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Characteristics of Golden-winged Warbler territories in plant communities associated with regenerating forest and abandoned agricultural fields

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ABSTRACT.   In the Appalachian portion of their breeding range, Golden-winged Warblers (*Vermivora chrysoptera*) nest in shrubland and regenerating forest communities created and maintained by disturbance. Because populations of Golden-winged Warblers have exhibited precipitous declines in population throughout their Appalachian breeding range, management activities that create or maintain early successional habitat are a priority for many natural resource agencies and their conservation partners. Within these early successional habitats, however, additional information is still needed concerning the relative importance of different vegetation features in selection of breeding territories by Golden-winged Warblers. Our objective, therefore, was to use logistic regression to estimate the probability of territory-level occupancy by Golden-winged Warblers in north-central Pennsylvania at two sites, each with its own early successional community, based on vegetation characteristics. Our communities were composed of shrublands and regenerating forest sites resulting from two disturbances: agriculture and forest fire. Despite differences in vegetation structure, portions of both study areas (regenerating forest and old field) supported territorial Golden-winged Warblers. Probability of territory occupancy by Golden-winged Warblers increased with percent blackberry (*Rubus*) cover in the regenerating forest community, and decreased as basal area and distance to microedge increased (i.e., as vegetation patchiness decreased) in both communities. These habitat features have also been found to influence other aspects of Golden-winged Warbler breeding ecology such as nest-site selection, pairing success, and territory abundance. Vegetation features influencing Golden-winged Warbler territory establishment can differ among shrubland and regenerating forest communities, and management decisions and outcomes may be affected by these differences. Our study provides a starting point for a more comprehensive hypothesis-driven occupancy survey to investigate features of the territories of Golden-winged Warblers across a broader geographic range and in different vegetation communities.

RESUMEN.   **Características de los territorios de la Reinita Alidorada en comunidades vegetales asociadas con la regeneración de bosques y campos agrícolas abandonados**
En la parte de los Apalaches de su rango de cría, la Reinita Alidorada (*Vermivora chrysoptera*) anidan en matorrales y en bosques que están regenerando, creadas y mantenidas por la perturbación natural. Debido a que las poblaciones de las Reinitas Alidoradas se han exhibido grandes reducciones a lo largo de su área de reproducción en los Apalaches, las actividades de gestión que crean o mantienen el estadio temprano de sucesión son prioridades para muchas agencias de recursos naturales y sus socios de la conservación. Sin embargo, dentro de estos hábitats sucesionales tempranos, todavía se necesita información adicional sobre la importancia relativa de las diferentes características de la vegetación en la selección de los territorios de cría por las Reinitas Alidoradas. Nuestro objetivo, por lo tanto, fue utilizar la regresión logística para estimar la probabilidad de ocupación en el territorio de las reinitas en el centro-norte de Pensilvania en dos sitios, cada uno con su propio comunidad vegetal en el estadio temprano de sucesión. Las comunidades vegetales estaban compuestas de matorrales y hábitats sucesionales tempranos, resultantes de dos perturbaciones: la agricultura y los incendios forestales. A pesar de las diferencias en la estructura de la vegetación, porciones de ambas áreas de estudio (las hábitats sucesionales tempranos y el antiguo campo agrícola) apoyaron las reinitas territoriales. La probabilidad de ocupación del territorio por las Reinitas Alidoradas se aumentó con el porcentaje de cubierta de zarzamora (*Rubus*) en la comunidad de sucesión, y disminuyó a medida que el área basal y la distancia al micro-borde del bosque se aumentó (es decir, cuando se disminuyó la forma irregular de la vegetación) en ambas comunidades. Se ha determinado que estas características del hábitat influye a otros aspectos de la ecología de la cría de la reinita, como la selección del lugar del nido, el éxito de emparejamiento, y la abundancia entre el territorio. Las características de la vegetación que influye el

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establecimiento del territorio se pueden diferir entre las comunidades de arbustos y bosques en regeneración, y las decisiones de gestión y los resultados correspondientes pueden verse afectados por estas diferencias. Nuestro estudio proporciona un punto de partida para una encuesta de ocupación basada en hipótesis para investigar las características de los territorios de las Reinitas Alidoradas a través de un rango geográfico más amplio y en diferentes comunidades de vegetación.

Creation and maintenance of shrublands and regenerating forests (hereafter, early successional communities) in eastern North America is a conservation priority because populations of many bird species that require such communities during a portion of their annual breeding cycle are declining (Rivera et al. 1998, Askins 2001, King et al. 2006, Schlossberg et al. 2010). For example, of 41 bird species identified as inhabitants of early successional communities in New England, 21 are declining and 12 more are of conservation concern (Schlossberg and King 2007). These declines have largely been attributed to reductions in the area of early successional communities (Trani et al. 2001, King and Schlossberg 2014). Historically, early successional communities in this region were created and maintained by a variety of natural disturbances such as wildfire, beaver (*Castor canadensis*) activity, tree falls, and weather events (i.e., wind and floods; DeGraaf and Yamasaki 2003). Current land uses or management methods that result in early successional communities include timber harvest, utility rights-of-way, farmland abandonment, shrubland management, and prescribed fire (Confer and Pascoe 2003, Bulluck and Buehler 2006, Fink et al. 2006). Different disturbance regimes often result in early successional communities that vary in plant composition and structure (Schulte and Niemi 1998, Franklin et al. 2000, Brawn et al. 2001, Bulluck and Buehler 2006) and, therefore, may not be equally suitable for all species of birds. Thus, maximizing the effectiveness of management programs requires knowledge of habitat selection by at-risk bird species in each vegetation community.

Golden-winged Warblers (*Vermivora chrysoptera*) are Neotropical migrant songbirds that nest in a variety of early successional and adjacent communities in the Great Lakes and Appalachian regions of North America (Confer et al. 2011). Populations in the Appalachian portion of their breeding range declined by an average of ~8.5% per year between 1966 and 2013 (Sauer et al. 2015). These declines are primarily attributed to habitat loss in both breeding and wintering areas, exacerbated by hybridization with closely related Blue-winged Warblers (*V. cyanoptera*; Buehler et al. 2007, Vallender et al. 2009, Toews et al. 2016). Of the threats affecting populations of Golden-winged Warblers in the Appalachian region, loss of nesting habitat is considered one of the most significant and, therefore, is currently a major focus of species-specific conservation (Roth et al. 2012, Rohrbaugh et al. 2016).

Creation and maintenance of breeding habitat for Golden-winged Warblers is needed at the landscape scale (i.e., ≥ 1 km extent), where habitat selection depends on percent forest cover and elevation (Bakermans et al. 2015a, Crawford et al. 2016), and the patch scale (i.e., 500 m extent), where key habitat-selection factors include stand age-class, density and patchiness of shrubs and saplings, and herbaceous ground cover (Bakermans et al. 2015a, Crawford et al. 2016, Frantz et al. 2016, Wood et al. 2016). Although development of the Golden-winged Warbler conservation plan and the results of more recent studies are important steps in the ongoing effort to increase populations in the Appalachian Mountains (Roth et al. 2012, Aldinger et al. 2015, Bakermans et al. 2015a), the primary focus of the conservation plan and recent studies has been on landscape- and nest site-scale (1 m²) habitat metrics, with less attention given to territory-scale attributes (i.e., Bellush et al. 2016, Frantz et al. 2016).

Territory-scale metrics are known to affect avian reproduction and survival (Weatherhead and Robertson 1977, Confer et al. 2003, Pearson and Knapp 2016), and thus are important for understanding how to effectively manage nesting habitat. For example, pairing success of male Golden-winged Warblers and nesting activity in Wisconsin aspen harvests were highest in stands with high

territory densities, and territory density was positively associated with availability of residual trees throughout the harvested areas (Roth et al. 2014).

We evaluated territory occupancy by Golden-winged Warblers in two early successional plant communities: abandoned agricultural land and regenerating forest. Specifically, we quantified within-territory vegetation attributes previously found to be important for Golden-winged Warblers to identify those most associated with territory occupancy in the two plant communities. Such information is needed to help refine and implement recently developed management guidelines at sites with similar plant communities in the central Appalachian breeding range of the Golden-winged Warbler (Rosenberg et al. 2016).

METHODS

Study areas. We collected data at Sproul State Forest in 2009 and 2010 and at Bald Eagle State Park in 2009. Although these two areas were only 30 km apart, we considered them separate study areas because they were located in different landscape contexts and had different land-use histories. We chose these locations because breeding populations of Golden-winged Warblers had previously been detected in the area.

Sproul State Forest (SSF, 41°14′N, 77°50′W) consisted of 112,000 ha located in western Clinton and northern Centre counties in north-central Pennsylvania. This study area was in the Mountainous High Allegheny Plateau physiographic province, a province characterized by high ridges and deep valleys created via headwater erosion of the West Branch of the Susquehanna River (Briggs 1999). Sproul State Forest was dominated by northern hardwood or dry oak (*Quercus* spp.) forests. Although there was active logging in SSF prior to and during our study, > 90% of forests were classified as sawtimber (> 25 cm dbh) and averaged 80–100 years old. Territorial Golden-winged Warblers monitored in our study were restricted to a 250-ha area regenerating after a 4000-ha stand-replacing wildfire in 1990. This regenerating forest was dominated by a mosaic of blackberry (*Rubus* spp.), huckleberry (*Gaylussacia* spp.), blueberry (*Vaccinium* spp.), mountain laurel

(*Kalmia latifolia*), sassafras (*Sassafras albidum*), birch (*Betula* spp.), black locust (*Robinia pseudoacacia*), and red maple (*Acer rubrum*) saplings. Black locust snags were also scattered throughout the regenerating forest community along with interspersed mature residual oak and birch. With the exception of sparsely distributed primitive cabins, a natural gas pipeline, and unimproved roads, there was little human development in this study area.

Bald Eagle State Park (BESP, 41°2′N, 77°39′W) consisted of 5900 ha located in northern Centre County and included a 730-ha reservoir. The remaining 4170 ha (71%) was a mosaic of fragmented forests, shrublands, and managed herbaceous openings resulting from historical agricultural land use and current wildlife management or utility rights-of-way maintenance. BESP is in the Ridge and Valley physiographic province, which is characterized by numerous long, narrow mountain ridges separated by valleys that vary in width and elevation (Way 2002). In BESP, we monitored Golden-winged Warblers on 243 ha (2009) of abandoned agricultural shrubland (hereafter, old field) that was annually mowed. Common tree and shrub species included yellow poplar (*Liriodendron tulipifera*), red maple, sugar maple (*A. saccharum*), elm (*Ulmus* spp.), black locust, black walnut (*Juglans nigra*), northern red oak (*Quercus rubra*), Virginia pine (*Pinus virginiana*), white pine (*P. strobus*), autumn-olive (*Eleagnus umbellata*), honeysuckle (*Lonicera* spp.), gray dogwood (*Cornus racemosa*), red osier dogwood (*C. sericea*), silky dogwood (*C. amomum*), hawthorn (*Crataegus* spp.), and arrowwood viburnum (*Viburnum dentatum*). The area surrounding BESP consisted of agricultural lands, low-density residential development, extensive tracts of forest, isolated forest patches, a state highway, and several secondary roads.

Territory mapping. We located and mapped territories of male Golden-winged Warblers from 1 May to 26 June 2009 (both communities) and 2010 (regenerating forest community only). We attempted to capture and color-band every territorial male to aid in identification during subsequent resighting attempts. This step was particularly necessary in areas with high densities of males. We used one 6-m mist-net (30-mm mesh), an MP3 audio lure of Golden-winged Warbler type I

and II songs (Stokes Field Guide to Bird Songs, Little, Brown, and Company, Boston, MA), and a model of a male Golden-winged Warbler to capture targeted males. We banded each captured bird with a standard USGS aluminum leg band and a unique combination of 1–3 colored plastic leg bands. We visited each community 2–3 times weekly during the breeding season (1 May to late June) to delineate territories by following individual males. We marked each song-post or observed location (e.g., foraging site) with male-specific unique color flagging and recorded geographic coordinates to the nearest 10 m using Garmin eTrex or Garmin 60CSx global positioning system (GPS, Garmin International, Olathe, KS). We used location data for each territorial male and ArcGIS to measure territory size and boundaries (minimum convex polygons, ESRI 2015). We refer to areas that we delineated via visual observation as defended territories. Although male Golden-winged Warblers are known to move outside defended territories (Streby et al. 2012, Frantz et al. 2016), Frantz et al. (2016) found that both radio-telemetry and visual observation of color-banded individuals can reliably delineate core-use areas of Golden-winged Warbler breeding territories.

Vegetation surveys. We measured several vegetation characteristics in all Golden-winged Warbler territories where we had ≥ 8 days of observations, and in unoccupied patches that appeared to contain similar Golden-winged Warbler nesting habitat to the occupied territories. Unoccupied patches were adjacent to or within 1 km of occupied territories and were surveyed two to three times weekly during the breeding season. We did not detect Golden-winged Warblers in these patches during any surveys. We hypothesized that territory occupancy would be influenced by a set of candidate variables we developed based on recent analyses regarding relationships between vegetation features and the breeding ecology of Golden-winged Warblers. These included: i) *Rubus* cover for foraging (Bellush et al. 2016), ii) variables potentially important for nest-site selection, including distance to forest edge (Aldinger and Wood 2014), *Rubus* cover (Aldinger and Wood 2014, Terhune et al. 2016), grass cover (Terhune et al. 2016), distance to microedge (change in vegetation structure;

Aldinger and Wood 2014), vegetation density (saplings and shrubs; Aldinger and Wood 2014, Terhune et al. 2016), and a quadratic response of vegetation density (Terhune et al. 2016), iii) grass cover, a variable potentially influencing nest success (Terhune et al. 2016), and iv) variables potentially influencing density and abundance, including basal area (Huffman 1997, Klaus and Buehler 2001, Roth et al. 2014, Bakermans et al. 2015a), a quadratic response to basal area (Bakermans et al. 2015a), and distance to microedge (Bakermans et al. 2015a, Wood et al. 2016). *Rubus* and grass cover were predicted to have positive relationships with territory occupancy, distance to forest edge and microedge were predicted to have negative relationships, and basal area and vegetation density were predicted to have quadratic responses to territory occupancy.

Unoccupied patches were delineated by centering a square equal to the area of the average Golden-winged Warbler territory (1.5 ha) on a random point created in ArcGIS 9.2 (ESRI 2009) using Hawth's Tools (Beyer 2001) and the generate random points function. Placement of random points used for delineating unoccupied patches was restricted to our study areas and these points were within the same disturbance footprint as the territories. Boundaries of unoccupied patches and territories did not overlap. We sampled vegetation in each Golden-winged Warbler territory and unoccupied patch using a systematic random sampling design of points along transects. All territory and unoccupied patch boundaries were delineated in ArcGIS. We used ArcGIS to select a random start location within each territory or unoccupied patch. We selected one random number for the distance between vegetation sampling points. This number was between 25 and 40 m so that points did not overlap and we could fit ≥ 30 points per territory or unoccupied patch. We also selected a random number between 0 and 359 to determine the compass direction of the transects in a given territory. If the chosen bearing pointed away from the territory or unoccupied patch, we used the opposite direction. We used ArcGIS and flagged territory boundaries to ensure that transect routes and points were entirely within and evenly distributed throughout each territory or unoccupied patch (ESRI 2009).

At each sampling point, we visually estimated the percent cover of grass and *Rubus* within a 1-m-radius circle. Because visual estimation methods can result in observer bias (Luscier et al. 2006), we trained all surveyors on the protocol as a group and worked in teams of two or more to minimize this potential (Kercher et al. 2003, Klimeš 2003, Symstad et al. 2008). This method is also consistent with those used in other studies where Golden-winged Warbler habitat features have been quantified (Confer et al. 2003, Aldinger et al. 2015, Bakermans et al. 2015a, Terhune et al. 2016). We also measured distance to the nearest microedge as a surrogate for vegetation patchiness at each point, with a microedge being any noticeable change in vegetation structure, i.e., change in vegetation height or species composition, such as a transition from grass to shrubs (Aldinger and Wood 2014, Bakermans et al. 2015a, Frantz et al. 2016, Wood et al. 2016). At every fifth sampling point (≥ 6 points per territory or unoccupied patch), we recorded basal area using a 10-factor prism, and the number of shrubs 1–2 m tall, shrubs > 2 m tall, and saplings (< 10 cm dbh and > 1 m tall) within a 5-m radius. We measured distance from the geometric center of each territory or unoccupied patch to the nearest mature forest edge using ArcMap (ESRI 2009) and aerial photographs.

Data analysis. We used the sum of shrubs and saplings to create a single covariate to represent "vegetation density." We calculated vegetation density for each 5-m-radius plot (stems per 79 m^2). We included vegetation density^2 and basal area^2 in some models containing vegetation density and basal area because Golden-winged Warblers are expected to select some optimal density (Roth et al. 2012, Bakermans et al. 2015a, Terhune et al. 2016) and the quadratic term permits a parabolic relationship. We averaged values for all vegetation covariates in each territory and unoccupied patch. We determined the Pearson's correlation among all pairs of variables and did not include two variables in the same model if the absolute value was > 0.7. One occupied territory at the regenerating forest study area had all vegetation measurements except basal area, so we used the mean basal area of all territories at this study area as the basal area value for that territory

(Cooch and White 2006). We standardized all continuous covariates to facilitate convergence given that our covariates had different scales (Schielzeth 2010).

We assumed that detection rate (p*) over the entire breeding season was close to 1, given a closed population, because the detection probability of individual male Golden-winged Warblers was estimated at 0.45 for a single visit (Aldinger and Wood 2015) and we visited each territory and unoccupied patch from 14 to 21 times. Given the equation $p^* = 1 - (1 - p)^n$, where p = detection probability for a single visit and n = the number of visits, our expected cumulative detection probability was 0.9998. We calculated the mean and standard error of each habitat characteristic (occupied territories and unoccupied patches combined) for each community to compare study areas. We performed two-tailed *t*-tests ($\alpha = 0.05$) to compare average values between study areas in R (version 3.2.4, R Core Team 2016). We performed logistic regression using the MuMIn package in R to model probability of occupancy based on vegetation characteristics (Barton 2016).

We ran all combinations of the variables of interest ($N = 8$) and their interaction with community type. We also included year in some models nested within our regenerating forest community to assess whether characteristics associated with this community differed between 2009 and 2010. These variables resulted in 8082 models, as we did not have a preconceived notion of the best combination of our covariates. We included an intercept-only null model. All possible subsets regression results in similar variable selection to stepwise regression and is an accepted method of selecting models (Murtaugh 2009). We used a model likelihood value of ≥ 0.125 to select supported models (Burnham and Anderson 2002). If there were multiple models with likelihood values ≥ 0.125, we employed model-averaged predictions and widths of 95% prediction intervals on model-averaged regression lines to infer the predictive ability of variables. Model-averaging was conducted with the AICcmodavg package in R (Mazerolle 2016, R Core Team 2016).

RESULTS

We delineated territory boundaries and conducted vegetation surveys in 62 Golden-

winged Warbler territories in the regenerating forest community (N_{2009} = 31, N_{2010} = 31) and 28 territories in the old field study area. We collected a mean of 31.3 ± 1.6 (SE) (range =8 – 62 points) mapped points per territory in the regenerating forest community and 36.4 ± 2.7 (range = 16 – 69 points) per territory in the old field area. We also conducted vegetation surveys in 33 unoccupied patches in regenerating forest (N_{2009} = 25, N_{2010} = 8) and 24 unoccupied patches in the old field community. Mean territory size was 1.53 ± 0.13 ha in the regenerating forest community and 1.47 ± 0.16 ha in the old field study area. Territory density at the regenerating forest community was 1.85 territories/10 ha in 2009 and 1.65 territories/10 ha in 2010. Territory density in the old field study area was 1.18 territories/10 ha. Several vegetation characteristics differed between old field and regenerating forest communities, including distance to forest edge, distance to microedge, percent *Rubus* cover, and percent grass cover (Fig. 1). We found no strong (> 0.70) correlations between any possible pair of habitat variables.

We identified 71 supported models (< 1% of all models) of Golden-winged Warbler territory occupancy (Table 1). *Rubus* cover, basal area, and community were included in all supported models. Vegetation patchiness (distance to microedge) and the year (regenerating forest community) effect were included in all but one supported model. Basal area^2 was included in over half of the supported models (N = 45 models). Vegetation density was included in 34 models, and the *Rubus* × community interaction was included in 31 models. No other variables were present in > 20 models. Because 71 models had a relative likelihood ≥ 0.125, we based our inferences on model-averaged predicted values.

Probability of Golden-winged Warbler occupancy at the regenerating forest community increased with percent *Rubus* cover. A probability of occupancy of ≥ 0.95 was associated with 40% or more *Rubus* cover in 2009 and 25% or more *Rubus* cover in 2010 (Fig. 2). *Rubus* cover was not strongly associated with probability of occupancy in the old field community, and occupancy probability ranged from 0.5 to 0.7 across all values of
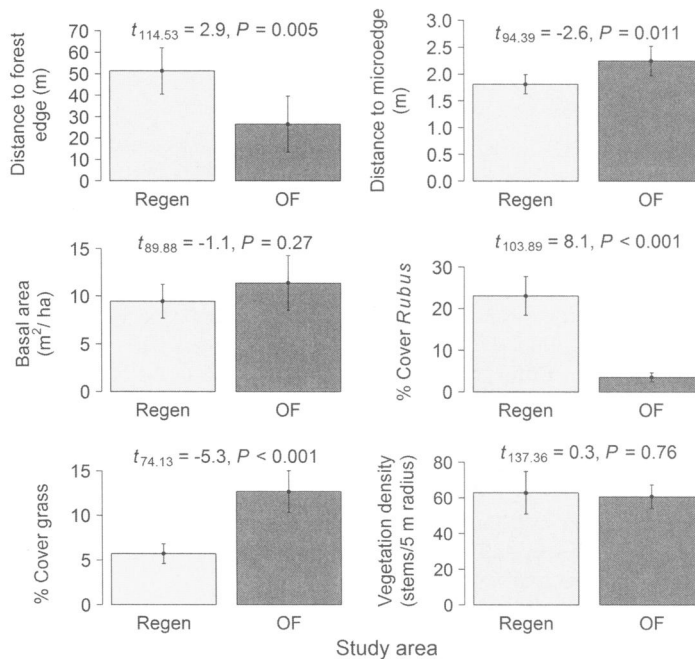

Fig. 1. Means (± SE) for variables measured in territories of Golden-winged Warblers and in randomly selected unoccupied patches. Communities were located in a regenerating forest (Regen) and an old field (OF) in central Pennsylvania in 2009 and 2010.

Table 1. Model descriptions, number of parameters, and information-theoretic selection criteria for models of probability of occupancy by Golden-winged Warblers in regenerating forest and abandoned agriculture communities in central Pennsylvania during 2009 and 2010. We selected supported models based on a likelihood value of ≥ 0.125, but, for brevity, only the null model and models with a difference in Akaike's Information Criterion (ΔAIC_c) of ≤ 2.0 are shown. There were 71 supported models out of 8082 models evaluated. The top model had an AIC_c of 127.93.

Model	Number of parameters	ΔAIC_c	Weight[a]	Likelihood[b]
Rubus + basal area + basal area^2 + distance to microedge + community + *Rubus* × community + community × year	8	0.00	0.24	1.000
Rubus + basal area + basal area^2 + distance to microedge + community + community × year	7	0.19	0.22	0.909
Rubus + basal area + distance to microedge + community + community × year	6	0.92	0.15	0.631
Rubus + basal area + basal area^2 + distance to microedge + community + *Rubus* × community + basal area × community + community × year	9	1.55	0.11	0.460
Rubus + basal area + basal area^2 + distance to microedge + community + vegetation density + vegetation density × community + community × year	9	1.73	0.10	0.420
Rubus + basal area + basal area^2 + distance to microedge + community + vegetation density + *Rubus* × community + community × year	9	1.76	0.10	0.414
Rubus + basal area + distance to microedge + community + *Rubus* × community + community × year	7	1.98	0.09	0.371
Null	1	70.41	0.00	0.000

[a]Akaike weight representing relative support for each model.
[b]Relative model likelihoods, calculated as $\exp(-0.5 \times \Delta AIC_c)$.

Rubus. Maximum occupancy probability in 2009 was 0.95 at 0 m^2/ha basal area in the regenerating forest community and ≥ 0.7 at 0 − 7 m^2/ha basal area in the old field community. Occupancy probabilities of 0.95 and higher occurred at 2 − 12 m^2/ha basal area at the regenerating forest community in 2010 (Fig. 3). Probability of occupancy by Golden-winged Warblers decreased as vegetation patchiness decreased, regardless of community. Occupancy probability was ≥ 0.7 at distances to microedge of 0.8 − 1.7 m in the old field community and 0.4 − 2.9 m in the regenerating forest community in 2010 (Fig. 4). Occupancy probability was highest (0.69) in the regenerating forest community in 2009 at 0.6 m to microedge (Fig. 4). The 95% confidence intervals for distance to microedge and the year (nested in regenerating forest community) effect did not overlap

zero in any of the three top models (Table 2). Confidence intervals for *Rubus*, basal area, and community did not overlap zero in two of the three top models (Table 2). The confidence interval for basal area^2 overlapped zero in both top models including this term (Table 2). Confidence intervals of the *Rubus* × community effect overlapped zero in the one top model including this term (Table 2). No other variables were in the top three models.

DISCUSSION

Despite many differences in vegetation structure, portions of both study areas (regenerating forest and old field) supported territorial Golden-winged Warblers. Territories had greater *Rubus* cover than adjacent unoccupied areas in the regenerating forest community.
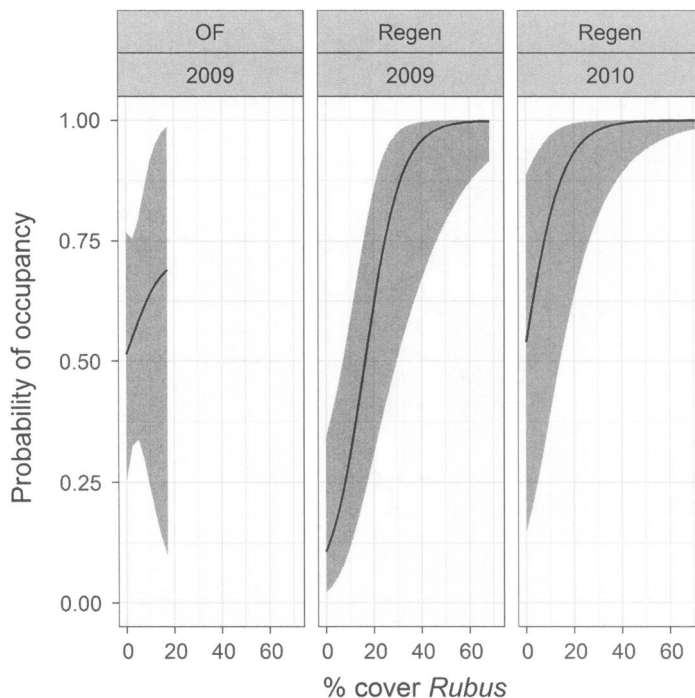
Fig. 2. Model-averaged probability of occupancy (± 95% prediction intervals) by Golden-winged Warblers as a function of percent cover of *Rubus* in our old field (OF) and regenerating forest (Regen) communities in central Pennsylvania in 2009 and 2010.

In both the regenerating forest and old field communities, warblers occupied territories with lower basal areas and greater vegetation patchiness. These associations between territory occupancy and vegetation characteristics should aid land managers attempting to create breeding habitat for Golden-winged Warblers in the central Appalachian portion of their breeding range.

Warblers in both communities exhibited the same general pattern of a higher probability of occupancy with lower values of basal area (0 − 12 m²/ha). In fact, the average basal areas for territories in the regenerating forest community (7.6 ± 0.8 m²/ha) and old field community (7.1 ± 0.9 m²/ha) were nearly identical. In comparison, mean basal areas for unoccupied patches were greater than 12 m²/ha in both study areas. Moreover, the range of basal areas occupied by Golden-winged Warblers in our regenerating forest and old field communities was similar to those reported in studies conducted in areas regenerating after timber harvests, another method commonly used to create nesting habitat for

this species (Klaus and Buehler 2001, Roth et al. 2014, Bakermans et al. 2015a). In Tennessee and North Carolina, portions of timber-harvested areas occupied by Golden-winged Warblers had lower basal areas (median basal area = 10 m²/ha) than those not occupied (median basal area = 40 m²/ha; Klaus and Buehler 2001). Similarly, abundance of Golden-winged Warblers in Pennsylvania peaked in areas regenerating after timber harvest with basal areas of ~7 m²/ha (Bakermans et al. 2015a) and, in Minnesota, Golden-winged Warbler abundance decreased when basal area values exceeded 9 m²/ha (Huffman 1997). Thus, our results regarding the importance of basal area to Golden-winged Warblers at the territory-scale support previous findings regarding the importance of this vegetation feature at the forest-stand level (Huffman 1997, Klaus and Buehler 2001, Roth et al. 2014, Bakermans et al. 2015a).

Ensuring that patches of low basal area are distributed across managed areas appears to be important for promoting occupancy by territorial Golden-winged Warblers. In both
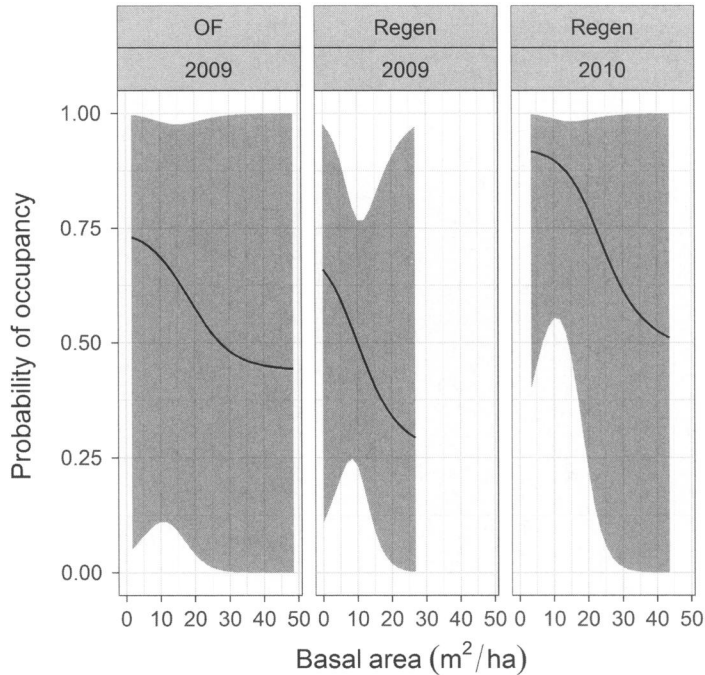
Fig. 3. Model-averaged probability of occupancy ($\pm$ 95% prediction intervals) by Golden-winged Warblers as a function of basal area at our old field (OF) and regenerating forest (Regen) communities in central Pennsylvania in 2009 and 2010.

of our study areas, the probability of occupancy declined sharply at basal areas > 3 to 10 m²/ha in 2009 and, in 2010, the probability of occupancy declined sharply for basal areas > 12 m²/ha in the regenerating forest study area. The lower bound for basal area in occupied territories in both study areas was 0 m²/ha. However, male Golden-winged Warblers in Wisconsin exhibited higher territory densities and greater pairing success in aspen (*Populus* spp.) harvests with scattered residual trees than in harvested areas with no residual trees (Roth et al. 2014). These authors suggested that residual basal area in timber harvests intended to benefit nesting Golden-winged Warblers should be at least 0.9 m²/ha, and that the optimal basal area was likely higher (Roth et al. 2014). Several territories in our study areas were adjacent to an intact forest edge, which likely compensated for the lack of residual basal area within the disturbance footprint. Breeding territories of Golden-winged Warblers are known to be restricted to areas adjacent to intact forest edge when early successional

communities associated with clearcuts, reclaimed surface mines, abandoned agricultural lands, and natural shrub wetlands lack large trees (Rossell 2001, Confer et al. 2003, Rossell et al. 2003, Patton et al. 2010). Distance from forest edge was found to influence nest-site selection by female Golden-winged Warblers nesting in shrublands and adjacent forest edge of the upper Great Lakes region, and ultimately, females that nested closest to forest-shrubland edges had the greatest predicted total fitness (nest and fledgling survival combined) (Streby et al. 2014b). The presence of shrubland-intact forest edges was likely important for occupancy by Golden-winged Warblers in our regenerating forest and old field study areas with low basal areas.

Occupancy of Golden-winged Warbler territories in our study was associated with high vegetation patchiness, with warblers establishing territories in areas where the average distance to microedge was $\leq 2 - 3$ m. Thus, territories were in areas with closer transitions among vegetation than unoccupied patches. Vegetation patchiness has been consistently
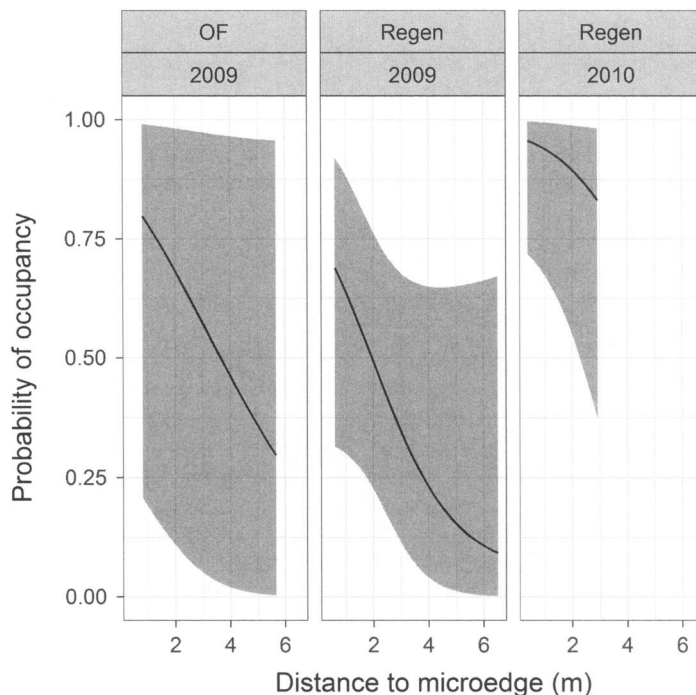
Fig. 4. Model-averaged probability of occupancy (± 95% prediction intervals) by Golden-winged Warblers as a function of distance to microedge, a surrogate for vegetation patchiness, at our old field (OF) and regenerating forest (Regen) communities in central Pennsylvania in 2009.

reported as a common feature of breeding territories of Golden-winged Warblers throughout much of their range and across many vegetation communities, including high-elevation wetlands in North Carolina (Rossell et al. 2003), shrub-pasture lands in West Virginia (Aldinger and Wood 2014), areas regenerating after timber harvests in Pennsylvania (Bakermans et al. 2015a), and abandoned farmlands in northern New York (Wood et al. 2016). The importance of vegetation patchiness to breeding Golden-winged Warblers may be a function of availability of potential nest sites because nests are typically located at microedges between shrubs and herbaceous cover (Aldinger and Wood 2014). Rossell et al. (2003) suggested that patchiness may deter nest predators, but did not specifically investigate this possibility.

The patchy vegetation structure associated with Golden-winged Warbler territories in our regenerating forest study area is characteristic of plant communities that can result from variation in intensity and frequency as fire moves across a landscape (Parshall et al.

2003). Vegetation heterogeneity resulting from prescribed fire has been found to be an important driver of avian communities in regenerating forests elsewhere (Fuhlendorf et al. 2006). Our regenerating forest community was the result of a large (4000 ha) stand-replacing wildfire that occurred 20 years prior to our study. Although much of the burned area had regenerated to closed-canopy pole-saplings stands, the area used by Golden-winged Warblers had retained complex vegetation structure consisting of a mosaic of scattered legacy trees, coppicing saplings, shrubs (i.e., mountain laurel, sweet-fern (*Comptonia peregrina*), and *Vaccinium* spp.), *Rubus* thickets, and herbaceous cover (i.e., ferns, grasses, and forbs).

Availability of patchy vegetation in our old field study area was limited, likely a result of two vegetation features: i) large patches of homogeneous herbaceous cover maintained by annual mowing, and ii) expansive areas of invasive shrubs (i.e., autumn-olive and honeysuckle) that formed monocultures of closed-canopy thickets with little to no other

Table 2. Regression parameter (Beta) estimates, standard errors, and 95% confidence intervals for parameters in the top three supported models of Golden-winged Warbler territory occupancy in regenerating forest and agriculture communities in Pennsylvania in 2009 and 2010. We selected supported models based on a likelihood value of ≥ 0.125; for brevity, only results from three models are shown. There were 71 supported models of 8082 in our candidate set. We made inferences based on model-averaged predicted values.

	Variable	Beta estimate	SE	Lower CI	Upper CI
Model 1	Intercept	−0.26	1.42	−3.05	2.54
	Rubus	−0.80	2.26	−5.23	3.63
	Regenerating forest community	0.35	1.54	−2.66	3.36
	Basal area	0.22	1.07	−1.88	2.31
	Basal area^2	−2.58	1.46	−5.44	0.28
	Distance to microedge	−0.73	0.27	−1.26	−0.20
	Rubus × regenerating forest community	3.88	2.49	−1.00	8.77
	Regenerating forest community × year	2.12	0.92	0.32	3.92
Model 2	Intercept	1.86	0.57	0.75	2.97
	Rubus	2.65	0.67	1.34	3.95
	Regenerating forest community	−1.96	0.58	−3.08	−0.83
	Basal area	−0.16	1.07	−2.26	1.94
	Basal area^2	−2.17	1.50	−5.11	0.77
	Distance to microedge	−0.60	0.25	−1.10	−0.11
	Regenerating forest community × year	2.25	0.91	0.47	4.03
Model 3	Intercept	1.85	0.52	0.84	2.87
	Rubus	2.43	0.59	1.28	3.58
	Regenerating forest community	−1.96	0.58	−3.09	−0.82
	Basal area	−1.76	0.39	−2.52	−0.99
	Distance to microedge	−0.62	0.25	−1.10	−0.14
	Regenerating forest community × year	2.36	0.89	0.61	4.10

vegetation strata intermixed. Prior to and during our study, most of our old field study area was managed via mechanical methods that followed habitat guidelines for American Woodcock (*Scolopax minor*; Bakermans et al. 2015b), including felling all trees in a shrubland matrix, shrubs mowed in a manner that yielded dense strips of single-aged shrub cover, and interspersed herbaceous fields ranging in area from ~1–3 ha. All three of these conditions contributed to the reduced patchiness of vegetation and greater distances to microedge. Given the importance of vegetation patchiness to nesting Golden-winged Warblers in our study areas and elsewhere, management activities that target these warblers should consider the need for creating and maintaining a mosaic of structurally diverse vegetation within disturbance footprints.

Rubus cover was another important predictor of territory occupancy by Golden-winged Warblers in our regenerating forest study area. Positive relationships between Golden-winged Warblers and *Rubus* cover have been noted previously for foraging, nest-site selection, and nest survival (Aldinger et al. 2015, Bellush et al. 2016, Terhune et al. 2016). In a study conducted in our regenerating forest study area, Bellush et al. (2016) found that *Rubus* had higher densities of caterpillars (typical Golden-winged Warbler prey; Confer et al. 2011, Streby et al. 2014a) than several other tree and shrub species. In addition, more *Rubus* was found in Golden-winged Warbler territories than in unoccupied areas, and Golden-winged Warblers selectively foraged on *Rubus* over several other shrub and tree species (Bellush et al. 2016). Our observed correlation between territory occupancy and vegetation known to host high amounts of Golden-winged Warbler prey is consistent with the results of other studies that suggest birds may select territories based on prey availability (Burke and Nol 1998, Marshall and Cooper 2004, Bellush et al. 2016).

Associations between *Rubus* and nest-site selection by Golden-winged Warblers have

been observed previously throughout their breeding range (Aldinger et al. 2015, Terhune et al. 2016). Nest-site availability is another factor thought to influence territory occupancy in songbirds (Martin and Roper 1988, Burke and Nol 1998, Jones and Robertson 2001). A range-wide study that included sites in seven states revealed that *Rubus* cover was an important positive predictor of nest-site selection by Golden-winged Warblers (Terhune et al. 2016) and a positive predictor of nest survival (Aldinger et al. 2015). The importance of *Rubus* cover for territory occupancy by Golden-winged Warblers in our regenerating forest study area may have been driven in part by the interplay between prey availability and high-quality nest sites. Finally, the fact that *Rubus* was an uncommon component in territories and unoccupied areas in our old field study area (< 5% cover; Fig. 1) demonstrates that, although *Rubus* has been a predictor of nest-site selection, nest survival, and territory placement throughout much of the Appalachian breeding range of Golden-winged Warblers, it is apparently not a requisite for occupancy in old field communities. Old field and forested systems regenerate differently, with old fields typically resulting in more shrub cover than forested systems (DeGraaf and Yamasaki 2003). Therefore, *Rubus* may not be as important in old field areas because other shrub species fill this niche.

CONCLUSION

Disturbance regimes like those we studied are known to affect habitat quality for a variety of bird species (Brawn et al. 2001), and we observed both similarities and discrepancies in Golden-winged Warbler territory occupancy in two study areas with different early successional plant communities created by different disturbance regimes. Our results regarding the importance of basal area, vegetation patchiness, and *Rubus* cover in territory occupancy by Golden-winged Warblers augment those of previous studies, where other aspects (i.e., foraging and nesting) of their breeding ecology were examined. Vegetation features known to influence territory occupancy could be incorporated into models that predict region-specific (i.e., Appalachian) and disturbance-specific effects of management on breeding populations of Golden-winged

Warblers. Our results, in combination with those of previous studies, suggest that goals for areas managed for breeding Golden-winged Warblers should include distances between changes in vegetation structure (e.g., changes among herbaceous and shrub patches) that do not exceed 3 m. We recommend managing regenerating forest communities in a manner that promotes the establishment of *Rubus*. In addition, maintaining basal area values of ~7 m^2/ha will be important in early successional communities that are not located along forest edges. Post-agricultural shrublands are often managed periodically using mechanical and chemical methods (i.e., brush hogging and herbicides) to restart succession (Dessecker and McAuley 2001). As such, care should be taken so that vegetation patchiness and tree cover are suitable for Golden-winged Warblers when territory occupancy by this species is a management goal. Ultimately, our results point toward a need to understand and convey how differences in vegetation structure and composition resulting from different disturbance regimes are associated with territory occupancy by Golden-winged Warblers.

Although our results only directly apply to our two study areas because our sampling was restricted to one example of each management type, they suggest variables to investigate and include in adaptive management plans where more replicates of each community are available. Our study provides a starting point for a more comprehensive hypothesis-driven occupancy survey that spans a broader geographic range. Such information will help ensure that limited conservation and management funds result in nesting habitat structure that optimizes the responses of target species, including occupancy and reproductive success (Peterson et al. 2016).

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