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Multiscale drivers of restoration outcomes for an imperiled songbird

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Habitat restoration is a cornerstone of conservation, particularly for habitat-limited species. However, restoration efforts are seldom rigorously monitored at meaningful spatial scales. Poor understanding of how species respond to habitat restoration programs limits conservation efficacy for habitat-restricted species like the Golden-winged Warbler (*Vermivora chrysoptera*, GWWA). We provide one of the first concerted assessments of a national conservation program aimed at restoring songbird habitat across its breeding range. We studied GWWA response to forest habitat restoration across two broad regions with opposing population trajectories and assessed factors driving species use of restored habitats across multiple spatial scales. From 2015 to 2017, we conducted 1,145 (*n* = 457 locations) and 519 point counts (*n* = 215 locations) across the Appalachian Mountains and Great Lakes (respectively) within restored habitats. Warbler abundance within restored habitats across the Great Lakes varied with latitude, longitude, elevation, forest type, and number of growing seasons. In the Appalachian Mountains, occupancy ($\hat{\psi}$) varied with longitude, elevation, forest type, and number of growing seasons. Detections were restricted to areas within close proximity to population centers (usually <24 km) in the Appalachian Mountains, where GWWAs are rare ($\hat{\psi}$ = 0.22, 95% confidence interval [CI]: 0.20–0.25), but not in the Great Lakes, where GWWAs remain common ($\hat{\psi}$ = 0.87, 95% CI: 0.84–0.90). Our study suggests that, even when best management practices are carefully implemented, restoration outcomes vary within/across regions and with multiscale habitat attributes. Although assessments of concerted habitat restoration efforts remain uncommon, our study demonstrates the value of monitoring data in the adaptive management process for imperiled species.

Key words: early-successional, forest management, habitat conservation, migratory birds, restoration

Implications for Practice

- Implementing species-specific best management practices has the capacity to yield quality nesting habitat for Golden-winged Warblers, especially when implemented within landscapes dominated by deciduous forest (≥75% deciduous cover at 1 km radius) and, in the Appalachian Mountains, <24 km from known breeding pairs.
- Warbler capacity to respond to habitat restoration not only varies across a single region (e.g. across the Western Great Lakes), but also between regions with different population trajectories.
- Golden-winged Warbler colonization of restored habitats often requires several years of vegetative succession, especially within the Appalachians; managers and biologists should judge restoration success with a degree of patience as restored habitats may take eight or more years to be colonized by Golden-winged Warblers.

Introduction

Habitat restoration is a cornerstone of conservation, particularly for habitat-limited species (Dobson et al. 1997; Perring et al. 2015). At best, restoration efforts are evidence-based, grounded in science, and guided by best management practices (BMPs; Brudvig 2017). However, even when restoration efforts are based on scientifically sound BMPs, outcomes are seldom monitored or rigorously evaluated (Török & Helm 2017). While restoring habitat can be a critical first step toward ensuring the survival of certain species, so too is evaluation and refinement to achieve intended outcomes (Suding 2011). Most studies of

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habitat restoration report mixed outcomes due to inadequate habitat outcomes, slow response by focal species, or both (Scott et al. 2001; Jones & Schmitz 2009), yet few empirical assessments of species response to restoration at meaningful scales exist (Menz et al. 2013; McIntosh et al. 2018). Understanding best practices in restoration is further complicated by the likely bias toward reporting positive outcomes (Suding 2011).

A wide variety of behavioral, ecological, and biological factors mediate the success of restoration programs (Palmer et al. 1997; Sudduth et al. 2011). For example, species capacity to colonize restored habitats is limited by the availability of dispersing individuals that may settle within restored sites (Snäll et al. 2003; Piqueray et al. 2013). Additionally, a species may behave differently across its range, especially if abundance varies widely (e.g. density-dependent factors; Einum et al. 2008). Landscape composition may contribute to variation in restoration outcomes by influencing the likelihood that new habitats will be discovered and colonized, given that landscape attributes can profoundly affect dispersal (Bond & Lake 2003; Crouzeilles et al. 2016; Wood et al. 2016). At local scales, factors including microhabitat structure (Triska et al. 2016; Corrêa et al. 2018) and plant species composition (Boves et al. 2013; Leuenberger et al. 2017) are important predictors of species response to restoration.

One group of species that may benefit from restoration are those reliant upon early-successional habitats in eastern North America (Amaral et al. 2016; Hazard-Daniel et al. 2017). Early-successional habitats are classic disturbance-dependent communities characterized by young and short-stature vegetation, like shrubs and saplings (Litvaitis 2001; DeGraaf & Yamasaki 2003). Changes to disturbance regimes (e.g. fire suppression, beaver [*Castor canadensis*] activity reduction) over the last several decades have reduced the availability of ephemeral habitats to the point that many associated wildlife species have declined (Askins 2001; Trani et al. 2001; Swanson et al. 2011). In response to these declines, early-successional species, such as the Golden-winged Warbler (*Vermivora chrysoptera*), have been widely studied to understand how best to create and maintain nesting habitat (i.e. BMPs; Bakermans et al. 2011; Roth et al. 2012). Moreover, a variety of programs have been initiated to implement BMPs for species like the Golden-winged Warbler (Ciuzio et al. 2013; WLFW 2016). To this end, we provide one of the first rigorous assessments of a national conservation program aimed at restoring habitat for an imperiled species across its range. More specifically, we studied species response (occupancy and abundance) to implementation of habitat restoration across two broad regions with opposing population trajectories and assessed factors driving species use of sites treated with BMPs (i.e. restoration success) across regional, landscape, and patch scales.

Methods

Focal Species

Golden-winged Warblers (hereafter, "GWWA") are Nearctic-Neotropical migratory songbirds that nest within early-successional communities in eastern North America (Confer et al. 2011). Like many early-successional specialists, GWWA populations have declined steadily since the 1960s (Sauer et al. 2017) or longer (Hill & Hagan 1991) due in part to loss of breeding habitat (Roth et al. 2012; Rosenberg et al. 2016). Breeding habitat loss is a persistent threat to species like GWWAs because the early-successional plant communities within which the species nests are ephemeral (Askins 2001), often persisting for only a few decades before natural succession renders a site unsuitable as nesting habitat (Confer et al. 2011; Rohrbaugh et al. 2016; Rosenberg et al. 2016). Today, GWWAs have become rare or patchily distributed across landscapes where they were once abundant (e.g. the Appalachian Mountains; Gill 2004; King & Schlossberg 2014) though populations in the Western Great Lakes are more secure (Sauer et al. 2017).

Habitat Guidelines and Restoration Implementation

In 2012, conservationists published a set of science-based BMPs detailing conservation strategies for GWWAs across its entire lifecycle (hereafter, the "Conservation Plan"; Bakermans et al. 2011; Roth et al. 2012; Bennett et al. 2016). The Conservation Plan has been readily adopted by multiple agencies and NGOs to help stem GWWA population declines (WLFW 2016; McNeil et al. 2017). Two of the most ambitious programs, Working Lands for Wildlife (WLFW) and Regional Conservation Partnership Program (RCPP), were initiated by USDA-NRCS in 2012 (WLFW) and 2016 (RCPP) to manage private lands for GWWA across the Appalachians and Great Lakes (Ciuzio et al. 2013; WLFW 2016). Since their inception, WLFW and RCPP have managed >9,000 ha of breeding habitat for GWWAs (WLFW: 6,400 ha, RCPP: 3,000 ha; J. Larkin, unpublished data) and hope to add to these values in 2020–2021 (WLFW 2016).

Among the most efficient habitat restoration tools recommended by the Conservation Plan are overstory removal timber harvests (Bakermans et al. 2015; McNeil et al. 2018). Overstory removal harvests (2.2–8.9 m^2/ha residual basal area; Bakermans et al. 2011) are rigorously demonstrated to provide quality habitat for GWWA territorial establishment (Bakermans et al. 2015), pairing (Roth et al. 2014), and nesting (McNeil et al. 2017), created from mature forest otherwise unsuitable for nesting. When implemented such that adequate regeneration occurs, overstory removal harvests are a convenient management type because they are often commercially viable and incorporate easily into forest management plans (Johnson et al. 2009; McCaskill et al. 2009). Although WLFW/RCPP use a variety of implementation tools for restoring and enhancing GWWA habitat across the breeding range (e.g. shrubland management; WLFW 2016), overstory removals are the most common method (NRCS 2017) and thus we sampled only habitats restored using overstory removal.

Study Area and Site Selection

We studied restored habitat patches across both the Great Lakes (high latitude) and Appalachian Mountains (high elevation) conservation regions (sensu Roth et al. 2012). The Great Lakes Conservation Region is estimated to host approximately 95% of the global breeding GWWA population (Roth et al. 2012). In the Western Great Lakes, we surveyed 17 counties in Minnesota and five counties in Wisconsin, ranging from 275 to 530 m above sea level. Upland deciduous forests dominate the region, intermixed with natural wetlands (Dyer 2006; Fry et al. 2011; Omernik & Griffith 2014). Red maple (*Acer rubrum*), birches (*Betula* spp.), aspens (*Populus* spp.), and oaks (*Quercus* spp.) are among the most common tree species in the region. Understory species are similarly varied but commonly include alder (*Alnus* spp.), willow (*Salix* spp.), and dogwood (*Cornus* spp.). We monitored all available locations that had been restored through WLFW/RCPP in Minnesota and Wisconsin between 2015 and 2017 (i.e. 0–2 growing seasons, posttreatment).

The 10 states within the Appalachian Mountains Conservation Region support approximately 5% of the global breeding population of GWWAs (Roth et al. 2012). Across the Appalachian Mountains, we sampled counties in Maryland (2), Pennsylvania (26), and New Jersey (2) that were located 188–989 m above sea level. Restored habitats in the Appalachian Mountains were dominated by Appalachian oak and northern hardwood forest communities (Dyer 2006; Fry et al. 2011) with maples (*Acer* spp.), birches, hickories (*Carya* spp.), and oaks the most common genera. A variety of understory plants occurred across the study area, including mountain laurel (*Kalmia latifolia*), witch-hazel (*Hamamelis virginiana*), black huckleberry (*Gaylussacia baccata*), and blueberry (*Vaccinium* spp.). We monitored all available locations that had been restored through WLFW/RCPP in Pennsylvania, Maryland, and New Jersey between 2012 and 2017 (i.e. 0–5 growing seasons, posttreatment). Additionally, we included a comparable sample of restored habitats on nearby public lands in the Appalachian Mountains, managed using the same prescription (Bakermans et al. 2011, 2015; McNeil et al. 2017; overstory removal, 0–9 growing seasons, posttreatment).

Point Count Surveys

Point counts were conducted from 2015 to 2017 following methods of McNeil et al. (2018); we recorded all GWWA males seen or heard at 1–2 random points (mean: 1.09 points/site) located >80 m from a habitat edge and spaced >250 m apart. Although not the focus of our study, we also recorded Blue-winged Warblers and hybrids during surveys. We sampled Golden-winged Warblers twice/breeding season by a single observer using a combined passive + playback method (Kubel & Yahner 2007; McNeil et al. 2014). Our point count protocol was identical to those of McNeil et al. (2018) except that we added a 3-minute conspecific playback immediately after our 10-minute point count surveys. In particular, playback consisted of a 1-minute digital recording of GWWA type 2 song (Ficken & Ficken 1967), a 1-minute digital recording of Eastern Screech-owl (*Megascops asio*)/Black-capped Chickadee (*Poecile atricapillus*) mobbing, and 1 minute of silence. This 3-minute recording was broadcast from an HDMX Jam Bluetooth Speaker (HDMX Audio USA) connected to a handheld MP3 player. We visually identified the plumage phenotype for each *Vermivora* spp. to avoid false-positive identifications based on song mismatch (Ficken & Ficken 1967; Highsmith 1989) and excluded birds detected outside the boundaries of restoration sites. Prior to field sampling, we extensively trained all technicians ($n = 45$) to consistently and accurately estimate distances to birds to the nearest 5 m interval (McNeil et al. 2018). This allowed us to record the distance from point count center to each GWWA (when first observed) for distance sampling analyses (see "Statistical Analyses" section, below). Data from the playback component of our point count (minutes 10–13) were not included in our distance analysis (Buckland et al. 2005; McNeil et al. 2014).

Surveys of Within-Patch Vegetation

We surveyed within-patch vegetation at each point from 15 June to 15 July each year following the methods of McNeil et al. (2018). Briefly, vegetative conditions were measured at 10-m intervals along three 100-m radial transects oriented 0°, 120°, and 240° from point count centers (James & Shugart 1970). Vegetation strata recorded at each stop consisted of the presence/absence of sapling, shrub, *Rubus* spp., forb, and sedge/grass (hereafter, "grass"). We also recorded the presence of woody stems within 1 m of the observer at each stop within the following categories: "0–1 m," "1–2 m," ">2 m," and "none." Basal area was quantified using a 10-factor basal area prism at the 0 m, 50 m, and 100 m locations along each transect ($n = 7$ total readings/point).

Remote-Sensed Landscape Data

We incorporated remotely sensed data from two primary sources: National Land Cover Database (2016 dataset; NLCD; Yang et al. 2018) and U.S. Forest Service Forest Inventory and Analysis (FIA) data (Forest Inventory Analysis Database 2019; Chojnacky 2000). We summarized land cover using ArcGIS 10.2 (ESRI 2011) at an ecologically meaningful scale to GWWAs (1-km radius; Bakermans et al. 2015) for the following land cover classes: (1) deciduous forest, (2) mixed forest, (3) coniferous forest, (4) shrubland, (5) forested wetland, (6) emergent wetland, (7) pasture, (8) row-crops, and (9) human development. From the FIA dataset, we summarized data for the following "forest type groups": (1) aspen-birch, (2) maple-beech (*Fagus* spp.), (3) oak-hickory, and (4) spruce (*Picea* spp.)—fir (*Abies* spp.). Each covariate was modeled as percent cover within a 1-km radius buffer.

Statistical Analyses

Preliminary analyses indicated that occupancy was high in the Great Lakes (naïve = 0.83) but low in the Appalachian Mountains (naïve = 0.20). With this in mind, although we modeled occupancy *and* abundance of GWWAs across sites in both conservation regions, we evaluated *variation* in region-specific response to habitat restoration using the greatest source of variation in each dataset: occupancy in the Appalachian Mountains (where most sites were un-occupied and abundance was usually = 0) and abundance in the Great Lakes (where most sites hosted at least one GWWA and occupancy was usually = 1). Given that occupancy models are designed for relatively uncommon species (MacKenzie et al. 2017), whereby occupancy is a proxy for abundance (MacKenzie & Nichols 2004) and abundance models are not ideal for species where most sites are unoccupied (Buckland et al. 2001; Kéry & Royle 2015), we believe our mixed analytical approach was ideal for meeting our objectives.

Occupancy Modeling. We modeled GWWA presence observations from both conservation regions using static occupancy models in the R package *unmarked* (Fiske & Chandler 2011; R Core Team 2018). We used only records of GWWA ≤100 m of the observer in all analyses. Package *unmarked* allows the user to fit linear models within a maximum likelihood framework that can be combined with an information theoretic approach (Andersen 2007) for model selection (e.g. using Akaike's information criterion adjusted for small sample size; AIC_c; Burnham & Andersen 2002). We formatted data using a stacked structure to allow multiple years of data to be modeled together (McClure & Hill 2012; Fogg et al. 2014). We used a four-step approach (Fig. S1A–D) to create our final candidate occupancy model set in the Appalachian Mountains (Fig. S1E). In the Great Lakes, we created occupancy models with only the goal of estimating mean regional rates of site occupancy as we explored habitat relationships using models of abundance (see Hierarchical Distance Modeling section). As such, we accounted for detection probability with the following approach but did not explore habitat patterns using occupancy models. We first modeled factors that influence detection probability ("detection" model set) using four survey covariates: (1) minutes since sunrise (mssr), (2) Julian date, (3) Beaufort wind index, and (4) cloud cover (%). To reduce the number of categories within the Beaufort wind index, we simplified values of ≤2 to "calm" and those >2 to "windy." We created all possible combinations of 0–4 survey covariates on detection probability (p) using the dredge function in the R package *MuMIn* (Barton 2018; R Core Team 2018; Fig. S1A) We considered covariates to be informative if they were in the competing set (<2.0; ΔAIC_c) and had β 95% confidence intervals (CIs) that did not include zero (Burnham & Andersen 2002). Dredge provided a useful approach for selecting informative detection covariates as we had no a priori expectation as to which combination of survey covariates might influence detection.

After establishing informative survey covariates on detection probability, we incorporated them into consecutive occupancy models assessing habitat patterns in the Appalachian Mountains. Our exploration of habitat associations began with broad geographic covariates ("regional" model set): latitude, longitude, and elevation using all possible combinations of additive covariates including quadratic relationships for latitude and longitude (i.e. $x + x^2$; Fig. S1B). We incorporated all the top model from this candidate set (detection + lat./long./elev. covariates) into all following model sets, as well as all additive combinations of additional covariates and null (intercept-only) models. We treated all competing models (e.g. ΔAIC_c <2.0; Burnham & Andersen 20022002) as plausible and included them in consecutive model sets. We next modeled all possible combinations of previous models + additive combinations with local structural vegetation ("patch" model set; Fig. S1C) and landscape covariates ("landscape" model set; Fig. S1D). Within our patch model set, we also included # growing seasons and habitat area (hectares) as covariates. Finally, using the supported models from both our patch and landscape habitat models (Fig. S1C & D), we created a global model that combined all supported covariates together and dredged this top model to create our final candidate set ("global" model set; Fig. S1E). The best ranked model from the global model set was that which we used to make occupancy predictions. Prior to each analysis, we calculated Pearson's correlation coefficient among all pairwise combinations of covariates and removed variables at the R = 0.7 threshold (Sokal & Rohlf 1969). During sampling, GWWA detections in the Appalachian Mountains appeared to be spatially clustered around population centers (e.g. the Pocono Mountains) while other sub-regions remained largely vacant of GWWA (e.g. portions of Pennsylvania's "Deep Valleys" region). To assess the extent to which detections in the Appalachians occur closer to other detections than expected by random chance (i.e. clumped), we also calculated Ripley's K for points with GWWA detections as compared to all sampling locations. Ripley's K function provides an empirical framework with which to test how clumped or dispersed objects in space (e.g. detections) may be with respect to the expectations of random chance.

Hierarchical Distance Modeling. We modeled GWWA abundance observations from both conservation regions with hierarchical distance models (HDM) using *gdistsamp* in the R package *unmarked* (Fiske & Chandler 2011; R Core Team 2018). We binned detections in 20-m-wide bins such that we had five distance bins to model observations (Buckland et al. 2001, 2005) and stacked data as with our occupancy analyses. We used a five-step approach (Fig. S1F–J) to creating our final candidate HDM model set (Fig. S1K). We assessed all available detection functions (hazard rate, half-normal, exponential, and uniform; Kéry & Royle 2015; Fig. S1F) prior to assessing factors that impact detection using four survey covariates: (1) mssr, (2) Julian date, (3) Beaufort wind index, and (4) cloud cover (binary). To avoid overfitting our HDMs and ensure model convergence, we created all possible combinations of 0–1 survey covariates on detection (while holding occupancy constant; "detection" model set; Fig. S1G). We then took the top-ranked detection model and incorporated it into all following HDM models for our Great Lakes observations. We did not explore habitat patterns on GWWA density in the Appalachian Mountains and simply used the top-ranked detection model to predict mean density within the region. As with occupancy in the Appalachian Mountains above, we tested covariates that assessed broad regional patterns of abundance in the Great Lakes:

latitude, longitude, and elevation using all possible combinations of additive covariates including quadratic relationships for latitude and longitude (i.e. $x + x^2$; Fig. S1H). We incorporated all the top models from this candidate set ("regional" model set; detection + lat./long./elev. covariates) into all following model sets, as well as all additive combinations of additional covariates and null (intercept-only) models. We next modeled all possible combinations of previous models + additive combinations with patch ("patch" model set; Fig. S1I) and landscape covariates ("landscape" model set; Fig. S1J). Finally, using the supported models from both our patch and landscape habitat models (Fig. S1I & J), we created all possible combinations of our top models from each set and compared them together using AIC_c ("global" model set; Fig. S1K). Using our top-ranked models in both occupancy- and distance model sets, we plotted functional relationships and mapped spatial predictions using the *predict* function in R, then visualized using ArcGIS.

Results

Correlation analyses indicated that our metric of "0–1 m" woody stem index was correlated with "none" woody stem index and the former was removed from modeling. Similarly, ">2 m" woody stem index was correlated with percent sapling cover and the former was removed from modeling. Basal area was correlated with canopy cover and so we removed canopy cover from our analyses. Finally, maple-beech forest cover was correlated with oak-hickory forest and the former was removed from modeling.

Appalachian Mountains Conservation Region

From 2015 to 2017, we conducted 1,145 point counts at 459 locations (n = 267 on private lands enrolled in NRCS's Working lands for Wildlife Partnership and n = 192 on state managed lands in Pennsylvania, New Jersey, and Maryland) in the Appalachian Mountains Conservation Region (Fig. 1). After accounting for detection probability (Table S1), mean occupancy probability of restored habitats across this region was $\hat{\lambda}$ = 0.22 (95% CI: 0.20–0.25). Mean density within restored habitats across this region was $\hat{\lambda}$ = 0.11 males/ha (95% CI: 0.09–0.13) which equates to 0.35 males (95% CI: 0.30–0.41)/point count. Occupancy probability was positively associated with longitude, and negatively associated with elevation (geographic model set; Table S2, Fig. 2). The best-ranked patch model included a positive association with # growing seasons with no competing models (patch model set; Table S3; Fig. 2). While stand conditions like basal area and habitat area remained relatively constant over the timescales we studied here (<10 years posttreatment), woody stem cover increased markedly over growing seasons as grass cover declined somewhat (Fig. S2). Habitats in their eighth growing season, therefore, hosted retained canopy and abundant regenerating woody stems while still supporting ample grass and forb cover (Fig. S2).

GWWA occupancy across the Appalachian Mountains was negatively associated with percent mixed forest and positively

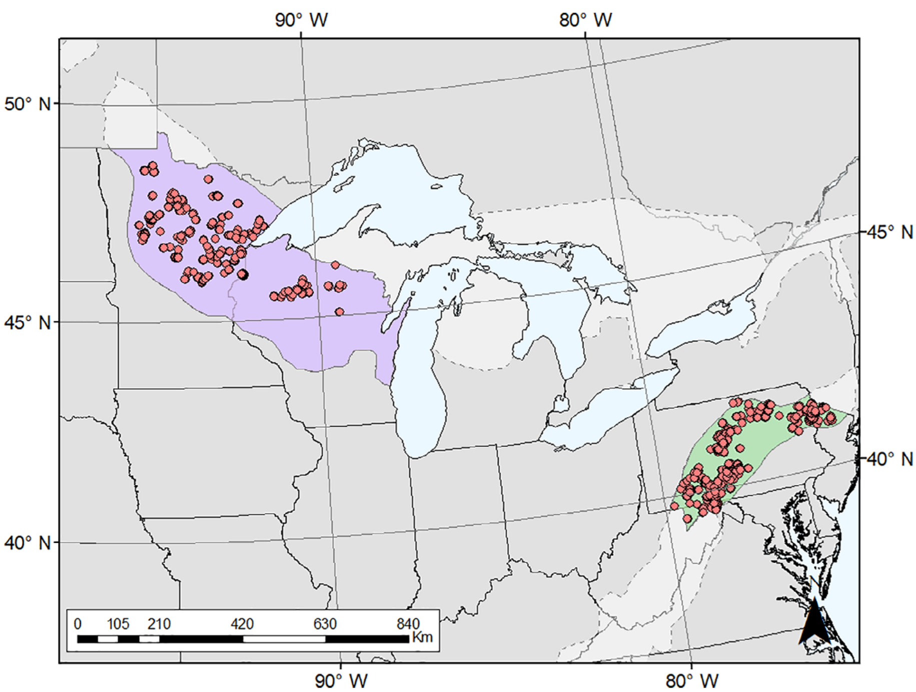

Figure 1. A map depicting locations where we conducted surveys (red points) for Golden-winged Warblers on restored early-successional habitats (i.e. overstory removals). We sampled portions of both the Great Lakes (violet) and Appalachian Mountain (green) conservation regions. All points are shifted 1–10 km in a random direction to maintain private landowner anonymity.

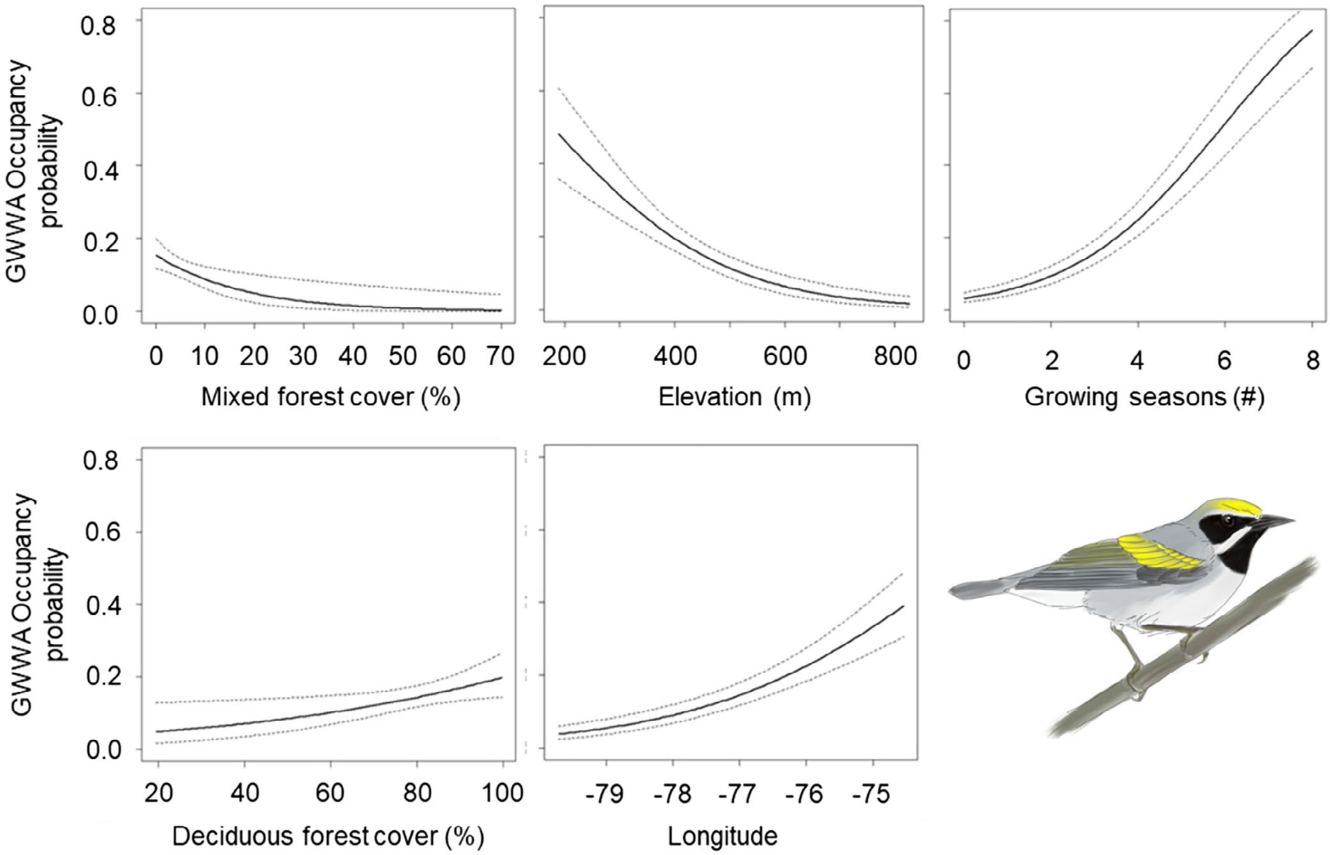

Figure 2. Functional relationships between Golden-winged Warbler occupancy within regenerating overstory removals across the sampled Appalachian Conservation Region. Shown are all covariate relationships for our top-ranked occupancy model. Solid lines represent occupancy estimates while dashed lines represent 95% confidence intervals.

associated with percent deciduous forest within 1 km (landscape model set; Table S4, Fig. 2). Our best-ranked occupancy model in the global model set included longitude (positive), elevation (negative), mixed forest cover (negative), deciduous forest cover (positive), and growing seasons (positive; Table S5, global model set; Fig. S3). Our best-ranked global model was found to fit our data reasonably well with only minor overdispersion ($\hat{c} = 1.14$; Kéry & Royle 2015). When we projected the best global model results across the sampled portion Appalachian Conservation Region, occupancy was predicted highest in eastern Pennsylvania (i.e. Pocono Mountains) and northwestern New Jersey ($\hat{\psi} = 0.40$–0.80) and intermediate in the Pennsylvania Wilds and south-central Pennsylvania ($\hat{\psi} = 0.10$–0.40). The species was rare elsewhere ($\hat{\psi} < 0.10$; Fig. 3). Ripley's K function values for point locations with GWWA detections as compared to all survey points revealed detections to be clustered at any scale below 70 km; however, the magnitude of differences between detections and all points indicated that clustering was most pronounced at the 24 km radius scale (Fig. S4). Aside from GWWA, other *Vermivora* spp. were consistently rare across all years: Blue-winged Warbler (*Vermivora cyanoptera*) naïve occupancy range: 6–7%, "Brewster's" + "Lawrence's" Warbler hybrids naïve occupancy range: 2–3%.

Great Lakes Conservation Region

From 2015 to 2017, we conducted 519 point counts at 215 locations all on private lands enrolled in NRCS's Regional Conservation Partnership Program in the Great Lakes Conservation Region (Fig. 1). Mean occupancy probability of restored habitats across this region was ($\hat{\psi} = 0.87$, 95% CI: 0.84–0.90). A half-normal detection function fit our distance data best with no competing models (second-ranked: hazard-rate, $\Delta AIC_c = 5.89$). After accounting for detection (detection model set; Table S1), mean density within restored habitats across this region was $\hat{\lambda} = 0.80$ males/ha (95% CI: 0.71–0.88) which equates to 2.50 males (95% CI: 2.23–2.76)/point count. Density was negatively associated with longitude, quadratically associated with latitude, and negatively associated with elevation (regional model set). A similar model with quadratic longitude was nearly competing ($\Delta AIC_c = 2.09$; Table S2, Fig. 4) so we considered both linear (longitude) and quadratic (longitude^2) terms for longitude in our consecutive model sets as a

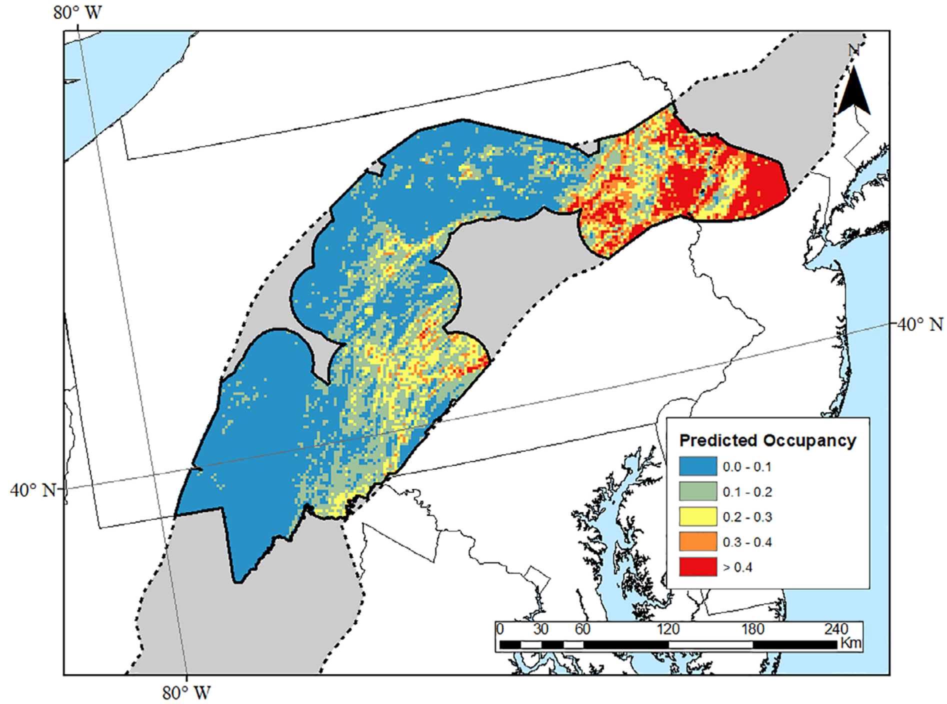

Figure 3. Patterns of Golden-winged Warbler predicted occupancy probability in restored habitats across sampled portions of the Appalachian Mountains Conservation Region. We predicted occupancy only within a 24-km radius of sampled survey locations using our top model that considered latitude, longitude, elevation, and percent mixed forest within a 1-km radius. Portions of the Appalachian Mountains Conservation Region outside our predicted area are shown in gray.

conservative measure. The best-ranked patch model included a positive association with # growing seasons with no competing models (patch model set, Table S3; Fig. 4). Likewise, GWWA density within Great Lakes restored habitats was negatively associated with percent mixed forest within 1 km (landscape model set, Table S4; Fig. 4). Our best-ranked density model (global model set) included latitude^2, longitude^2, elevation (negative), mixed forest cover (negative), and # growing seasons (positive; Table S5, Fig. S3–S5). Our best-ranked model was not overdispersed ($\hat{c} = 0.94$). When we projected these model results across the sampled portion Great Lakes Conservation Region, density was lowest in eastern Wisconsin and along the northern shore of Lake Superior ($\hat{\lambda} = 0$–0.5 males/ha) and highest in central Minnesota ($\hat{\lambda} \geq 1.25$ males/ha; Fig. 5). Like the Appalachian Mountains Conservation Region, non-GWWA *Vermivora* spp. were consistently rare across all years: Blue-winged Warbler naïve occupancy range: 0–1%; neither Brewster's nor Lawrence's Warblers' phenotypes were detected in the Great Lakes region.

Discussion

BMPs have been developed for a wide array of species of conservation concern but are seldom implemented or systematically monitored at meaningful spatial scales (McIntosh et al. 2018). Our study demonstrates that even when BMPs are carefully implemented, restoration outcomes (occupancy and abundance) vary across regions and with multiscale attributes. Additionally, the extent of restoration success was conditional upon regional abundance with most sites occupied in the Great Lakes (though abundance varied) while fewer sites were occupied in the Appalachians. With this in mind, the WLFW and RCPP had mixed success in achieving stated goals, like many habitat restoration efforts before (Scott et al. 2001; Jones & Schmitz 2009). Our results thus provide both a rare case-study of a national conservation program aimed at avian habitat restoration as well as a critical step in adaptive management for GWWAs (Rohrbaugh et al. 2016).

Across both regions, older sites were most used by GWWAs, likely due to regeneration of a structurally diverse understory vegetation over time. As indicated by our patch data, "number of growing seasons" serves as a reasonable proxy for a suite of structural vegetation characteristics (Klaus & Buehler 2001; Confer et al. 2003; Patton et al. 2010). Importantly, the relationship between GWWA abundance and number of growing seasons is expected to be strongly nonlinear (Otto & Roloff 2012), with suitability of sites initially improving with age but then deteriorating over 15–20 years of succession as stands enter the sapling stage (Bakermans et al. 2011; Otto & Roloff 2012). One limitation of our study is, while sites varied in age from 0 to 8 years postharvest in the Appalachians, sites were only 0–2 years posttreatment in the Great Lakes. Given that habitat quality appears to increase over at least nine growing seasons, we believe our estimates of GWWA density in the Great Lakes are conservative as ecological succession will likely

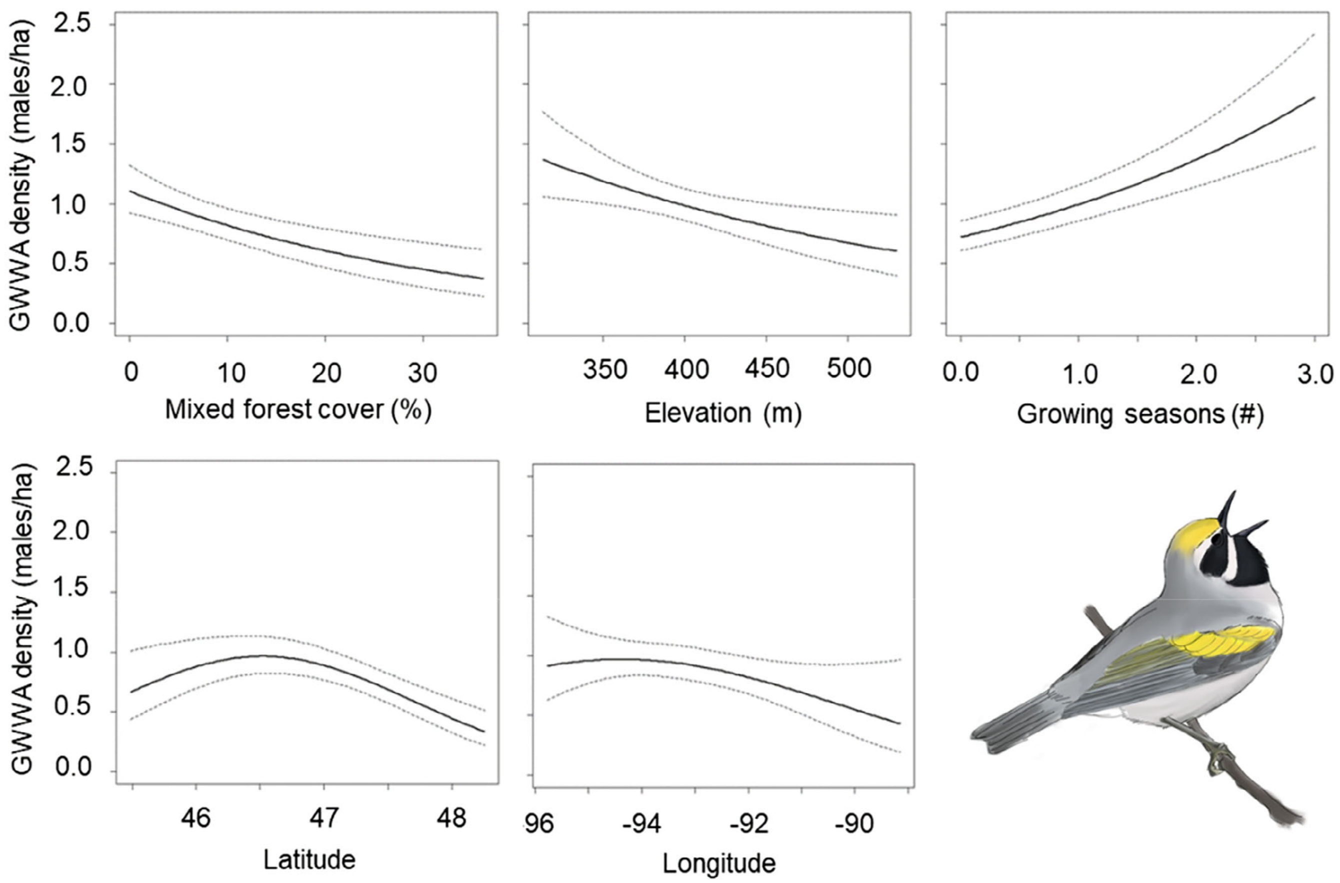

Figure 4. Functional relationships between Golden-winged Warbler density (males/ha) within regenerating overstory removals across the sampled Great Lakes Conservation Region. Shown are all covariate relationships for our top-ranked hierarchical distance model. Solid lines represent density estimates while dashed lines represent 95% confidence intervals.

continue to enhance for at least several additional years (Otto & Roloff 2012). Future work monitoring stands beyond their third growing season may elucidate how habitat associations may change as stands continue to age in the Great Lakes Conservation Region. As forest stands age into the sapling stage, though no longer nesting habitat for GWWAs, they provide habitat to postfledging GWWAs and other species (Streby & Andersen 2013; Streby et al. 2016; Fiss 2018), highlighting the need for a mosaic of forest successional stages. A major challenge for programs like WLFW and RCPP that focus on private lands will be to maintain adequate young forest cover for nesting GWWA populations in the face of extreme land parcelization (Haines et al. 2011). Indeed, land parcelization results in an increased number of landowners owning a finite area of potential GWWA habitat (Haines et al. 2011). Consequently, landscapes with highly fragmented ownership (i.e. highly parcelized) may preclude the forest age class diversification essential to sustainable GWWA populations.

Within both conservation regions, mixed forest cover was negatively associated with GWWA use of restored habitats. Although GWWAs are known to avoid coniferous-dominated landscapes (Buehler et al. 2007; Roth et al. 2012), our results demonstrate that even modest mixed forest cover (e.g. 10% at a 1-km radius) may stifle restoration success in this system. Like mixed forest cover, elevation was associated with negative GWWA response in both regions. This relationship was particularly interesting in the Appalachian Mountains Conservation Region wherein habitat management emphasizes montane habitats, in an effort to reduce sympatry with Blue-winged Warblers (Bakermans et al. 2011, 2015; Wood et al. 2016). With this in mind, the patterns we report may be landscape-specific, and land managers wishing to conserve GWWAs should consider multiple factors (including local abundance) when selecting forests for restoration (≥75% deciduous cover, 200–500 m elevation).

Our finding that GWWAs failed to colonize restored habitats across portions of the Appalachian Mountains speaks to sparse distribution of populations in this region. Historically, GWWAs were comparatively abundant across both regions of their breeding range (Gill 1980, 2004; Roth et al. 2012); however, populations have declined by an estimated 95% within the Appalachian Mountains (Wilson et al. 2012; Sauer et al. 2017). Chronic regional population declines were reflected by sparse occupancy in restored habitats across the Appalachian Mountains wherein restored habitats >24 km from local population centers were

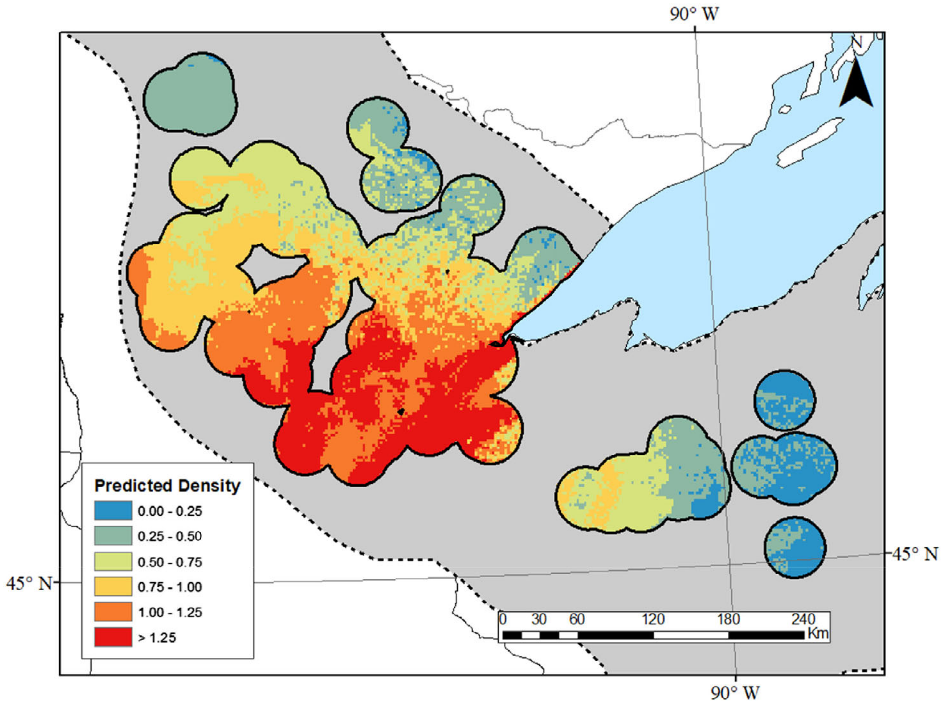

Figure 5. Patterns of Golden-winged Warbler predicted density (males/ha) in restored habitats across sampled portions of the Great Lakes Conservation Region. We predicted occupancy only within a 24-km radius of sampled survey locations using our top model that considered latitude, longitude, elevation, and percent mixed forest within a 1-km radius. Portions of the Great Lakes Conservation Region outside our predicted area are shown in gray.

least likely to be occupied. Only one landscape in the Appalachians—the Pocono Mountains—had consistently high occupancy. Across this landscape, GWWAs are known to occur in abundance in both managed forests like those studied here and natural wetlands that perforate this landscape (McNeil et al. 2018). One interesting prediction from our map was that GWWA were expected to be common in northwestern New Jersey, although we never detected the species in restored habitats in the state. New Jersey's capacity to support GWWAs, unlike the Poconos, may be compromised by extremely low GWWA abundance coupled with locally common BWWAs and a limited ability to conduct management near source populations or other factors not assessed by our study (e.g. widespread coverage of wetlands by invasive *Phragmites australis*; Roth et al. 2012).

Although our study is among the first to assess the success of a national habitat restoration program aimed at recovering songbird populations, many parallels can be drawn between the efforts of WLFW/RCPP and habitat management for Kirtland's Warblers (*Setophaga kirtlandii*; Bocetti et al. 2014). Like the GWWA, Kirtland's Warbler is a Nearctic-Neotropical migratory songbird dependent upon early-successional forests in eastern North America. By the 1970s, fewer than 200 males were detected on annual population surveys and all detections were restricted to northern portions of Michigan's Lower Peninsula (Probst et al. 2003; Donner et al. 2008). In response to the critical state of the Kirtland's Warbler population, a multiagency effort was initiated to manage thousands of hectares of habitat on public lands (Donner et al. 2008). By the early 1990s, the Kirtland's Warbler population began to grow in response to habitat management and, by 2003, 1,200 singing males were recorded (Donner et al. 2008). Although it took several decades of concerted effort, the Kirtland's Warbler was ultimately removed from the Endangered Species List in response to the species' robust recovery (USFWS 2019). Although concerted habitat restoration intended to benefit GWWA is still early in the implementation stage, that similar approaches have been successful elsewhere is promising. With this in mind, rigorous assessments of GWWA population growth in response to programs like WLFW/RCPP will require systematic sampling of the GWWA population including range-wide measurements of abundance over time, especially in the Appalachian Mountains where the species is rare and difficult to detect (Roth et al. 2012).

While the restored habitats we studied were not uniformly occupied by GWWAs, management of early-successional habitat remains essential to avoid regional extirpation of GWWA, especially in the Appalachian region (Rohrbaugh et al. 2016). Given that overstory removal harvests are already an accepted method of managing hardwood forests (Johnson et al. 2009), our results demonstrate that habitat restoration for GWWAs is highly compatible with standard forestry practices (Nyland 2002). Though outside the scope of our study, assessments of GWWA use of other managed habitat types (e.g. alder shearing) would also be valuable in improving our understanding of how GWWA respond to BMP implementation. Although our study was focused on GWWA, we commonly observed other disturbance-dependent species (e.g. Prairie Warblers, *Setophaga discolor*) within restored GWWA habitats, suggesting the potential for GWWA BMP implementation to benefit a broad suite of animal species. Furthermore, a precursor to overstory removal harvests in oak forest types is frequently a series of shelterwood harvests (Johnson et al. 2009). Shelterwood harvests tend to have too much tree canopy to support nesting GWWAs, but they often support other imperiled species like Cerulean Warblers (*S. cerulea*) and, thus, further support the notion that standard forestry practices may benefit numerous bird species (Wood et al. 2013; Boves et al. 2015). Although our study is limited to a single restoration initiative, our results demonstrate that programs aimed at early-successional habitat restoration, when implemented in the framework of adaptive forest management, have the potential to benefit habitat-limited species while remaining within the realm of sustainable forestry.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Models of detection probability for Golden-winged Warblers within restored early-successional forests in the Appalachian Mountains (top) and Great Lakes (bottom).
Table S2. Regional models of occupancy and density for Golden-winged Warblers within restored early-successional forests in the Appalachian Mountains (top) and Great Lakes (bottom).
Table S3. Patch models of occupancy and density for Golden-winged Warblers within restored early-successional forests in the Appalachian Mountains (top) and Great Lakes (bottom).
Table S4. Landscape models of occupancy and density for Golden-winged Warblers within restored early-successional forests in the Appalachian Mountains (top) and Great Lakes (bottom).
Table S5. Global models of occupancy and density for Golden-winged Warblers within restored early-successional forests in the Appalachian Mountains (top) and Great Lakes (bottom).
Figure S1. A workflow diagram depicting components of occupancy- and hierarchical distance modeling for the Appalachian Mountains (left) and Great Lakes (right), respectively.
Figure S2. Patterns of vegetative succession within restored Golden-winged Warbler habitat over growing seasons.
Figure S3. Projections of Golden-winged Warbler occupancy in eastern Pennsylvania (A), central Pennsylvania (B), and southcentral Pennsylvania (C).
Figure S4. Values of Ripley's K for sampling points where Golden-winged Warblers were detected (circles) as compared to all our sampling locations (thin black line).
Figure S5. Projections of GWWA density in western MN (A), central MN (B), and the MN/WI boarder (C).

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