\tan\beta)$, where A_s is the specific catchment area (area (m²) per unit width orthogonal to the flow direction) and β is the slope angle (in radians; Gessler et al. 1995).

We manually digitized land cover at a scale of 1:10,000 using 2011 National Agriculture Imagery Program (NAIP) imagery (1-m cell size collected during the growing season). We chose the 2011 imagery because it corresponded with the approximate midpoint of our study. Two sites experienced major land cover change during 2014–2015 because of timber harvests, so we created annual land cover maps for these sites. We digitized land cover for polygons ≥ 0.2 ha to avoid overly tedious manual digitization while accounting for the minimum reported size of a Golden-winged Warbler territory (0.2 ha; Confer et al. 2011). Our land cover classes included barren (no vegetation), forest (nearly 100% closed canopy consisting of trees >10 cm dbh), herbaceous (dominated by grasses and forbs with $<30\%$ woody cover), shrubland ($\geq 30\%$ shrub cover generally dominated by ≤ 10 cm dbh stems of species such as autumn olive [*Elaeagnus umbellata*], hawthorn [*Crataegus* spp], multiflora rose [*Rosa multiflora*], and shrubby St. Johnswort [*Hypericum prolificum*], with scattered canopy trees and herbaceous understory), and young forest (regenerating forest stands generally resulting from timber harvest, dominated by saplings ≤ 10 cm dbh, displaying distinct edges against surrounding forest, and often dissected by logging roads).

We incorporated open water (West Virginia GIS Technical Center 2006), man-made structure (West Virginia GIS Technical Center 2003), and road (West Virginia GIS Technical Center 2010) polygons into our land cover map. We buffered structures, represented as points, with a 154 m² square, representing the median house size outside metropolitan statistical areas during 1973–2010 (U.S. Census Bureau 2010). We buffered road

TABLE 1. Summary statistics for covariates (see Table 2 for covariate notation) used in Golden-winged Warbler density modeling and redundancy analysis in West Virginia, USA, 2008–2015. Summary statistics are based on site-level covariate values, derived by averaging covariate values across years for each point count location ($n = 273$), then averaging across point count locations within each site ($n = 121$).

Covariate	Minimum	1st quartile	Median	Mean	3rd quartile	Maximum
5-km geospatial covariates: annual dispersal scale						
Northing (km)	4,156.6	4,230.7	4,245.4	4,256.2	4,285.7	4,385.6
Forest cover (%)	59	81	87	85	92	97
Herbaceous cover (%)	0	3	6	8	12	31
Young forest cover (%)	0	0	1	1	2	9
Shrubland cover (%)	0	2	3	4	6	13
Shannon's equitability index	0.1	0.2	0.3	0.3	0.4	0.8
Edge (km/km²) [a]	0.2	0.6	0.8	0.9	1.2	2.2
Minimum elevation (m)	265	616	679	694	781	969
1.5-km geospatial covariates: extraterritorial movement scale						
Forest cover (%)	37	6	86	83	93	100
Herbaceous cover (%)	0	2	5	9	10	51
Young forest cover (%)	0	0	0	1	2	10
Shrubland cover (%)	0	2	4	6	9	30
Shannon's equitability index	0.0	0.2	0.3	0.3	0.5	0.8
Edge (km/km²) [a]	0.0	0.7	1.1	1.3	1.7	4.2
Minimum elevation (m)	318	675	794	800	916	1,106
100-m geospatial covariates: intraterritorial movement scale						
Forest cover (%)	0	14	29	35	53	100
Herbaceous cover (%)	0	0	7	13	22	84
Young forest cover (%)	0	0	0	8	0	100
Shrubland cover (%)	0	9	44	42	70	100
Shannon's equitability index	0.0	0.3	0.4	0.4	0.5	0.8
Edge (km/km²) [a]	0.0	3.3	6.0	6.5	9.2	19.8
Minimum elevation (m)	540	786	925	940	1,097	1,309
TWI [b]	5.0	6.0	6.3	6.6	7.0	15.0
Field vegetation covariates: local resource utilization scale [c]						
Vegetation density (%)	8	46	60	61	78	99
Basal area (m²/ha)	0.0	2.1	6.3	10.9	12.5	87.5
Grass cover (%)	18	66	85	76	93	100
Forb cover (%)	31	68	80	78	91	100
Vine cover (%)	0	0	1	7	7	52
Rubus cover (%)	0	3	10	17	25	77
Shrub cover (%)	0	11	21	25	39	70
Sapling cover (%)	0	0	4	10	13	73
Canopy cover (%)	0	1	5	14	19	90
Shrub layer height (m)	0.3	1.3	2.0	2.1	2.9	4.2
Sapling layer height (m)	0.0	0.8	1.8	2.1	3.0	5.9

[a] Density of shrubland–forest and young forest–forest edge.
[b] Topographic wetness index.
[c] Sample size: $n = 75$ sites with field vegetation data.

centerlines based on their type, with primary roads (e.g., Interstate 68) buffered by 8 m, secondary roads by 5 m (e.g., U.S. Route 219), local neighborhood roads, rural roads, and city streets by 3.7 m (e.g., County Route 1), and all other roads by 1.35 m. We vetted open water, man-made structure, and road polygons against 2011 NAIP imagery and corrected inconsistencies to increase the accuracy of our final land cover map.

We delineated edges between early-successional woody vegetation (shrubland and young forest) and forest (hereafter, Edge). We considered early-successional woody vegetation and forest to share an edge if they were within 3 m of each other as a means of separating ecotones from rural road edges. We calculated Shannon's equitability index (Pielou 1966) as $H/\ln(S)$, where H is Shannon's diversity index ($-\sum_{i=1}^{s} p_i \times \ln(p_i)$; Shannon 1948) and $\ln(S)$ is the natural log of the number of land cover classes (S). We used the proportions (p_i) of herbaceous, forest, shrubland, and young forest land cover classes in the calculation for each buffer. Values for Shannon's equitability index range from 0 to 1, with 1 representing even proportions of the 4 land cover classes.

Field vegetation data. At a subset of point count locations ($n = 967$ point counts at 174 point count

locations in 75 sites), we collected breeding season–specific (median date: June 30, range: June 7–September 14) vegetation data within an 11.3-m radius plot centered on the point count location. At our sites, most plants had reached full leaf development by June 7. We measured the basal area of woody plants from the plot center using a 10-factor prism. Similarly to Nudds (1977), we estimated vegetation density by placing a board (2 m tall, 40 cm wide) 10 m from the plot center in each of the 4 cardinal directions and recording how many of the 20 20-cm squares were <50% visible to another observer standing at the plot center. We divided the number of squares that were <50% visible by the total number of squares (20) on the board to obtain the vegetation density percentage for each direction, then averaged the 4 percentages for a single estimate of vegetation density per point count location. Across the 11.3-m radius plot, we visually estimated the average height of the shrub and sapling layer. At least 2 observers independently estimated height, then averaged the estimates and rounded to the nearest 0.25 m. We also measured the percent cover of grasses, forbs, vines, *Rubus*, shrubs, saplings (1–10 cm diameter and $\geq$1 m tall), and canopy trees (>10 cm dbh) based on ocular tube "hits" (James and Shugart 1970) at 5 points along 11.3-m transects radiating out from the plot center in each cardinal direction. Observers recorded whether each cover type intersected the ocular tube crosshairs when viewing through the ocular tube straight toward the ground and straight upward. We divided the number of hits per cover type by the total number of possible hits (20) for a single estimate of cover per cover type per point count location. For all field vegetation data, analyses, results, and interpretation, we considered *Rubus* separately from other shrubs and woody plants because of its abundance and importance to Golden-winged Warblers in our study sites (Aldinger and Wood 2014).

Data Analysis

Golden-winged Warbler detection probability. To account for imperfect detection of Golden-winged Warbler males during 100-m radius point counts, we combined distance-sampling (Buckland et al. 2001) and time-removal (Farnsworth et al. 2002) methods following Sólymos et al. (2013) to model the 2 components of detection probability (the probability that a bird is detected during a point count): availability (the probability that a bird is available for detection), and perceptibility (the probability that an observer detects a bird, given that it is available for detection). We then used estimates of availability and perceptibility and the area sampled ($\pi \times$ point count radius^2) as offsets to convert counts to density.

We used package detect 0.3-2 (Sólymos et al. 2014) in program R (used for this and all subsequent analyses; R Core Team 2016) to formulate conditional multinomial maximum likelihood models of availability and perceptibility as functions of covariates. We considered each point count ($n = 1,096$) as an independent sample when modeling detection probability (Sólymos et al. 2013). Candidate availability models included continuous covariates for date and time since sunrise, which we rescaled by dividing by their maximum possible values of 365 days and 1,440 min, respectively (Sólymos et al. 2013). We used package maptools 0.8-36 (Lewin-Koh and Bivand 2015) to obtain sunrise times. Candidate perceptibility models included continuous covariates for herbaceous, forest, and shrubland cover within a 100-m radius and categorical covariates for sky and wind codes and observer. We pooled 2 observers with the fewest point counts ($n = 43$ point counts pooled) so that the observer model would run without error. To compare among candidate models for availability and perceptibility, we used Akaike's information criterion (AIC; Burnham and Anderson 2002) in package MuMIn 1.15.6 (Bartoń 2016). We accounted for model-selection uncertainty by using a parametric bootstrap procedure ($n = 1,000$ replicates with replacement) to produce model-averaged detection probability offsets (see the supporting information in Sólymos et al. 2013). The probability of selecting a candidate availability or perceptibility model was proportional to its Akaike model weight.

Golden-winged Warbler density modeling. We used package lme4 1.1-11 (Bates et al. 2015) to formulate Poisson lognormal mixed effect Golden-winged Warbler density models fitted with Laplace approximation. In each model, we included random intercepts for year and for point count ID nested within site. This random-effects structure accounted for annual variation in density (Sauer et al. 2017), nonindependence of point count locations within sites, and repeated measurements at individual point count locations within sites (Bates et al. 2015). Golden-winged Warblers can be detected nearly perfectly with 10-min point counts, especially with repeated counts (Aldinger and Wood 2015), so we did not use zero-inflated models (Martin et al. 2005).

Variables at different spatial scales may be important for predicting Golden-winged Warbler density (Thogmartin 2010), so we organized candidate models into 5 model suites. Model suites I–IV each represented a different spatial scale. A priori candidate density models for model suites I (5.0-km scale), II (1.5-km scale), and III (100-m scale) included fixed effects for geospatial covariates (Table 2) and used all 1,096 point counts. A priori candidate density models for model suite IV included fixed effects for vegetation covariates measured in the field (Table 2) and used all point counts for which we had field vegetation data ($n = 967$). The fifth and final model suite integrated all spatial scales by using all possible combinations of the plausible models from model suites I–IV.

TABLE 2. Descriptions, notations, and justifications for covariates in model suites evaluating the association of geospatial (model suites I, II, and III) and field vegetation (model suite IV) covariates with Golden-winged Warbler density in West Virginia, USA, 2008–2015. We used the covariates in each model suite in 2 models: one with a linear term and one with a linear and a quadratic term. Each model suite also included an intercept-only model.

Covariate [abbreviation]	Justification
UTM (km) [Northing] [a]	Positive association between density and latitude, possibly due to climate (Thogmartin 2010).
Land cover (%)	
Forest [a,b,c]	Positive association between density and forest cover within 5 km (Thogmartin 2010); recommended ≥60% forest cover within 2.5 km (Crawford et al. 2016).
Herbaceous [c]	Can be the predominant component of territories (Rossell et al. 2003); needed to fragment shrub or sapling stands used for nesting (Klaus and Buehler 2001, Bakermans et al. 2015).
Young forest [a,b,c]	Positive association between abundance and young forest cover within 1 km (Bakermans et al. 2015).
Shrubland [a,b,c]	Commonly used nesting cover at high elevations in West Virginia (Aldinger and Wood 2014) and throughout the breeding range (Confer et al. 2011).
Shannon's equitability index using 4 land covers (forest, herbaceous, young forest, shrubland) [c]	Variety of successional stages used during the breeding season, including herbaceous (Rossell et al. 2003), shrubland (Aldinger and Wood 2014), young forest (Bakermans et al. 2015), and forest (Frantz et al. 2016).
Density (km/km^2) of shrubland–forest and young forest–forest edge [Edge] [b,c]	Edge between shrubland or young forest and later successional forest is a component of nearly all territories (Patton et al. 2010, Confer et al. 2011, Frantz et al. 2016).
Minimum elevation [b,c]	Elevation >500 m predicts occurrence and likely limits contact with Blue-winged Warblers in Appalachian Mountains region (Crawford et al. 2016).
Median topographic wetness index [TWI] [c]	Wetlands may provide local (0.5–5.0 ha) refugia with increased genetic purity and nest survival (Confer et al. 2010; but see Peterson et al. 2016).
Basal area (m^2/ha) at point count location [d]	Recommended 1.9–3.7 m^2/ha basal area for breeding territories in the Appalachian region (Golden-winged Warbler Working Group 2013).
Vegetation density (%) within 10 m [d]	Vegetation within 10 m of nest locations was denser than random locations (Aldinger and Wood 2014); recommended 10–35% vegetation density within 10 m of nests (Terhune et al. 2016).

Mean vegetation height (m) within 11.3 m [d]
  Shrub height
  Sapling height
	Height of woody vegetation may be associated with density (Roth and Lutz 2004).

Cover (%) within 11.3 m [d]
  Grass
  Forb
  Vine
  Rubus
  Shrub
  Sapling
  Canopy
	Vegetation communities used for breeding are characterized by a complex mosaic of herbaceous and woody vegetation and canopy trees (Confer et al. 2011, Roth et al. 2012).

[a] Model suite I (5-km geospatial covariates: annual dispersal scale).
[b] Model suite II (1.5-km geospatial covariates: extraterritorial movement scale).
[c] Model suite III (100-m geospatial covariates: intraterritorial movement scale).
[d] Model suite IV (field vegetation covariates: local resource utilization scale).

We chose a 5.0-km radius for covariates in model suite I because ~5.0 km was the largest between-season movement that we observed for color-banded Golden-winged Warblers (K. Aldinger personal observation). Model suite I also included the northing of the point count location because sites followed a primarily latitudinal gradient spanning 230 km (Figure 1). The 1.5-km radius for covariates in model suite II reflected the distance of within-season movements of radio-tagged Golden-winged Warbler males (Frantz et al. 2016). The 100-m radius for covariates in model suite III corresponded with the spot-mapped territory size of Golden-winged Warblers from this region (2.4 ha ± 0.5 SE; Frantz et al. 2016) and matched our point count radius.

Geospatial covariates representing the same characteristic at different but spatially nested extents tend to be highly positively correlated because each spatial scale partly measures the same information (Zuur et al. 2009). Therefore, we created 3 nonoverlapping concentric rings (0–100 m, >100 m–1.5 km, and >1.5–5.0 km) around each point count location. Concentric rings represent a premodeling method of reducing collinearity analogous to the model-based approach of constructing linear combinations of spatially nested covariates (Chatterjee and Price 1991), with the advantage that regression coefficients retain a simple interpretation. Creating concentric rings was necessary because model suite V contained covariates from multiple spatial scales. Hereafter, we refer to each scale by the outer radius of the concentric ring followed by the covariate name (Table 2). For example, forest cover within the 1.5–5.0-km ring is called "5.0-km forest cover."

For each covariate in each model suite, we included a model with a linear term and a model with linear and quadratic terms. We included quadratic terms because Golden-winged Warbler breeding habitat includes a complex mosaic of different vegetation types (Confer et al. 2011), and the correlation of density with vegetative cover may change direction as the vegetation community becomes more or less homogeneous. For model suites I, II, and III, we included models that combined covariates for minimum elevation and forest cover, elevation and shrubland cover, elevation and young forest cover, and shrubland and young forest cover (i.e. nesting cover). For model suite IV, we included models that combined covariates for grass and forb (i.e. herbaceous) cover; *Rubus*, sapling, and shrub (i.e. woody) cover; grass, forb, vine, *Rubus*, shrub, and sapling cover (i.e. nesting gestalt); shrub and sapling height (i.e. woody plant height); and vegetation density and grass and forb cover. All model suites also included an intercept-only model for comparison.

We used a nonparametric bootstrap technique ($n = 1,000$ replicates with replacement) to incorporate uncertainty associated with parameter estimates from availability and perceptibility models into our density models and to estimate regression parameters and associated errors for those density models (Sólymos et al. 2013). We created an index for the bootstrap iterations that accounted for the study design by resampling sites first and then point count locations within sites ($n = 1,096$ samples). We used the same bootstrap index for all candidate density models so that replicates ($B_1, B_2, \ldots B_n$) could be directly compared among models (i.e. replicate B_i used the same set of n samples across all candidate density models). We derived fixed-effect coefficients, random-effect standard deviations, and model predictions for a model by calculating the median across the 1,000 bootstrap model replicates, and estimated 95% quantile confidence intervals (QCI)

using the 2.5% and 97.5% quantiles of those replicates (Breiman 1996).

Covariate and model selection. Within and between scales we excluded one of any pair of covariates with a Pearson's product moment correlation coefficient $\geq |0.9|$ from density modeling to be conservative in excluding potentially important covariates. For each pair, we generally retained the covariate that we felt had simpler interpretation or management application. For example, we chose to retain 1.5-km forest cover over 1.5-km Shannon's equitability index because the proportion of forest cover in an area is simpler to understand and manage than an index representing the relative proportions of 4 different land cover classes. We excluded 5-km Edge (vs. 5-km shrubland cover), 5-km Shannon's equitability index and 5-km herbaceous cover (vs. 5-km forest cover), 5-km minimum elevation (vs. 1.5-km minimum elevation), 1.5-km Shannon's equitability index (vs. 1.5-km forest cover), and 1.5-km herbaceous cover (vs. 1.5-km forest cover).

To compare among candidate models in each model suite, we used AIC (Burnham and Anderson 2002) in package MuMIn 1.15.6 (Bartoń 2016). We calculated the evidence ratio (E), or the normalized relative likelihood, for each candidate model as $E = e^{0.5(\Delta\text{AIC})}$, where ΔAIC is the AIC value of the candidate model minus the minimum AIC value in the model suite (Burnham and Anderson 2002). Given our nonparametric bootstrap approach, we calculated E during each bootstrap replicate, then calculated the median E across all bootstrap replicates. We defined models with median $E \leq 2.7$ as plausible (Burnham and Anderson 2002). We considered median E to be a conservative indicator of the plausibility of each candidate model for Golden-winged Warbler density. For each model, we also calculated the proportion (M) of bootstrap replicates ($n = 1,000$) when that model was plausible.

When we had identified plausible models within each model suite, we used the plausible models to build model suite V, representing a hierarchical resource utilization process (Johnson 1980) for Golden-winged Warblers. We formulated new models using all possible combinations of the plausible models in model suites I–IV and used the same analytic approach described above for model suites I–IV. For all model suites, we considered covariates in plausible models to be biologically important if the fixed effect coefficient 95% QCI did not overlap zero.

Avian community structure. We used the cca function in package vegan 2.3-5 (Oksanen et al. 2016) to perform canonical correspondence analysis (CCA), a constrained ordination technique that combines multiple regression and correspondence analysis, to depict avian community structure. We used nonflyover detections of adult male birds within a 100-m radius to construct a matrix of

species' annual mean relative abundances at sites ($n = 121$ sites) with which to run the CCA. To derive this matrix, we calculated the maximum number of males detected across within-year visits to each point count location, then averaged across point count locations within each site, then averaged across years for each site. We excluded species with males detected in <10% of sites. Removing rare species can have negligible effects on ordinations (McCune and Grace 2002, Pos et al. 2014). We also excluded the Ruby-throated Hummingbird (*Archilochus colubris*) because it was usually detected by sight only (69% of detections), suggesting a markedly different detection process than that for more vocal songbirds. We excluded the American Goldfinch (*Spinus tristis*) because it bred primarily after our point count period (McGraw and Middleton 2009). We used biologically important covariates (i.e. covariates for which the fixed effect coefficient 95% QCI did not overlap zero) from the plausible models in model suite V as constraining covariates in the CCA. We evaluated the CCA ordination by examining partitioned variance, correlation (R^2), adjusted R^2 (Peres-Neto et al. 2006), and significance of permutation tests ($n = 1,000$ permutations; Borcard et al. 2011), and considered results statistically significant at $\alpha = 0.05$.

To further examine the relationships between the constraining covariates and avian community structure, we used the ordisurf function in package vegan 2.3-5 to fit smooth surfaces for each constraining covariate using generalized additive models with thin plate splines (Oksanen et al. 2016). To derive a single site-level covariate value to correspond with the matrix of species' relative abundances, we averaged covariate values across year for each point count location, then averaged across point count locations within each site. We used symmetric scaling for ordination diagrams (Gabriel 2002) and displayed linear combination scores so that the surface created by the ordisurf function was analogous to environmental vectors traditionally used with CCA (Oksanen et al. 2016). We used a surface created by the ordisurf function rather than the environmental vectors traditionally used with CCA so that we could evaluate the position of each species in the ordination relative to values of the constraining covariates. We considered a species to be associated with Golden-winged Warblers if it was plotted within the range of values of the constraining covariates known to be associated with greater-than-median Golden-winged Warbler density based on our density modeling.

RESULTS

Golden-winged Warbler Detection Probability
Across 1,096 100-m radius point counts conducted during May–June, 2008–2015, we recorded 225 detections of male Golden-winged Warblers (range: 0–3 males per point count). The most-supported model of availability included linear and quadratic terms for date, and 2 additional models had a $\Delta AIC \leq 2.0$ (Table 3). The most-supported model of perceptibility included a linear term for 100-m forest cover, and a model with linear and quadratic terms for 100-m forest cover was also plausible ($\Delta AIC = 1.4$; Table 3). Among plausible models, availability was negatively associated with date and time since sunrise, and perceptibility was negatively associated with 100-m forest cover.

Golden-winged Warbler Density
Two models were plausible in model suite I (5-km geospatial covariates: annual dispersal scale): one with a linear term for northing ($E = 1.0$, $M = 0.9$) and one with a linear and a quadratic term for northing ($E = 2.0$, $M = 0.8$; Appendix Figure 5). Both models indicated that Golden-winged Warbler density was inversely associated with latitude (Table 4).

A single model with a linear and a quadratic term for 1.5-km minimum elevation was plausible ($E = 1.0$, $M = 0.9$) in model suite II (1.5-km geospatial covariates: extraterritorial movement scale; Appendix Figure 5). Density peaked at intermediate values for 1.5-km minimum elevation (Table 4). A similar pattern should extend to the 5-km scale because of the highly positive correlation (correlation coefficient = 0.90) between 1.5-km and 5-km minimum elevation, which led us to exclude the latter covariate.

In model suite III (100-m geospatial covariates: intraterritorial movement scale), a model with linear terms for 100-m minimum elevation and 100-m shrubland cover ($E = 1.0$, $M = 0.8$) and a model with linear and quadratic terms for 100-m shrubland cover ($E = 1.8$, $M = 0.6$) were plausible (Appendix Figure 5). Golden-winged Warbler density was positively associated with 100-m shrubland cover and negatively associated with 100-m minimum elevation (Table 4).

No models from model suite IV (field vegetation covariates: local resource utilization scale) had median $E \leq 2.7$ (Appendix Figure 6) and therefore no models were considered plausible based on our model-selection criterion. Thus, we did not carry over any models from model suite IV into model suite V and were able to use the full set of point count data ($n = 1,096$ point counts) for model suite V rather than the subset with field vegetation data ($n = 967$). However, although none of the models in suite IV were plausible, covariates for vegetation density or sapling cover appeared in each of the 5 top-ranked models, suggesting that these covariates may be worth investigating using a slightly different scale or metric.

For model suite V, we evaluated all possible combinations of the plausible models from model suites I–III. The top-ranked model ($E = 1.0$, $M = 1.0$) had linear terms for 1.5-km minimum elevation, 100-m minimum elevation, and 100-m shrubland cover, and a quadratic term for 1.5-km minimum

TABLE 3. We formulated conditional multinomial maximum likelihood models of availability and perceptibility of Golden-winged Warblers during point count surveys in West Virginia, USA, 2008–2015, as functions of covariates using package detect 0.3-2 (Sólymos et al. 2014) in program R (R Core Team 2016). For continuous covariates (e.g., Date), we formulated models with quadratic terms (e.g., Date + Date^2) because we expected that detection probability would not always demonstrate a straight-line pattern. We evaluated competing models using differences in Akaike's information criterion (ΔAIC) and model weights (w_i; Burnham and Anderson 2002). K is the number of parameters in the model, and $-2\ln L$ is the maximum log-likelihood. We present all candidate models.

Model	K	$-2\ln L$	ΔAIC	w_i
Availability models				
Date + Date^2	3	541.6	0.0 [a]	0.37
Date	2	544.7	1.1	0.21
Date + Date^2 + TSS [b]	4	541.6	2.0	0.14
Date + TSS	3	544.6	3.0	0.08
Date + TSS + TSS^2	4	542.7	3.1	0.08
Intercept only	1	549.9	4.3	0.04
TSS + TSS^2	3	546.6	5.0	0.03
Date + Date^2 + TSS + TSS^2	5	542.7	5.1	0.03
TSS	2	549.9	6.3	0.02
Perceptibility models [c]				
100-m forest cover	2	512.8	0.0 [d]	0.55
100-m forest cover + 100-m forest cover^2	3	512.2	1.4	0.28
100-m shrubland cover	2	517.0	4.2	0.07
Intercept only	1	520.7	5.9	0.03
Wind [e]	6	516.8	5.9	0.03
100-m shrubland cover + 100-m shrubland cover^2	3	510.7	6.0	0.03
100-m herbaceous cover	2	520.7	7.9	0.01
Sky [f] + Wind	10	506.0	8.8	0.01
100-m herbaceous cover + 100-m herbaceous cover^2	3	518.2	9.9	0.00
Observer [g]	8	520.7	10.0	0.00
Sky	5	510.8	11.4	0.00

[a] Minimum AIC = 547.6.
[b] TSS = Time since sunrise.
[c] See Table 2 for covariate notation.
[d] Minimum AIC = 516.8.
[e] Wind categorized as: no wind, smoke drifts, wind felt on face, leaves rustle, small branches move, or trees sway (Hamel et al. 1996).
[f] Sky categorized as: no or few clouds; partly cloudy; cloudy or overcast; or fog, mist, or drizzle (Hamel et al. 1996).
[g] Observer = observer ID.

elevation (Appendix Figure 7). A second plausible model had the same structure but with the addition of a linear term for northing ($E = 2.5$, $M = 0.9$). In both models, Golden-winged Warbler density peaked when 1.5-km minimum elevation was 804 m, was negatively associated with 100-m minimum elevation, and was positively associated with 100-m shrubland cover (Table 4, Figure 3). Unlike in model suite I, the 95% QCI for the northing fixed-effect coefficient overlapped zero (Table 4).

Avian Community Structure

We detected 129 species and 2 hybrid phenotypes (Brewster's and Lawrence's Warblers) during point counts in 2008–2015 (Table 5). We used 52 species for the CCA after excluding 77 species and the 2 hybrid phenotypes because they either occurred on <10% of sites or exhibited characteristics that made them unsuitable for analysis (American Goldfinch, Ruby-throated Hummingbird). The constrained axes explained 11% (axis 1 = 7%, axis 2 = 3%, axis 3 = 1%) of the variance in the avian community, which when adjusted (adjusted R^2) decreased to 8% (axis 1 = 5%, Axis 2 = 2%, Axis 3 = 1%). The unconstrained axes explained the vast majority (adjusted R^2 = 92%) of the variation in the avian community, but permutation tests suggested that the global CCA model ($F_{3,117} = 4.6$, $P = 0.001$, all canonical axes (axis 1: $F_{1,117} = 8.5$, $P = 0.001$; axis 2: $F_{1,117} = 3.6$, $P = 0.001$; axis 3: $F_{1,117} = 1.6$, $P = 0.02$), and all constraining covariates (100-m shrubland cover: $F_{1,117} = 3.8$, $P = 0.001$; 100-m minimum elevation: $F_{1,117} = 8.3$, $P = 0.001$; 1.5-km minimum elevation: $F_{1,117} = 1.7$, $P = 0.02$) were statistically significant.

By fitting surfaces (rather than vectors) for constraining covariates, we could objectively determine which species grouped with the Golden-winged Warbler (Table 5, Figure 4) based on the range of values predicted to be associated with greater-than-median densities of Golden-winged Warblers (Figure 3). The White-eyed Vireo (*Vireo griseus*), Blue-gray Gnatcatcher (*Polioptila caerulea*), Gray Catbird

TABLE 4. Median fixed effect coefficients, median random effect standard deviations, and 95% quantile confidence limits (QCL) for plausible models (median evidence ratio $\leq$ 2.7) in each model suite of Golden-winged Warbler density in West Virginia, USA, 2008–2015. Model suite I = 5-km geospatial (annual dispersal) scale, model suite II = 1.5-km geospatial (extraterritorial movement) scale, model suite III = 100-m geospatial (intraterritorial movement) scale, model suite IV = local resource utilization scale, and model suite V = all possible combinations of plausible models from model suites I–III (Appendix Figures 5–7). Model suite IV had no plausible models.

Model suite	Fixed effect	Fixed effect coefficient (95% QCL)	Random effect standard deviation (95% QCL)		
			Point count ID	Site	Year
I	Intercept	−0.5 (−1.5, 0.6)	1.2 (0.8, 1.8)	1.7 (1.0, 3.2)	0.4 (0.2, 0.6)
	Northing	−4.5 (−6.1, −3.0)			
	Intercept	−2.6 (−5.5, 0.0)	1.2 (0.8, 1.8)	1.7 (0.9, 3.0)	0.4 (0.2, 0.6)
	Northing	4.8 (−5.1, 15.4)			
	Northing^2	−8.9 (−18.7, −0.3)			
II	Intercept	−59.4 (−76.3, −43.3)	1.4 (0.9, 2.0)	0.4 (0.0, 1.4)	0.4 (0.2, 0.6)
	1.5-km minimum elevation	149.8 (107.8, 194.2)			
	1.5-km minimum elevation^2	−95.7 (−124.1, −69.1)			
III	Intercept	−0.6 (−2.7, 1.2)	1.0 (0.7, 1.5)	0.4 (0.0, 1.7)	0.4 (0.2, 0.6)
	100-m minimum elevation	−4.8 (−6.9, −2.5)			
	100-m shrubland cover	4.3 (3.2, 5.5)			
	Intercept	−7.0 (−10.6, −5.3)	0.8 (0.5, 1.2)	1.3 (0.5, 2.5)	0.4 (0.2, 0.6)
	100-m shrubland cover	12.1 (6.9, 22.0)			
	100-m shrubland cover^2	−6.4 (−13.2, −2.7)			
V	Intercept	−60.9 (−79.2, −45.2)	0.7 (0.4, 1.0)	0.0 (0.0, 0.2)	0.4 (0.2, 0.6)
	1.5-km minimum elevation	161.4 (119.4, 209.6)			
	1.5-km minimum elevation^2	−102.1 (−132.1, −76.0)			
	100-m shrubland cover	3.9 (2.9, 4.9)			
	100-m minimum elevation	−6.6 (−8.8, −4.7)			
	Intercept	−61.0 (−85.5, −41.0)	0.7 (0.4, 1.0)	0.0 (0.0, 0.2)	0.4 (0.2, 0.6)
	Northing	0.1 (−2.3, 2.8)			
	1.5-km minimum elevation	161.7 (111.7, 220.4)			
	1.5-km minimum elevation^2	−102.3 (−138.1, −71.1)			
	100-m shrubland cover	3.9 (2.8, 4.9)			
	100-m minimum elevation	−6.7 (−9.1, −4.6)			

(*Dumetella carolinensis*), Brown Thrasher (*Toxostoma rufum*), and Yellow Warbler (*Setophaga petechia*) were plotted with Golden-winged Warblers within the optimum (for Golden-winged Warblers) ranges of all constraining covariate surfaces (100-m shrubland cover = 52–100%, 100-m minimum elevation = 540–914 m, 1.5-km minimum elevation = 602–1,006 m; Figure 4). We thus consider these species as most likely to benefit from
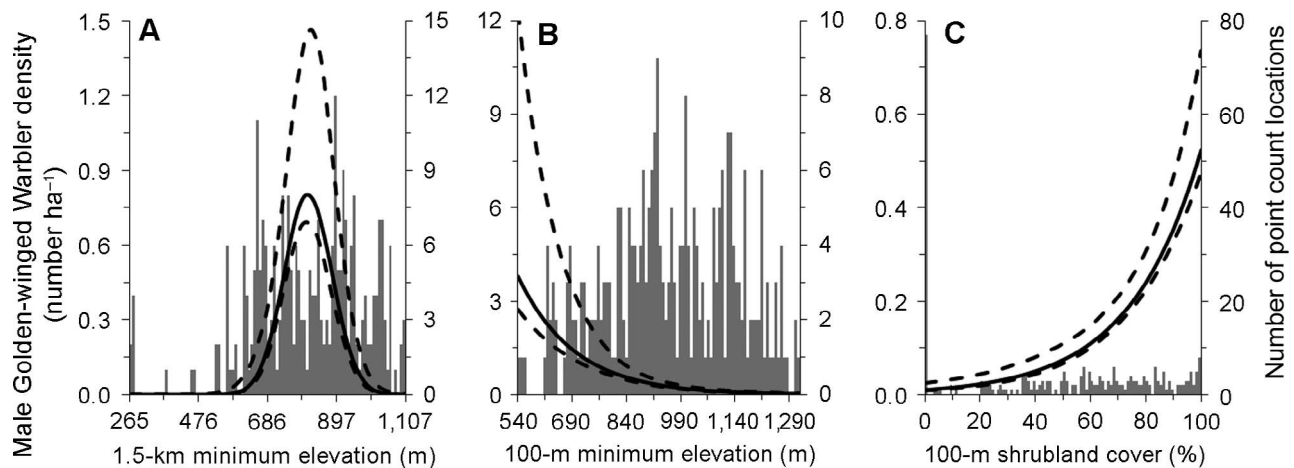
FIGURE 3. Median marginal predicted male Golden-winged Warbler density (solid line) and 95% quantile confidence interval (dashed lines) in West Virginia, USA, 2008–2015. Predictions are based on the top density model including fixed effects for (**A**) 1.5-km minimum elevation, (**B**) 100-m minimum elevation, and (**C**) 100-m shrubland cover, and random effects for point count location ID, site, and year (Table 4). Gray bars represent the number of point count locations sampled. See Table 2 for covariate descriptions.

conservation strategies aimed at maximizing Golden-winged Warbler density. Twenty-one species were plotted within the optimum ranges of 1.5-km and 100-m minimum elevation (Figure 4). We consider these species most likely to be affected, either positively or negatively to varying degrees, by management for Golden-winged Warblers, because they predominantly occur at elevations that would be considered for management. Species that were plotted closer to the 52% line for 100-m shrubland cover, such as the American Redstart (*Setophaga ruticilla*), are more likely to benefit from, or at least tolerate, increases to 100-m shrubland cover. Conversely, species that were plotted at lower values for 100-m shrubland cover, such as the Hooded Warbler (*Setophaga citrina*), are more likely to be negatively affected by increases to 100-m shrubland cover.

DISCUSSION

Our results confirm and refine existing knowledge about Golden-winged Warbler populations in the Appalachian Mountain region, particularly with regard to elevation (Crawford et al. 2016) and shrubland cover (Aldinger and Wood 2014). We found evidence of a previously undocumented hierarchical resource utilization process (Johnson 1980), wherein Golden-winged Warbler density showed spatial scale–dependent associations with elevation. At the 100-m radius scale, Golden-winged Warbler density was negatively associated with minimum elevation and peaked at 540 m, the lowest 100-m minimum elevation value that we sampled. But at the 1.5-km radius scale, Golden-winged Warbler density peaked at 804 m, near the midpoint of the range of 1.5-km minimum elevation values that we sampled. This knowledge can enhance conservation planning as it identifies the most important variables favoring high densities of Golden-winged Warblers in a way that accounts for multiple spatial scales relevant to the species' life history. Finally, we extended our findings to the broader avian community and formulated objective criteria that identified 5 species likely to benefit from Golden-winged Warbler management and 21 species likely to be affected positively or negatively in proportion to their affinity for early-successional vegetation communities. Our results provide information for future comprehensive modeling efforts (e.g., Peterson et al. 2016) and for organizations involved in local conservation efforts in West Virginia (e.g., USDA Forest Service, U.S. Natural Resources Conservation Service, and West Virginia Division of Natural Resources).

Golden-winged Warbler Density
The connection between Golden-winged Warblers and elevation is well documented, the prevailing knowledge being that higher elevations (>500 m) are preferred up to a point (<1,200 m) in the central Appalachian Mountains (Crawford et al. 2016, Rosenberg et al. 2016a). Studies in the Appalachian Mountain region have explicitly evaluated elevation as a covariate (Welton 2003, Patton et al. 2010, Bakermans et al. 2015) or considered it an important study design component (Bulluck and Buehler 2008, Aldinger and Wood 2015). Nonetheless, our understanding of the role of elevation is incomplete because these previous studies generally did not consider multiple spatial scales concurrently. This is reflected in the practice of selecting sites for Golden-winged Warbler management based on whether the site itself, not the surrounding area, is above an elevational threshold (K. Aldinger personal observation). Had we evaluated a single spatial scale corresponding to our point count radius, we might have incompletely concluded that Golden-winged Warbler management was suitable at a much broader range of sites, given the shape and direction of the association between density and 100-m minimum elevation (optimum 100-m minimum elevation = 540–914 m with the peak at 540 m; Figure 3). However, many of these sites would not be suitable for Golden-winged Warblers because their elevations within 1.5 km are <602 m or >1,006 m. And while it is important not to make inferences outside the range of data in general (Conn et al. 2015), it could be tempting to forecast the density–elevation association below the range of our data, given its shape and direction.

Applying results without the context of the larger geographical landscape and existing knowledge in this case could have led to decisions that exacerbated Golden-winged Warbler population declines by encouraging contact with Blue-winged Warblers (*Vermivora cyanoptera*) along the western slopes of the Allegheny Mountains at elevations around 500 m (Crawford et al. 2016). Blue-winged Warblers consistently replace Golden-winged Warblers through hybridization within 50 yr of initial contact (Gill 1980, Rosenberg et al. 2016a). Concurrently modeling multiple scales instead led to the conclusion that high-elevation landscapes (optimum 1.5-km minimum elevation = 602–1,006 m, with the peak at 804 m) could provide refugia for Golden-winged Warblers, perhaps even at local (100-m scale) elevations that would otherwise be inhabited by Blue-winged Warblers. Because the 1.5-km and 5.0-km scales correspond to within-season extraterritorial movements (Frantz et al. 2016) and annual dispersal (K Aldinger personal observation), respectively, these mid- to high-elevation landscapes may buffer Golden-winged Warbler populations from extrapair mating attempts and immigration by Blue-winged Warblers.

We consider 2 hypotheses to be likely explanations for the shape and direction of the 100-m spatial scale association between Golden-winged Warbler density and elevation (Figure 3). First, during much of the 20th century in West Virginia, Golden-winged Warblers nested at

TABLE 5. Species detected during point counts conducted in May–June, 2008–2015, in West Virginia, USA. For canonical correspondence analysis (Figure 4), we excluded species when nonflyover detections of males occurred in fewer than 10% of sites across 2008–2015 (see "% male occurrence" column). We also excluded Ruby-throated Hummingbirds because they exhibited limited vocalizations and American Goldfinches because they were somewhat nonterritorial, wide-ranging, gregarious, and bred later than most other songbirds. An "X" in the appropriate column indicates whether the species' position in the ordination overlapped the range of values for the constraining variable associated with greater-than-median Golden-winged Warbler density (1.5-km minimum elevation = 602–1,006 m, 100-m minimum elevation = 540–914 m, 100-m shrubland cover = 52–100%).

Common name	Abbreviation	Scientific name	% male occurrence	1.5-km minimum elevation	100-m minimum elevation	100-m shrubland cover
Canada Goose	CANG	*Branta canadensis*	0			
Wood Duck [e]	WODU	*Aix sponsa*	0			
Northern Bobwhite [a,e]	NOBO	*Colinus virginianus*	1			
Ruffed Grouse [a,e]	RUGR	*Bonasa umbellus*	9			
Wild Turkey [f]	WITU	*Meleagris gallopavo*	1			
Mourning Dove	MODO	*Zenaida macroura*	24	X	X	
Yellow-billed Cuckoo	YBCU	*Coccyzus americanus*	15	X	X	
Black-billed Cuckoo [a,d,h]	BBCU	*Coccyzus erythropthalmus*	21	X		
Common Nighthawk [a]	CONI	*Chordeiles minor*	0			
Chimney Swift [a,d]	CHSW	*Chaetura pelagica*	1			
Ruby-throated Hummingbird	RTHU	*Archilochus colubris*	17			
Killdeer	KILL	*Charadrius vociferus*	0			
American Woodcock [a,c]	AMWO	*Scolopax minor*	0			
Great Blue Heron [b]	GBHE	*Ardea herodias*	0			
Green Heron [b]	GRHE	*Butorides virescens*	0			
Turkey Vulture	TUVU	*Cathartes aura*	0			
Northern Harrier [b,e]	NOHA	*Circus hudsonius*	0			
Sharp-shinned Hawk [e]	SSHA	*Accipiter striatus*	0			
Cooper's Hawk	COHA	*Accipiter cooperii*	0			
Red-shouldered Hawk	RSHA	*Buteo lineatus*	0			
Broad-winged Hawk [a,e]	BWHA	*Buteo platypterus*	0			
Red-tailed Hawk	RTHA	*Buteo jamaicensis*	2			
Great Horned Owl	GHOW	*Bubo virginianus*	0			
Barred Owl	BADO	*Strix varia*	0			
Belted Kingfisher	BEKI	*Megaceryle alcyon*	1			
Red-headed Woodpecker [b,e,h]	RHWO	*Melanerpes erythrocephalus*	0			
Red-bellied Woodpecker	RBWO	*Melanerpes carolinus*	3			
Yellow-bellied Sapsucker [b,d]	YBSA	*Sphyrapicus varius*	2			
Downy Woodpecker	DOWO	*Picoides pubescens*	3			
Hairy Woodpecker	HAWO	*Picoides villosus*	4			
Northern Flicker [e]	NOFL	*Colaptes auratus*	3			
Pileated Woodpecker	PIWO	*Dryocopus pileatus*	2			
American Kestrel [a]	AMKE	*Falco sparverius*	1			
Olive-sided Flycatcher [a,e,h]	OSFL	*Contopus cooperi*	0			
Eastern Wood-pewee [e]	EAWP	*Contopus virens*	44	X	X	
Acadian Flycatcher [d]	ACFL	*Empidonax virescens*	20	X	X	
Alder Flycatcher [b,f]	ALFL	*Empidonax alnorum*	11			X
Willow Flycatcher [e]	WIFL	*Empidonax traillii*	5			
Least Flycatcher [b]	LEFL	*Empidonax minimus*	35	X		X
Eastern Phoebe	EAPH	*Sayornis phoebe*	19	X	X	
Great Crested Flycatcher	GCFL	*Myiarchus crinitus*	12	X	X	
Eastern Kingbird	EAKI	*Tyrannus tyrannus*	1			
White-eyed Vireo	WEVI	*Vireo griseus*	10	X	X	X
Yellow-throated Vireo [e]	YTVI	*Vireo flavifrons*	11		X	
Blue-headed Vireo	BHVI	*Vireo solitarius*	44	X		
Warbling Vireo	WAVI	*Vireo gilvus*	2			
Red-eyed Vireo	REVI	*Vireo olivaceus*	98	X	X	
Blue Jay	BLJA	*Cyanocitta cristata*	0			
American Crow	AMCR	*Corvus brachyrhynchos*	0			
Common Raven	CORA	*Corvus corax*	0			
Tree Swallow	TRES	*Tachycineta bicolor*	2			
Northern Rough-winged Swallow	NRWS	*Stelgidopteryx serripennis*	0			
Barn Swallow	BARS	*Hirundo rustica*	2			

TABLE 5. Continued.

Common name	Abbreviation	Scientific name	% male occurrence	1.5-km minimum elevation	100-m minimum elevation	100-m shrubland cover
Black-capped Chickadee [e]	BCCH	*Poecile atricapillus*	55	X	X	
Tufted Titmouse	TUTI	*Baeolophus bicolor*	59	X	X	
Red-breasted Nuthatch	RBNU	*Sitta canadensis*	0			
White-breasted Nuthatch	WBNU	*Sitta carolinensis*	3			
Brown Creeper [b]	BRCR	*Certhia americana*	1			
House Wren	HOWR	*Troglodytes aedon*	23	X	X	
Winter Wren	WIWR	*Troglodytes hiemalis*	5			
Carolina Wren	CARW	*Thryothorus ludovicianus*	12	X	X	
Blue-gray Gnatcatcher	BGGN	*Polioptila caerulea*	20	X	X	X
Golden-crowned Kinglet	GCKI	*Regulus satrapa*	18	X		
Ruby-crowned Kinglet	RCKI	*Regulus calendula*	2			
Eastern Bluebird	EABL	*Sialia sialis*	22	X	X	
Veery [b]	VEER	*Catharus fuscescens*	31	X		
Swainson's Thrush [b]	SWTH	*Catharus ustulatus*	4			
Hermit Thrush	HETH	*Catharus guttatus*	8			
Wood Thrush [a,c,h]	WOTH	*Hylocichla mustelina*	35	X	X	
American Robin	AMRO	*Turdus migratorius*	51	X		X
Gray Catbird	GRCA	*Dumetella carolinensis*	57	X	X	X
Brown Thrasher [e]	BRTH	*Toxostoma rufum*	33	X	X	X
Northern Mockingbird	NOMO	*Mimus polyglottos*	3			
European Starling	EUST	*Sturnus vulgaris*	2			
Cedar Waxwing	CEDW	*Bombycilla cedrorum*	9			
House Finch	HOFI	*Haemorhous mexicanus*	1			
Purple Finch	PUFI	*Haemorhous purpureus*	1			
Red Crossbill [b,d]	RECR	*Loxia curvirostra*	0			
American Goldfinch	AMGO	*Spinus tristis*	54			
Eastern Towhee [e]	EATO	*Pipilo erythrophthalmus*	88	X		X
Chipping Sparrow	CHSP	*Spizella passerina*	49	X		
Clay-colored Sparrow [b]	CCSP	*Spizella pallida*	0			
Field Sparrow [a,d]	FISP	*Spizella pusilla*	65	X		X
Vesper Sparrow [a]	VESP	*Pooecetes gramineus*	7			
Savannah Sparrow	SAVS	*Passerculus sandwichensis*	3			
Grasshopper Sparrow [a,e]	GRSP	*Ammodramus savannarum*	1			
Song Sparrow	SOSP	*Melospiza melodia*	43	X	X	
Swamp Sparrow	SWSP	*Melospiza georgiana*	1			
White-throated Sparrow [e]	WTSP	*Zonotrichia albicollis*	0			
Dark-eyed Junco	DEJU	*Junco hyemalis*	33	X		
Yellow-breasted Chat [a,e]	YBCH	*Icteria virens*	9			
Bobolink [a,h]	BOBO	*Dolichonyx oryzivorus*	2			
Eastern Meadowlark [a,e]	EAME	*Sturnella magna*	7			
Orchard Oriole	OROR	*Icterus spurius*	1			
Baltimore Oriole	BAOR	*Icterus galbula*	21		X	
Red-winged Blackbird	RWBL	*Agelaius phoeniceus*	16	X	X	
Brown-headed Cowbird	BHCO	*Molothrus ater*	32	X	X	
Common Grackle	COGR	*Quiscalus quiscula*	3			
Ovenbird	OVEN	*Seiurus aurocapilla*	48	X		
Worm-eating Warbler [a,c]	WEWA	*Helmitheros vermivorum*	3			
Louisiana Waterthrush [a,d]	LOWA	*Parkesia motacilla*	3			
Golden-winged Warbler [a,c,g]	GWWA	*Vermivora chrysoptera*	26	X	X	X
Blue-winged Warbler [b,c]	BWWA	*Vermivora cyanoptera*	10		X	
Brewster's Warbler	BRWA	*Vermivora chrysoptera × cyanoptera*	6			
Lawrence's Warbler	LAWA	*Vermivora chrysoptera × cyanoptera*	0			
Black-and-white Warbler [e]	BAWW	*Mniotilta varia*	46	X	X	
Tennessee Warbler	TEWA	*Oreothlypis peregrina*	2			
Mourning Warbler	MOWA	*Geothlypis philadelphia*	27	X		
Kentucky Warbler [a,c,h]	KEWA	*Geothlypis formosa*	2			
Common Yellowthroat	COYE	*Geothlypis trichas*	66	X		X
Hooded Warbler [d]	HOWA	*Setophaga citrina*	41	X	X	
American Redstart	AMRE	*Setophaga ruticilla*	57	X	X	

TABLE 5. Continued.

Common name	Abbreviation	Scientific name	% male occurrence	1.5-km minimum elevation	100-m minimum elevation	100-m shrubland cover
Cerulean Warbler [a,c,h]	CERW	*Setophaga cerulea*	9			
Northern Parula [e]	NOPA	*Setophaga americana*	10			
Magnolia Warbler	MAWA	*Setophaga magnolia*	29	X		
Bay-breasted Warbler [e]	BBWA	*Setophaga castanea*	1			
Blackburnian Warbler [b,e]	BLBW	*Setophaga fusca*	35	X		
Yellow Warbler	YEWA	*Setophaga petechia*	25	X	X	X
Chestnut-sided Warbler	CSWA	*Setophaga pensylvanica*	85	X		
Blackpoll Warbler [f]	BLPW	*Setophaga striata*	7			
Black-throated Blue Warbler [b]	BTBW	*Setophaga caerulescens*	22	X		
Pine Warbler	PIWA	*Setophaga pinus*	2			
Yellow-rumped Warbler	YRWA	*Setophaga coronata*	3			
Yellow-throated Warbler [e]	YTWA	*Setophaga dominica*	2			
Prairie Warbler [a,c,h]	PRAW	*Setophaga discolor*	2			
Black-throated Green Warbler	BTNW	*Setophaga virens*	53	X		
Canada Warbler [a,d,h]	CAWA	*Cardellina canadensis*	7			
Scarlet Tanager [e]	SCTA	*Piranga olivacea*	69	X	X	
Northern Cardinal	NOCA	*Cardinalis cardinalis*	41	X	X	
Rose-breasted Grosbeak	RBGR	*Pheucticus ludovicianus*	41	X		X
Indigo Bunting [e]	INBU	*Passerina cyanea*	95	X		

[a] Priority 1 (West Virginia Division of Natural Resources 2015).
[b] Priority 2 (West Virginia Division of Natural Resources 2015).
[c] Highest priority (Appalachian Mountains Joint Venture Management Board 2008).
[d] High priority (Appalachian Mountains Joint Venture Management Board 2008).
[e] Moderate priority (Appalachian Mountains Joint Venture Management Board 2008).
[f] Low priority (Appalachian Mountains Joint Venture Management Board 2008).
[g] Red Watch List: Species with extremely high vulnerability due to small population and range, high threats, and rangewide declines (Rosenberg et al. 2016b).
[h] "D" Yellow Watch List: Species with population declines and moderate to high threats (Rosenberg et al. 2016b).

elevations considerably lower (nearly to the Ohio River; Brooks 1940) than the current occupied elevational range (Crawford et al. 2016). This warbler may actually be a relatively new inhabitant of the West Virginia highlands (Rives 1898, Brooks 1944). Thus, the inverse correlation between density and elevation at the 100-m scale may be a relic of the species' historic distribution preserved by the surrounding higher-elevation landscape (1.5-km minimum elevation: 602–1,006 m). Our second hypothesis is that vegetation communities capable of supporting higher densities of Golden-winged Warblers occur more often on lower-elevation side slopes and valleys than on higher-elevation mountain peaks. The former are generally better suited for agriculture, the predominant source of Golden-winged Warbler nesting cover in our study area (Aldinger and Wood 2014, Aldinger et al. 2015). A study using controlled experimental plots at different elevations may be able to address these hypotheses.

The other biologically important covariate in our top Golden-winged Warbler density model, shrubland cover, has also been previously identified as important (Hanowski 2002, Bulluck and Buehler 2008, Roth et al. 2012, Aldinger and Wood 2014). In the most similar study that we found,

Golden-winged Warblers were absent from point counts in Minnesota and Wisconsin, USA, when 100-m shrubland cover was <10% (Hanowski 2002). Our raw point count data showed that we likewise failed to detect Golden-winged Warblers when 100-m shrubland cover was <11%, but density did not reach higher-than-median levels until 100-m shrubland cover was >52%. At the other end of the compositional spectrum, our models suggested that density was greatest when 100-m shrubland cover was 100%. A 100-m radius circle composed purely of shrubland (3.1 ha) is one-quarter the size of the largest recommended contiguous circular patch (12.6 ha) of early-successional cover for the species (<200 m to nearest older age-class forest; Rohrbaugh et al. 2016). A minimum of 9–10 ha of shrubland may be preferred by nesting Golden-winged Warblers (Confer and Knapp 1981, Roth et al. 2014). Therefore, managing roughly circular or regularly shaped patches of contiguous shrubland cover of 9.0–12.6 ha in size surrounded by older age-class forest may ensure that Golden-winged Warblers use the entire patch. Higher densities may be achieved within each patch by arranging multiple patches in a network with <2 km between patches (Bakermans et al. 2015). Irregularly shaped patches
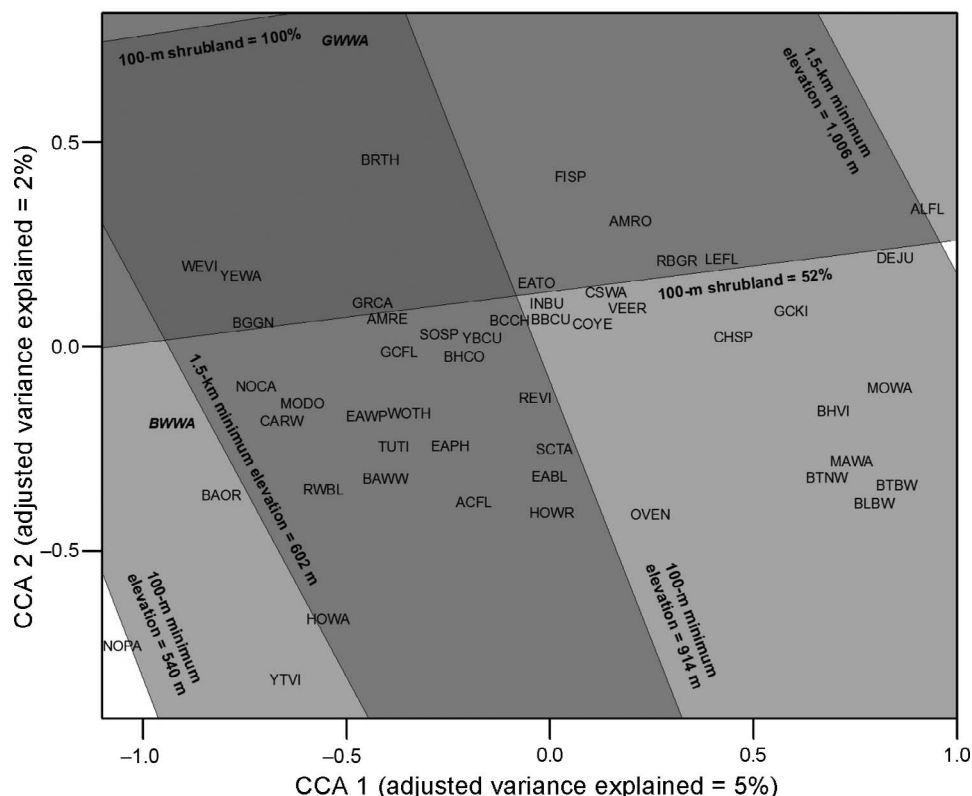
FIGURE 4. Canonical correspondence analysis results for species within the ranges of fitted covariate surface values predicted to be associated with greater-than-median densities of Golden-winged Warblers (100-m shrubland cover = 52–100%, 100-m minimum elevation = 540–914 m, 1.5-km minimum elevation = 602–1,006 m; Appendix Figure 5). The Blue-winged Warbler (BWWA, in bold italicized font) is highlighted because the species hybridizes with the Golden-winged Warbler (GWWA, also in bold italicized font). Darker shading represents overlapping covariate ranges. See Table 5 for species abbreviations.

or patches with embedded islands of canopy trees (Roth et al. 2014) may be preferred to create larger extents of Golden-winged Warbler nesting cover. A scale-variant compositional analysis conditioned on Golden-winged Warbler abundance or occupancy in which cover type is evaluated as a function of scale would further improve guidelines for the optimum proportion of shrubland in a given area.

Consistent in density modeling and field observations was an emphasis on shrubland rather than young forest cover. We detected no Golden-winged Warblers during point counts in locations classified as young forest ($n = 79$ point counts, $n = 27$ point count locations, $n = 13$ sites), despite the range of ages (1–20+ breeding seasons after timber harvest) and, consequently, stages of vegetative succession sampled. While our data show a preference for shrublands over young forest, Golden-winged Warblers do breed in young forest cover elsewhere in their range (Klaus and Buehler 2001, Patton et al. 2010, Bakermans et al. 2015) and occasionally in West Virginia (R. Bailey personal communication). Historically, in West Virginia, the Golden-winged Warbler was a fixture of the "chestnut sprout

association" (Brooks 1940), a term describing the young forest cover resulting from mass die-off of American chestnuts (*Castanea dentata*). Thus, an alternative explanation for the apparent preference for shrublands over young forests is that contemporary forest management practices in our area may be inadequate for nesting Golden-winged Warblers. The most common timber-harvest method in West Virginia is partial harvesting, especially diameter-limit harvests in which only merchantable trees greater than a designated diameter are cut (62% of harvests: McGill et al. 2004; 80% of harvests: Fajvan et al. 1998). Partial harvesting generally does not remove enough trees to create nesting cover for Golden-winged Warblers (Weakland et al. 2002). Furthermore, partial harvesting can decrease forest productivity and shift tree species composition toward shade-tolerant species (Schuler 2004), which could reduce future opportunities to harvest timber in a way that would benefit Golden-winged Warblers. The young forests that we sampled were the result of even-aged forest management in which nearly all trees in an area were cut, which is an uncommon practice in West Virginia (Fajvan et al. 1998). When even-aged

management does occur, it is unlikely that adequate Golden-winged Warbler nesting cover will develop because management practices, including timber harvesting, that are implemented specifically to create nesting cover can still fall short of attaining recommended vegetation characteristics (Roth et al. 2012, McNeil et al. 2017). Critical steps for the conservation of the species in West Virginia may therefore be to (1) create and maintain shrubland vegetation communities (Golden-winged Warbler Working Group 2013) and (2) promote species-specific forest management guidelines (Bakermans et al. 2011), especially within 2 km of known Golden-winged Warbler breeding populations in shrublands (Bakermans et al. 2015). The latter step could elucidate whether Golden-winged Warblers exhibit a preference for shrubland over young forest or if changes to forest management practices are needed.

Avian Community Structure

Our second objective was to translate covariate levels associated with greater-than-median densities of Golden-winged Warblers into implications for the broader avian community. The most important covariates associated with Golden-winged Warbler density explained just 8% of the variation in the avian community, probably due to our short list of constraining variables. Still, the global CCA model, all constrained axes, and all constraining variables were statistically significant, and the ordination plot and fitted surfaces were intuitive and corroborated our Golden-winged Warbler density modeling, thus warranting further interpretation.

The list of species most closely associated with high densities of Golden-winged Warblers was relatively short, suggesting that the species may have limited value as a surrogate for conservation of the larger avian community (Caro and O'Doherty 1999). However, a broader consideration of temporal and spatial scales is warranted before dismissing the surrogate species concept altogether. Our data represent a temporal snapshot of the nesting period for most songbirds in our study area, based on morning singing behavior. Vegetation communities used during morning singing bouts during the nesting period may not be representative of the range of vegetation communities used throughout the course of an entire day. Golden-winged Warblers in Minnesota used forest cover more in the afternoon than in the morning, presumably for prolonged foraging bouts (Streby et al. 2012). Ovenbirds (*Seiurus aurocapilla*) in Saskatchewan, Canada, on the other hand, displayed the opposite trend and moved away from interior forest in the afternoon (Mazerolle and Hobson 2003). Similarly, cover types used for nesting may not be representative of the range of cover types used during the entire breeding season. Songbird species that nest in early-successional vegetation communities may

raise their fledglings in forest cover and vice versa (King and Schlossberg 2014, Streby et al. 2016a). Analogous arguments may be made for spatial scale. Core areas of a bird's territory used for conspicuous activities such as nesting and singing may differ markedly from peripheral areas used for foraging or rearing fledglings (McDermott and Wood 2010, Streby et al. 2016a). Finally, the scales of our constraining covariates were relatively local compared with the species' geographic distribution across the Allegheny Mountains of West Virginia. Thus, at longer temporal and broader spatial scales, management for Golden-winged Warbler nesting cover likely will benefit, or at least be compatible with, more species than our results indicate. A management approach that aims to create dynamic forested landscapes (Roth et al. 2012) with empirically derived age-class distribution targets (Johst et al. 2011) across broad scales (>5-km radius) may be the preferred approach to benefit Golden-winged Warblers and many other bird species.

Specifically for shrubland-nesting birds, our ordination suggests that Golden-winged Warblers may be the most area-sensitive in our study area because they were plotted farther along the 100-m shrubland cover gradient than any other species. This pronounced area sensitivity, along with hybridization with Blue-winged Warblers, may help to explain why Golden-winged Warbler populations have declined faster than all but those of the Bewick's Wren (*Thryomanes bewickii*) among shrubland-nesting birds in the Appalachian Mountains Bird Conservation Region (Sauer et al. 2017). Given our results, management for Golden-winged Warblers would apparently meet the needs of other shrubland-nesting bird species that require relatively smaller areas of shrubland (Watson et al. 2001). Such an interpretation has merit because many songbirds in eastern North America are threatened primarily by limited abundance of early-successional vegetation communities (King and Schlossberg 2014). Still, incorporating the unique ecology of each species and tracking individual species through an adaptive management framework to the greatest extent possible remain important facets of a conservation strategy focused on a single species (Lindenmayer et al. 2002).

Of the 5 species most likely to benefit from Golden-winged Warbler management (Table 5, Figure 4), only the Brown Thrasher is listed as a priority species in the region (Appalachian Mountains Joint Venture Management Board 2008). Of the 21 species most likely to be affected because they predominantly occur at elevations associated with greater-than-median densities of Golden-winged Warblers (Table 5), 7 are listed as priority species (Appalachian Mountains Joint Venture Management Board 2008, West Virginia Division of Natural Resources 2015, Rosenberg et al. 2016b). One of the most pertinent of these species is the Wood Thrush (*Hylocichla mustelina*),

because of its high priority ranking by multiple conservation groups (Table 5) and association with large tracts of unbroken forest (Evans et al. 2011), placing the species seemingly at odds with the Golden-winged Warbler. Forest fragmentation and edge density, both of which potentially increase in the landscape when managing for Golden-winged Warblers, are negatively associated with the nest survival of Wood Thrushes (Driscoll et al. 2005). However, Wood Thrushes require shrubland and young forest during the postbreeding period (Vega Rivera et al. 1998). Furthermore, landscape forest cover recommendations for Golden-winged Warblers in the Appalachian Mountains region ($\geq$75%; Wood et al. 2016) would likely moderate edge effects for the Wood Thrush (Driscoll and Donovan 2004) and other species (Hunter et al. 2001). Therefore, recommendations calling for 15% of heavily forested landscapes to be maintained in shrubland and young forest cover (Bakermans et al. 2015) could benefit both the Wood Thrush and Golden-winged Warbler, among other species, if planned to minimize fragmentation of large tracts of later-successional forest (Bonnot et al. 2013).

Brown-headed Cowbirds (*Molothrus ater*) were also plotted within elevations associated with greater-than-median densities of Golden-winged Warblers. Cowbirds are sometimes listed as an important threat to Golden-winged Warbler populations because of brood parasitism (Buehler et al. 2007, Confer et al. 2011). A review of published literature found that parasitism rates varied geographically from 0% to 35% (Aldinger 2010), and a recent book on Golden-winged Warblers mentioned Brown-headed Cowbirds only one time (Streby et al. 2016b). These disparate reports suggest that the impacts of Brown-headed Cowbird brood parasitism on Golden-winged Warblers are localized. In fact, across 2 studies including 429 Golden-winged Warbler nests in West Virginia, no nests were parasitized (Canterbury et al. 1996, Aldinger and Wood 2014). The lack of parasitism may have been due to the >82% forest cover within the Golden-winged Warbler's range in West Virginia (Morin et al. 2016). Forest cover is negatively associated with parasitism rate (Cox et al. 2012). However, given that cowbirds occurred at 32% of sites (Table 5), more abundant alternate hosts also may have diluted the effects of parasitism on the rarer Golden-winged Warbler (Barber and Martin 1997). To avoid increasing parasitism rates, the relative positions of the Golden-winged Warbler and Brown-headed Cowbird in our ordination suggest maximizing 100-m shrubland cover, which reduces 100-m herbaceous cover that likely attracts Brown-headed Cowbirds.

Blue-winged Warblers merit mention because they hybridize with and generally replace Golden-winged Warblers (Gill 1980, Rosenberg et al. 2016a). However, the Blue-winged Warbler's position in our ordination only overlapped the range of 100-m minimum elevation associated with greater-than-median densities of Golden-winged Warblers. This result contextualizes our findings from the density modeling and provides a more mechanistic understanding of the complex relationship between Golden-winged Warblers, Blue-winged Warblers, and elevation. We infer that an important pathway for Blue-winged Warblers to hybridize with and replace Golden-winged Warblers is through extraterritorial movements of Blue-winged Warblers at lower elevations seeking extrap-air copulation with nearby (within ~1.5 km) Golden-winged Warblers at higher elevations. We sampled multiple sites during 2008–2015 with Golden-winged Warblers and hybrids without documenting any Blue-winged Warbler males or females in any sites during intensive banding, territory mapping, and nest searching activities (K. Aldinger personal observation). Focusing conservation efforts on higher values for 100-m minimum elevation and to the right-hand side of the peak (804 m) of 1.5-km minimum elevation (Figure 3) may reduce the risk of contact between the 2 species.

Conclusion

Our results indicate that for single-species management of Golden-winged Warblers in the West Virginia highlands, the most important variables are 1.5-km minimum elevation of 602–1,006 m, 100-m minimum elevation of 540–914 m, and 100-m shrubland cover of 52–100%. The important practical application of these results for conservation planners in our area is to consider minimum elevation 1.5 km or even 5.0 km beyond the site boundary, which will influence whether extraterritorial movements and dispersal into the site will consist of Golden-winged Warblers or Blue-winged Warblers. Twenty-six species seemed likely to be affected in some way by management for Golden-winged Warblers, yet only White-eyed Vireos, Blue-gray Gnatcatchers, Gray Catbirds, Brown Thrashers, and Yellow Warblers were strongly associated with the values of shrubland cover and elevation favored by Golden-winged Warblers. Still, we suggest that Golden-winged Warblers may be the most shrubland area–sensitive songbird in our study area, while still requiring heavily forested landscapes (Wood et al. 2016). Management meeting these requirements could concurrently meet the needs of Golden-winged Warblers and these 26 other species.
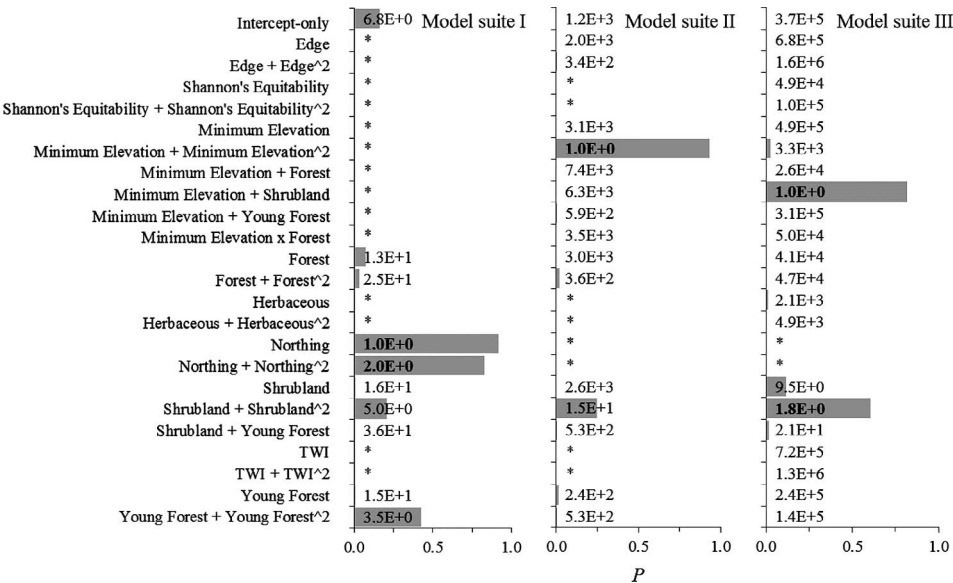
ACKNOWLEDGMENTS

LITERATURE CITED

Aldinger, K. R. (2010). Playback surveys and breeding habitat characteristics of Golden-winged Warblers (*Vermivora chrysoptera*) on high-elevation pasturelands on the Monongahela National Forest, West Virginia. M.S. thesis, West Virginia University, Morgantown, WV, USA.

Aldinger, K. R., and P. B. Wood (2014). Reproductive success and habitat characteristics of Golden-winged Warblers in high-elevation pasturelands. The Wilson Journal of Ornithology 126:279–287.

Aldinger, K. R., and P. B. Wood (2015). Variables associated with detection probability, detection latency, and behavioral responses of Golden-winged Warblers (*Vermivora chrysoptera*). The Condor: Ornithological Applications 117:364–375.

Aldinger, K. R., T. M. Terhune, II, P. B. Wood, D. A. Buehler, M. H. Bakermans, J. L. Confer, D. J. Flaspohler, J. L. Larkin, J. P. Loegering, K. L. Percy, A. M. Roth, and C. G. Smalling. (2015). Variables associated with nest survival of Golden-winged Warblers (*Vermivora chrysoptera*) among vegetation communities commonly used for nesting. Avian Conservation and Ecology 10:art.6.

Appalachian Mountains Joint Venture Management Board (2008). Implementation Plan for the Appalachian Mountains Joint Venture: A Foundation for All-Bird Conservation in the Region (B. W. Smith, Editor). Appalachian Mountains Joint Venture, Frankfort, KY, USA.

Bakermans, M. H., J. L. Larkin, B. W. Smith, T. M. Fearer, and B. C. Jones (2011). Golden-winged Warbler Habitat Best Manage-ment Practices for Forestlands in Maryland and Pennsylvania. American Bird Conservancy, The Plains, VA, USA.

Bakermans, M. H., B. W. Smith, B. C. Jones, and J. L. Larkin (2015). Stand and within-stand factors influencing Golden-winged Warbler use of regenerating stands in the central Appalachian Mountains. Avian Conservation and Ecology 10:art.10.

Barber, D. R., and T. E. Martin (1997). Influence of alternate host densities on Brown-headed Cowbird parasitism rates in Black-capped Vireos. The Condor 99:595–604.

Bartoń, K. (2016). MuMIn: Multi-model inference. R package version 1.15.6. http://CRAN.R-project.org/package=MuMIn

Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker (2015). Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Bonnot, T. W., F. R. Thompson, III, J. J. Millspaugh, and D. T. Jones-Farrand (2013). Landscape-based population viability models demonstrate importance of strategic conservation planning for birds. Biological Conservation 165:104–114.

Borcard, D., F. Gillet, and P. Legendre (2011). Numerical Ecology with R. Springer, New York, NY, USA.

Breiman, L. (1996). Bagging predictors. Machine Learning 24:123–140.

Brooks, M. (1940). The breeding warblers of the central Allegheny Mountain region. The Wilson Bulletin 52:249–266.

Brooks, M. (1944). A Check-List of West Virginia Birds. West Virginia Agriculture Experiment Station Bulletin 316, West Virginia University, Morgantown, WV, USA.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas (2001). Introduction to Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, Oxford, UK.

Buehler, D. A., A. M. Roth, R. Vallender, T. C. Will, J. L. Confer, R. A. Canterbury, S. B. Swarthout, K. V. Rosenberg, and L. P. Bulluck (2007). Status and conservation priorities of Golden-winged Warbler (*Vermivora chrysoptera*) in North America. The Auk 124:1439–1445.

Bulluck, L. P., and D. A. Buehler (2008). Factors influencing Golden-winged Warbler (*Vermivora chrysoptera*) nest-site selection and nest survival in the Cumberland Mountains of Tennessee. The Auk 125:551–559.

Burnham, K. P., and D. R. Anderson (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second edition. Springer, New York, NY, USA.

Canterbury, R. A., D. M. Stover, and J. J. Kotesovec, Jr. (1996). Population Ecology of Golden-winged Warblers in Southern West Virginia. West Virginia Division of Natural Resources, Elkins, WV, USA.

Caro, T. M., and G. O'Doherty (1999). On the use of surrogate species in conservation biology. Conservation Biology 13:805–814.

Chatterjee, S., and B. Price (1991). Regression Analysis by Example, second edition. John Wiley & Sons, New York, NY, USA.

Confer, J. L., and K. Knapp (1981). Golden-winged Warblers and Blue-winged Warblers: The relative success of a habitat specialist and a generalist. Auk 98:108–114.

Confer, J. L., K. W. Barnes, and E. C. Alvey (2010). Golden- and Blue-winged warblers: Distribution, nesting success, and genetic differences in two habitats. The Wilson Journal of Ornithology 122:273–278.

Confer, J. L., P. Hartman, and A. Roth (2011). Golden-winged Warbler (*Vermivora chrysoptera*). In The Birds of North America Online (P. G. Rodewald, Editor). Cornell Lab of

Ornithology, Ithaca, NY, USA. http://bna.birds.cornell.edu/bna/species/gowwar

Conn, P. B., D. S. Johnson, and P. L. Boveng (2015). On extrapolating past the range of observed data when making statistical predictions in ecology. PLOS One 10:e0141416.

Cox, W. A., F. R. Thompson, III, and J. Faaborg (2012). Landscape forest cover and edge effects on songbird nest predation vary by predator. Landscape Ecology 27:659–669.

Crawford, D. L., R. W. Rohrbaugh, A. M. Roth, J. D. Lowe, S. Barker Swarthout, and K. V. Rosenberg (2016). Landscape-scale habitat and climate correlates of breeding Golden-winged and Blue-winged warblers. In Golden-winged Warbler Ecology, Conservation, and Habitat Management (H. M. Streby, D. E. Andersen, and D. A. Buehler, Editors). Studies in Avian Biology 49:41–66.

Driscoll, M. J. L., and T. M. Donovan (2004). Landscape context moderates edge effects: Nesting success of Wood Thrushes in central New York. Conservation Biology 18:1330–1338.

Driscoll, M. J. L., T. M. Donovan, R. Mickey, A. Howard, and K. K. Fleming (2005). Determinants of Wood Thrush nest success: A multi-scale, model selection approach. The Journal of Wildlife Management 69:699–709.

Evans, M., E. Gow, R. R. Roth, M. S. Johnson, and T. J. Underwood (2011). Wood Thrush (*Hylocichla mustelina*). In The Birds of North America Online (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. http://bna.birds.cornell.edu/bna/species/woothr

Fajvan, M. A., S. T. Grushecky, and C. C. Hassler (1998). The effects of harvesting practices on West Virginia's wood supply. Journal of Forestry 96:33–39.

Farnsworth, G. L., K. H. Pollock, J. D. Nichols, T. R. Simons, J. E. Hines, and J. R. Sauer (2002). A removal model for estimating detection probabilities from point-count surveys. The Auk 119:414–425.

Frantz, M. W., K. R. Aldinger, P. B. Wood, J. Duchamp, T. Nuttle, A. Vitz, and J. L. Larkin (2016). Space and habitat use of breeding Golden-winged Warblers in the central Appalachian Mountains. In Golden-winged Warbler Ecology, Conservation, and Habitat Management (H. M. Streby, D. E. Andersen, and D. A. Buehler, Editors). Studies in Avian Biology 49:81–94.

Gabriel, K. R. (2002). Goodness of fit of biplots and correspondence analysis. Biometrika 89:423–436.

Gehlke, C. E., and K. Biehl (1934). Certain effects of grouping upon the size of the correlation coefficient in census tract material. Journal of the American Statistical Association 29:169–170.

Gessler, P. E., I. D. Moore, N. J. McKenzie, and P. J. Ryan (1995). Soil-landscape modelling and spatial prediction of soil attributes. International Journal of Geographic Information Systems 9:421–432.

Gill, F. B. (1980). Historical aspects of hybridization between Blue-winged and Golden-winged warblers. The Auk 97:1–18.

Golden-winged Warbler Working Group (2013). Best Management Practices for Golden-winged Warbler Habitats in the Appalachian Region: A Guide for Land Managers and Landowners. www.gwwa.org/plan

Hamel, P. B., W. P. Smith, D. J. Twedt, J. R. Woehr, E. Morris, R. B. Hamilton, and R. J. Cooper (1996). A land manager's guide to point counts of birds in the Southeast. USDA Forest Service General Technical Report SO-120.

Hanowski, J. M. (2002). Habitats and landscapes used by breeding Golden-winged Warblers in western Great Lakes forests. The Loon 74:127–133.

Hunter, W. C., D. A. Buehler, R. A. Canterbury, J. L. Confer, and P. B. Hamel (2001). Conservation of disturbance-dependent birds in eastern North America. Wildlife Society Bulletin 29:440–455.

James, F. C., and H. H. Shugart, Jr. (1970). A quantitative method of habitat description. Audubon Field Notes 24:727–736.

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Johst, K., M. Drechsler, A. J. A. van Teeffelen, F. Hartig, C. C. Vos, S. Wissel, F. Wätzold, and P. Opdam (2011). Biodiversity conservation in dynamic landscapes: Trade-offs between number, connectivity and turnover of habitat patches. Journal of Applied Ecology 48:1227–1235.

King, D. I., and S. Schlossberg (2014). Synthesis of the conservation value of the early-successional stage in forests of eastern North America. Forest Ecology and Management 324:186–195.

Klaus, N. A., and D. A. Buehler (2001). Golden-winged Warbler breeding habitat characteristics and nest success in clearcuts in the southern Appalachian Mountains. The Wilson Bulletin 113:297–301.

Lewin-Koh, N. J., and R. Bivand (2015). maptools: Tools for reading and handling spatial objects. R package version 0.8-36. https://cran.r-project.org/package=maptools

Lindenmayer, D. B., A. D. Manning, P. L. Smith, H. P. Possingham, J. Fischer, I. Oliver, and M. A. McCarthy (2002). The focal species approach and landscape restoration: A critique. Conservation Biology 16:338–345.

Martin, T. G., B. A. Wintle, J. R. Rhodes, P. M. Kuhnert, S. A. Field, S. J. Low-Choy, A. J. Tyre, and H. J. Possingham (2005). Zero-tolerance ecology: Improving ecological inference by modelling the source of zero observations. Ecology Letters 8:1235–1246.

Mazerolle, D. F., and K. A. Hobson (2003). Do Ovenbirds (*Seiurus aurocapillus*) avoid boreal forest edges? A spatiotemporal analysis in an agricultural landscape. The Auk 120:152–162.

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

McDermott, M. E., and P. B. Wood (2010). Influence of cover and food resource variation on post-breeding use of timber harvests with residual canopy trees. The Wilson Journal of Ornithology 122:545–555.

McGill, D. W., D. J. Magill, J. Kochenderfer, M. Ford, and T. Schuler (2004). Information transfer during the timber transaction period in West Virginia, USA. In Communication Strategies for Multiple Partner Involvement in Forest Extension. Proceedings of the 7th Extension Working Party Symposium, IUFRO (International Union of Forestry Research Organizations) Working Party S6.06-03 Extension, Orvieto and Rome, Italy. pp. 159–170.

McGraw, K. J., and A. L. Middleton (2009). American Goldfinch (*Spinus tristis*). In The Birds of North America Online (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://birdsna.org/Species-Account/bna/species/amegfi

McNeil, D. J., K. R. Aldinger, M. H. Bakermans, J. A. Lehman, A. C. Tisdale, J. A. Jones, P. B. Wood, D. A. Buehler, C. G. Smalling, L. Siefferman, and J. L. Larkin (2017). An evaluation and comparison of conservation guidelines for an at-risk migratory songbird. Global Ecology and Conservation 9:90–103.

Morin, R. S., G. W. Cook, C. J. Barnett, B. J. Butler, S. J. Crocker, M. A. Hatfield, C. M. Kurtz, T. W. Lister, W. G. Luppold, W. H.
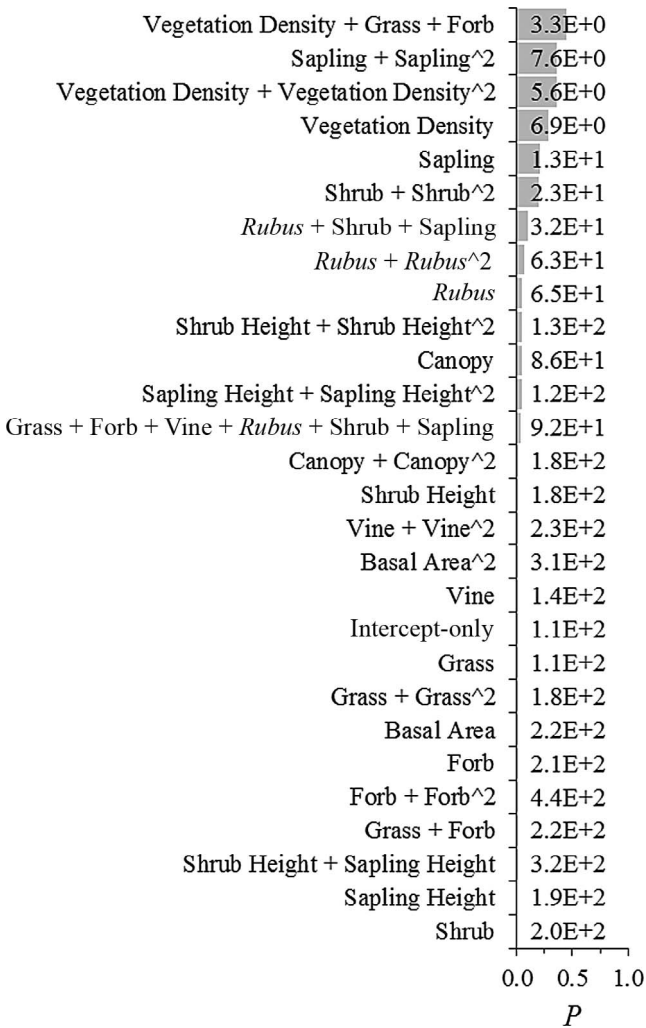
McWilliams, P. D. Miles, et al. (2016). West Virginia Forests, 2013. USDA Forest Service Resource Bulletin NRS-105.

Nudds, T. D. (1977). Quantifying the vegetative structure of wildlife cover. Wildlife Society Bulletin 5:113–117.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Sólymos, M. H. H. Stevens, and H. Wagner (2016). vegan: Community Ecology Package. R package version 2.3-5. https://CRAN.R-project.org/package=vegan

Patton, L. L., D. S. Maehr, J. E. Duchamp, S. Fei, J. W. Gassett, and J. L. Larkin (2010). Do the Golden-winged Warbler and Blue-winged Warbler exhibit species-specific differences in their breeding habitat use? Avian Conservation and Ecology 5: art.2.

Peres-Neto, P. R., P. Legendre, S. Dray, and D. Borcard (2006). Variation partitioning of species data matrices: Estimation and comparison of fractions. Ecology 87:2614–2625.

Peterson, S. M., H. M. Streby, and D. E. Andersen (2016). Spatially explicit models of full-season productivity and implications for landscape management of Golden-winged Warblers in the western Great Lakes region. In Golden-winged Warbler Ecology, Conservation, and Habitat Management (H. M. Streby, D. E. Andersen, and D. A. Buehler, Editors). Studies in Avian Biology 49:141–160.

Pielou, E. C. (1966). Shannon's formula as a measure of species diversity: Its use and misuse. The American Naturalist 100: 463–465.

Pos, E., J. E. Guevara Andino, D. Sabatier, J.-F. Molino, N. Pitman, H. Mogollón, D. Neill, C. Cerón, G. Rivas, Di Fiore, A. R. Thomas, et al. (2014). Are all species necessary to reveal ecologically important patterns? Ecology and Evolution 4: 4626–4636.

Ralph, C. J., J. R. Sauer, and S. Droege (Technical Editors) (1995). Monitoring bird populations by point counts. USDA Forest Service General Technical Report PSW-GTR-149.

R Core Team (2016). R: A Language and Environment for Statistical Computing. Version 3.2.5. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Rich, T. D., C. J. Beardmore, H. Berlanga, P. J. Blancher, M. S. W. Bradstreet, G. S. Butcher, D. W. Demarest, E. H. Dunn, W. C. Hunter, E. E. Iñigo-Elias, J. A. Kennedy, et al. (2004). Partners in Flight North American Landbird Conservation Plan. Cornell Lab of Ornithology, Ithaca, NY, USA.

Rives, W. V. (1898). The summer birds of the West Virginia spruce belt. The Auk 15:131–137.

Rohrbaugh, R. W., D. A. Buehler, S. B. Swarthout, D. I. King, J. L. Larkin, K. V. Rosenberg, A. M. Roth, R. Vallender, and T. Will (2016). Conservation perspectives: Review of new science and primary threats to Golden-winged Warblers. In Golden-winged Warbler Ecology, Conservation, and Habitat Manage- ment (H. M. Streby, D. E. Andersen, and D. A. Buehler, Editors). Studies in Avian Biology 49:207–215.

Rosenberg, K. V., and P. J. Blancher (2005). Setting numerical population objectives for priority landbird species. In Bird Conservation and Implementation in the Americas: Proceed- ings of the Third International Partners in Flight Conference, volume 1 (C. J. Ralph and T. D. Rich, Editors). USDA Forest Service General Technical Report PSW-GTR-191. pp. 57–67.

Rosenberg, K. V., J. A. Kennedy, R. Dettmers, R. P. Ford, D. Reynolds, J. D. Alexander, C. J. Beardmore, P. J. Blancher, R. E. Bogart, G. S. Butcher, A. F. Camfield, et al. (2016b). Partners in Flight Landbird Conservation Plan: 2016 Revision for Canada

and Continental United States. Partners in Flight Science Committee.

Rosenberg, K. V., T. Will, D. A. Buehler, S. Barker Swarthout, W. E. Thogmartin, R. E. Bennett, and R. B. Chandler (2016a). Dynamic distributions and population declines of Golden- winged Warblers. In Golden-winged Warbler Ecology, Con- servation, and Habitat Management (H. M. Streby, D. E. Andersen, and D. A. Buehler, Editors). Studies in Avian Biology 49:3–28.

Rossell, C. R., Jr., S. C. Patch, and S. P. Wilds (2003). Attributes of Golden-winged Warbler territories in a mountain wetland. Wildlife Society Bulletin 31:1099–1104.

Roth, A. M., and S. Lutz (2004). Relationship between territorial male Golden-winged Warblers in managed aspen stands in northern Wisconsin, USA. Forest Science 50:153–161.

Roth, A. M., D. J. Flaspohler, and C. R. Webster (2014). Legacy tree retention in young aspen forest improves nesting habitat quality for Golden-winged Warbler (*Vermivora chrysoptera*). Forest Ecology and Management 321:61–70.

Roth, A. M., R. W. Rohrbaugh, K. R. Aldinger, M. H. Bakermans, S. Barker Swarthout, D. A. Buehler, J. L. Confer, D. Crawford, C. Friis, R. M. Fowlds, J. L. Larkin, et al. (2012). Golden-winged Warbler breeding season conservation plan. In Golden- winged Warbler Status Review and Conservation Plan (A. M. Roth, R. W. Rohrbaugh, T. Will, and D. A. Buehler, Editors). www.gwwa.org/plan

Sauer, J. R., D. K. Niven, J. E. Hines, D. J. Ziolkowski, Jr., K. L. Pardieck, J. E. Fallon, and W. A. Link (2017). The North American Breeding Bird Survey, Results and Analysis 1966– 2015. Version 02.07.2017. USGS Patuxent Wildlife Research Center, Laurel, MD, USA.

Schuler, T. M. (2004). Fifty years of partial harvesting in a mixed mesophytic forest: Composition and productivity. Canadian Journal of Forest Research 34:985–997.

Scott, J. M., D. D. Goble, A. M. Haines, J. A. Wiens, and M. C. Neel (2010). Conservation-reliant species and the future of conservation. Conservation Letters 3:91–97.

Shannon, C. E. (1948). A mathematical theory of communication. Bell System Technical Journal 27:379–423.

Sólymos, P., S. M. Matsuoka, E. M. Bayne, S. R. Lele, P. Fontaine, S. G. Cumming, D. Stralberg, F. K. A. Schmiegelow, and S. J. Song (2013). Calibrating indices of avian density from non- standardized survey data: Making the most of a messy situation. Methods in Ecology and Evolution 4:1047–1058.

Sólymos, P., M. Moreno, and S. R. Lele (2014). detect: Analyzing wildlife data with detection error. R package version 0.3-2. https://cran.r-project.org/package=detect

Streby, H. M., D. E. Andersen, and D. A. Buehler (Editors) (2016b). Golden-winged Warbler Ecology, Conservation, and Habitat Management. Studies in Avian Biology 49.

Streby, H. M., J. P. Loegering, and D. E. Andersen (2012). Spot- mapping underestimates song-territory size and use of mature forest by breeding Golden-winged Warblers in Minnesota, USA. Wildlife Society Bulletin 36:40–46.

Streby, H. M., S. M. Peterson, and D. E. Andersen (2016a). Survival and habitat use of fledgling Golden-winged Warblers in the western Great Lakes region. In Golden-winged Warbler Ecology, Conservation, and Habitat Management (H. M. Streby, D. E. Andersen, and D. A. Buehler, Editors). Studies in Avian Biology 49:127–140.

Terhune, T. M., II, K. R. Aldinger, D. A. Buehler, D. J. Flaspohler, J. L. Larkin, J. P. Loegering, K. L. Percy, A. M. Roth, C. Smalling, and P. B. Wood (2016). Golden-winged Warbler nest-site

habitat selection. In Golden-winged Warbler Ecology, Conservation, and Habitat Management (H. M. Streby, D. E. Andersen, and D. A. Buehler, Editors). Studies in Avian Biology 49:109–125.

Thogmartin, W. E. (2010). Modeling and mapping Golden-winged Warbler abundance to improve regional conservation strategies. Avian Conservation and Ecology 5: art.2.

U.S. Census Bureau (2010). Median and average square feet of floor area in new single-family houses completed by location. U.S. Census Bureau, Washington, DC, USA. www.census.gov/const/C25Ann/sftotalmedavgsqft.pdf

U.S. Natural Resources Conservation Service (2012). Golden-winged Warbler. USDA Natural Resources Conservation Service, Washington, DC, USA. www.nrcs.usda.gov/wps/portal/nrcs/detailfull/national/programs/financial/whip/?cid=stelprdb1046990

Vega Rivera, J. H., J. H. Rappole, W. J. McShea, and C. A. Haas (1998). Wood Thrush postfledgling movements and habitat use in northern Virginia. The Condor 100:69–78.

Watson, J., D. Freudenberger, and D. Paull (2001). An assessment of the focal-species approach for conserving birds in variegated landscapes in southeastern Australia. Conservation Biology 15:1364–1373.

Weakland, C. A., P. B. Wood, and W. M. Ford (2002). Responses of songbirds to diameter-limit cutting in the central Appalachians of West Virginia, USA. Forest Ecology and Management 155:115–129.

Welton, M. (2003). Status and distribution of the Golden-winged Warbler in Tennessee. Migrant 74:61–82.

West Virginia Division of Natural Resources (2015). 2015 West Virginia State Wildlife Action Plan. West Virginia Division of Natural Resources, Wildlife Resources Section, South Charleston, WV, USA. http://www.wvdnr.gov/Wildlife/Action_Plan.shtm

West Virginia GIS Technical Center (1999). Digital Elevation Dataset (30-meter NED). West Virginia GIS Technical Center, Morgantown, WV, USA. www.wvgis.wvu.edu/data/dataset.php?ID=29

West Virginia GIS Technical Center (2003). SAMB Building Points and Polygons. West Virginia GIS Technical Center, Morgantown, WV, USA. wvgis.wvu.edu/data/dataset.php?ID=288

West Virginia GIS Technical Center (2006). Streams (SAMB 1: 4,800 scale). West Virginia GIS Technical Center, Morgantown, WV, USA. wvgis.wvu.edu/data/dataset.php?ID=265

West Virginia GIS Technical Center (2010). Roads and Railroads (1990, 2000, and 2010 Census TIGER/Line). West Virginia GIS Technical Center, Morgantown, WV, USA. wvgis.wvu.edu/data/dataset.php?ID=238

Wood, E. M., S. E. Barker Swarthout, W. M. Hochachka, J. L. Larkin, R. W. Rohrbaugh, K. V. Rosenberg, and A. D. Rodewald (2016). Intermediate habitat associations by hybrids may facilitate genetic introgression in a songbird. Journal of Avian Biology 47:508–520.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith (2009). Mixed Effects Models and Extensions in Ecology with R. Springer, New York, NY, USA.

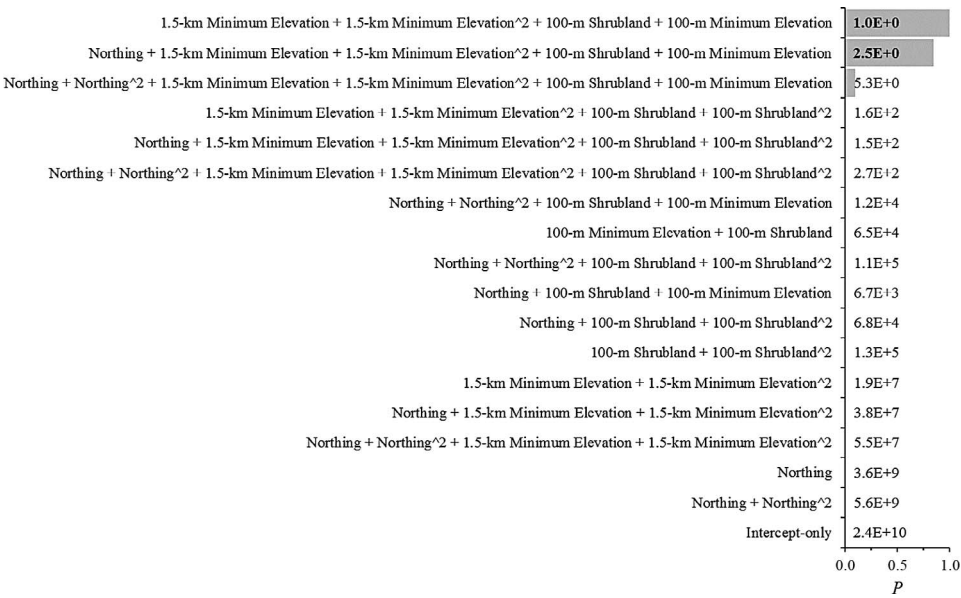| Model	Model suite I	Model suite II	Model suite III
Intercept-only	6.8E+0	1.2E+3	3.7E+5
Edge	*	2.0E+3	6.8E+5
Edge + Edge^2	*	3.4E+2	1.6E+6
Shannon's Equitability	*	*	4.9E+4
Shannon's Equitability + Shannon's Equitability^2	*	*	1.0E+5
Minimum Elevation	*	3.1E+3	4.9E+5
Minimum Elevation + Minimum Elevation^2	*	**1.0E+0**	3.3E+3
Minimum Elevation + Forest	*	7.4E+3	2.6E+4
Minimum Elevation + Shrubland	*	6.3E+3	**1.0E+0**
Minimum Elevation + Young Forest	*	5.9E+2	3.1E+5
Minimum Elevation x Forest	*	3.5E+3	5.0E+4
Forest	1.3E+1	3.0E+3	4.1E+4
Forest + Forest^2	2.5E+1	3.6E+2	4.7E+4
Herbaceous	*	*	2.1E+3
Herbaceous + Herbaceous^2	*	*	4.9E+3
Northing	**1.0E+0**	*	*
Northing + Northing^2	**2.0E+0**	*	*
Shrubland	1.6E+1	2.6E+3	9.5E+0
Shrubland + Shrubland^2	**5.0E+0**	**1.5E+1**	**1.8E+0**
Shrubland + Young Forest	3.6E+1	5.3E+2	2.1E+1
TWI	*	*	7.2E+5
TWI + TWI^2	*	*	1.3E+6
Young Forest	1.5E+1	2.4E+2	2.4E+5
Young Forest + Young Forest^2	**3.5E+0**	5.3E+2	1.4E+5

P

APPENDIX FIGURE 5. We used Akaike's information criterion (AIC; Burnham and Anderson 2002) to compare among candidate Golden-winged Warbler density models for model suites I (5-km geospatial covariates: annual dispersal scale), II (1.5-km geospatial covariates: extraterritorial movement scale), and III (100-m geospatial covariates: intraterritorial movement scale). We calculated the evidence ratio ($E = e^{0.5(\Delta AIC)}$, where ΔAIC is the AIC value of the candidate model minus the minimum AIC value in the model suite) for each model in each bootstrap replicate ($n = 1,000$ replicates). M is the proportion of bootstrap replicates when $E \leq 2.7$ (gray bars). Data labels represent median E across all bootstrap replicates. Models with median $E \leq 2.7$ (labels highlighted in bold font) were considered plausible. All models had random intercepts for year and for point count ID nested within site. Asterisks denote models not included in the model suite. See Table 2 for covariate descriptions (TWI = topographic wetness index).

Vegetation Density + Grass + Forb	3.3E+0
Sapling + Sapling^2	7.6E+0
Vegetation Density + Vegetation Density^2	5.6E+0
Vegetation Density	6.9E+0
Sapling	1.3E+1
Shrub + Shrub^2	2.3E+1
Rubus + Shrub + Sapling	3.2E+1
Rubus + *Rubus*^2	6.3E+1
Rubus	6.5E+1
Shrub Height + Shrub Height^2	1.3E+2
Canopy	8.6E+1
Sapling Height + Sapling Height^2	1.2E+2
Grass + Forb + Vine + *Rubus* + Shrub + Sapling	9.2E+1
Canopy + Canopy^2	1.8E+2
Shrub Height	1.8E+2
Vine + Vine^2	2.3E+2
Basal Area^2	3.1E+2
Vine	1.4E+2
Intercept-only	1.1E+2
Grass	1.1E+2
Grass + Grass^2	1.8E+2
Basal Area	2.2E+2
Forb	2.1E+2
Forb + Forb^2	4.4E+2
Grass + Forb	2.2E+2
Shrub Height + Sapling Height	3.2E+2
Sapling Height	1.9E+2
Shrub	2.0E+2

0.0   0.5   1.0

P

APPENDIX FIGURE 6. We used Akaike's information criterion (AIC; Burnham and Anderson 2002) to compare among candidate Golden-winged Warbler density models in model suite IV (field vegetation covariates: local resource utilization scale). We calculated the evidence ratio ($E = e^{0.5(\Delta AIC)}$, where ΔAIC is the AIC value of the candidate model minus the minimum AIC value in the model suite) for each model in each bootstrap replicate ($n = 1{,}000$ replicates). M is the proportion of bootstrap replicates when $E \leq 2.7$ (gray bars). Data labels represent median E across all bootstrap replicates. No models were considered plausible (all median $E > 2.7$). All models had random intercepts for year and for point count ID nested within site. See Table 2 for covariate descriptions.

APPENDIX FIGURE 7. We used Akaike's information criterion (AIC; Burnham and Anderson 2002) to compare among candidate Golden-winged Warbler density models in model suite V, which featured all possible combinations of plausible models from model suites I–IV (Appendix Figures 5, 6). We calculated the evidence ratio ($E = e^{0.5(\Delta AIC)}$, where ΔAIC is the AIC value of the candidate model minus the minimum AIC value in the model suite) for each model in each bootstrap replicate ($n = 1,000$ replicates). M is the proportion of bootstrap replicates when $E \leq 2.7$ (gray bars). Data labels represent median E across all bootstrap replicates. Models with median $E \leq 2.7$ (labels highlighted in bold font) were considered plausible. All models had random intercepts for year and for point count ID nested within site. See Table 2 for covariate descriptions.