Regional abundance and local breeding productivity explain occupancy of restored habitats in a migratory songbird

Darin J. McNeil[a,b,*], Amanda D. Rodewald[a,b], Orin J. Robinson[b], Cameron J. Fiss[d], Kenneth V. Rosenberg[b], Viviana Ruiz-Gutierrez[b], Kyle R. Aldinger[c], André A. Dhondt[b,e], Sharon Petzinger[f], Jeffery L. Larkin[d,g]

[a] *Department of Natural Resources, Cornell University, Ithaca, NY 14850, USA*
[b] *Cornell Laboratory of Ornithology, Ithaca, NY 14850, USA*
[c] *West Virginia Cooperative Fish and Wildlife Research Unit, Division of Forestry and Natural Resources, West Virginia University, Morgantown, WV 26506, USA*
[d] *Department of Biology, Indiana University of Pennsylvania, Indiana, PA 15705, USA*
[e] *Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14850, USA*
[f] *New Jersey Division of Fish and Wildlife, Lebanon, NJ 08833, USA*
[g] *American Bird Conservancy, The Plains, VA 20198, USA*

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ABSTRACT

Ecological restoration is a key tool in offsetting habitat loss that threatens biodiversity worldwide, but few projects are rigorously evaluated to determine if conservation objectives are achieved. We tested whether restoration outcomes for an imperiled bird, the Golden-winged Warbler (*Vermivora chrysoptera*; GWWA) met the assumptions of the 'Field of Dreams' hypothesis or whether local and regional population dynamics impacted restoration success. From 2015 to 18, we surveyed 514 points located in recently restored successional habitats. We used new- and published data on the survival of 341 nests and 258 fledglings to estimate GWWA breeding productivity. Occupancy and colonization of restored habitats were significantly higher in our Western Study Region (Minnesota and Wisconsin) than our Eastern Study Region (Maryland, Pennsylvania, and New Jersey), a pattern that mirrored broader regional population trends. At local scales, productivity was high in Eastern Pennsylvania (> 3 independent juveniles/pair/year) but low in Central Pennsylvania (1 juvenile/pair/year) while both Western and Central Minnesota hosted intermediate productivity (between 1 and 2 juveniles/pair/year). Productivity and occupancy covaried locally in the Eastern Study Region, while occupancy was high in the Western Study Region, despite intermediate productivity. These differences have profound implications for restoration outcomes, as GWWA possessed robust capacity to respond to habitat restoration in both regions, but this capacity was conditional upon local productivity where the species is rare. Our findings suggest that, even when restoration efforts are focused on a single species and use comparable prescriptions, interactions among processes governing habitat selection, settlement, and productivity can yield variable restoration outcomes.

1. Introduction

Habitat loss and degradation remain among the greatest threats to biodiversity, worldwide (Andrén, 1994; Wilcove et al., 1998; Butchart et al., 2010; Jantz et al., 2015). As the global human population continues to grow, anthropogenic impacts on natural systems are expected to increase (Foley et al., 2005; Crist et al., 2017). Although land conversion drives most habitat loss (Purvis et al., 2000) and fragmentation (Wilson et al., 2016), habitats may be degraded or otherwise rendered unsuitable for species due to changes in natural disturbance regimes that once created or maintained disturbance-dependent ecosystems

(e.g., wildfire; Askins, 2001, DeGraaf and Yamasaki, 2003). Restoration ecology was born partly to address these system-level impacts (Palmer et al., 2016), with habitat restoration being the most common practical extension of the field (Suding, 2011).

Despite the popularity of habitat restoration (Lerner et al., 2007; Cullinane et al., 2016; Török and Helm, 2017), surprisingly few studies have evaluated how species respond to interventions (Menz et al., 2013). Several habitat-based conservation efforts have successfully led to the recoveries of species of conservation concern (Scott et al., 2001; Suding, 2011), including Kirtland's Warbler (*Setophaga kirtlandii*; Probst et al., 2003), Black-capped Vireo (*Vireo atricapilla*; Wilsey et al., 2014),

and black-footed ferret (*Mustela nigripes*; Jachowski and Lockhart, 2009). Few habitat restoration efforts have yielded greater success than those initiated as part of the North American Waterfowl Management Plan, which have recovered or steadied populations of many once-ailing waterbirds (Nichols et al., 1995; Williams et al., 1999; Sauer et al., 2017; USFWS, 2017). Restoration efforts, however, do not always fit a binary view of success versus failure (Scott et al., 2001), and most are considered partially successful (i.e., mixed measures of recovery; Jones and Schmitz, 2009). Thus, despite the conceptually appealing lens of "if you build it, they will come" (i.e., the 'Field of Dreams' Hypothesis, Palmer et al., 1997, Sudduth et al., 2011), habitat restoration outcomes are highly variable and require more rigorous monitoring and evaluation (Suding, 2011; Piqueray et al., 2013).

Few studies have explicitly studied how processes operating across a broad range of spatial and temporal scales, such as habitat selection, dispersal, and demography, can influence restoration outcomes (George and Zack, 2001; Scott et al., 2001). With passive wildlife restoration efforts (i.e., those relying upon natural colonization of restored habitats rather than active reintroduction), successful occupancy of restored habitat is understood to reflect hierarchical decisions about habitat selection made by dispersing individuals (Hildén, 1965; Hutto, 1985). Even for habitats restored to suitable conditions for a focal species, demographic and dispersal attributes of patches remain key determinants of colonization potential (Scott et al., 2001). For instance, restored sites near densely populated areas are often more quickly colonized than isolated sites or those in sparsely occupied parts of the species range (Skellam, 1951, Andrén, 1994, Paracuellos and Tellería, 2004). Likewise, local demography should affect colonization, by way of source-sink dynamics (Pulliam, 1988; Stout et al., 2007). Avian response to habitat enhancement efforts in northern Oregon provided some support for the Field of Dreams hypothesis, however, capacity to benefit from habitat enhancement varied markedly among species with disturbance-dependent birds colonizing sites the fastest (Cahall et al. 2013). Although the Field of Dreams hypothesis has been tested by several regionally focused studies (Cahall et al. 2013, Frick et al., 2014, Schumann, 2017), predictions about population responses to habitat restoration remain largely grounded in theory (Huxel and Hastings, 1999; Brudvig, 2011) rather than empirical demonstrations at appropriate spatial scales (Menz et al., 2013; McIntosh et al., 2018).

With persistent constraints on human and fiscal resources, the conservation community must ensure that restorations achieve, or at least make meaningful progress towards, conservation goals (Scott et al., 2001; Cullinane et al., 2016). Meeting this challenge requires understanding the conditions that yield high restoration success (i.e., a field of dreams) and those unlikely to benefit focal species (Palmer et al., 1997). Although it has been demonstrated that response to habitat restoration varies among species (Cahall et al. 2013) and with landscape composition (Skellam, 1951; Andrén, 1994; Paracuellos and Tellería, 2004), demographic factors are another important component of habitat quality (Pulliam, 1988) that may also drive variation in restoration success. Herein, we test the Field of Dreams hypothesis by examining whether occupancy of restored habitats by an imperiled, disturbance-associated songbird will rise with (a) regional abundance or (b) local breeding productivity (i.e., annual production of independent juveniles). We considered support for either pattern to be inconsistent with the Field of Dreams hypothesis, since such support suggests that habitat restoration does not necessarily result in focal species colonization.

2. Materials and methods

2.1. Focal species

The Golden-winged Warbler (*Vermivora chrysoptera*; hereafter, "GWWA") is an imperiled long-distance migratory songbird that has been declining for at least a half century (Rosenberg et al., 2016; Sauer

et al., 2017) and is currently being considered for listing on the Endangered Species Act (Sewell, 2010; population size: ~400,000; Roth et al., 2012). This species provided an excellent opportunity to examine restoration outcomes because altered disturbance regimes have dramatically reduced availability of early-successional habitat on which the species depends (Confer et al., 2011; Rosenberg et al., 2016). Widespread loss of early-successional nesting habitat (King and Schlossberg, 2014) has caused the species to become rare and patchily distributed across the eastern United States where GWWAs were once common (Rosenberg et al., 2016; Sauer et al., 2017). While habitat loss is one of the primary drivers behind the species' decline (Rosenberg et al., 2016), other important drivers include competition/hybridization with Blue-winged Warblers (*V. cyanoptera*; Confer et al., 2003), brood parasitism by Brown-headed Cowbirds (*Molothrus ater*; Confer et al., 2003, Confer et al. 2011), and degradation of the non-breeding grounds (Bennett et al., 2016). Consequently, GWWAs have experienced a mean annual rate of decline of 2.28%/year, with the most pronounced declines in the Appalachian portion of the breeding range (8.56% decline/year) while populations in the western Great Lakes are more stable (e.g., Minnesota: 0.37% increase/year; Sauer et al., 2017). Additionally, the current GWWA breeding population in the Great Lakes is estimated to be ~20 times larger than the Appalachian GWWA population (Roth et al., 2012).

2.2. Habitat guidelines and restoration implementation

In hopes of stemming persistent population declines, researchers and practitioners developed an evidence-based conservation plan for the GWWA (Roth et al., 2012). This conservation plan synthesized numerous past studies on GWWA habitat ecology and management to develop a series of regional- and habitat-specific best management practices (BMPs; i.e., Bakermans et al., 2011), which, in turn, have been implemented by multiple agencies and non-government organizations as part of restoration activities. The most ambitious effort, Working Lands for Wildlife (WLFW; Ciuzio et al., 2013, WLFW, 2016b), was launched in 2012 by the US Department of Agriculture Natural Resource Conservation Service (NRCS). Over the ensuing six years, the WLFW effort, in concert with the Regional Conservation Partnership Program (RCPP), facilitated the creation of > 6000 ha of early-successional habitat across the eastern (Appalachian) and western (Great Lakes) portions of the GWWA's breeding range (WLFW, 2016a). The WLFW program aims to restore an additional 6000 ha of breeding habitat by 2021 to offset habitat losses via ecological succession (WLFW, 2016a) and economic-driven changes in timber harvest practices (Nyland, 1992).

2.3. Study area

We employed a study design that required consideration of species response to habitat management across multiple spatial scales: "study regions", "focal landscapes", and "sites". At the broadest extent, we studied GWWA use of habitats within two study regions: Northern Minnesota and Wisconsin ("Western Study Region"), and Pennsylvania, Maryland, and New Jersey ("Eastern Study Region"). Within these two study regions, we identified four ecologically distinct focal landscapes within which nest and fledgling survival data were available. Within both study regions and focal landscapes, we monitored "sites" where habitat had recently been restored following GWWA BMPs.

2.3.1. Study regions

Our Western Study Region included northern portions of Minnesota and Wisconsin (Fig. 2). The region (elevation: 249–540 m) was dominated by eastern deciduous, boreal-hardwood transition, and aspen forests (Dyer, 2006; Omernik and Griffith, 2014) interspersed with mosaics of upland and wetland vegetation communities (Fry et al., 2011), both of which serve as breeding habitat for GWWA (Roth et al.,

2012; Roth et al., 2014). Common tree species within the communities we sampled were red maple (*Acer rubrum*), birch (*Betula* spp.), aspen (*Populus* spp.), and oak (*Quercus* spp.) with a varied understory (e.g., *Alnus* spp., *Salix* spp., *Cornus* spp.). This region falls within the 'Great Lakes Conservation Region' as outlined by Roth et al. (2012). The Eastern Study Region (elevation: 416–677 m) included high-elevation portions of Pennsylvania, Maryland, and New Jersey (Fig. 2). The region was dominated by Appalachian oak and northern hardwood forest communities (Dyer, 2006; Fry et al., 2011), though wetland communities are common within the Pocono Mountains of northeastern Pennsylvania (McNeil et al., 2017). Common tree species within the communities we sampled were maples, birch, hickory (*Carya* spp.), and oak with a varied understory (e.g., *Kalmia latifolia*, *Vaccinium* spp.). This region falls within the 'Appalachian Mountains Conservation Region' as outlined by Roth et al. (2012).

2.3.2. Focal landscapes

We examined four ecologically distinct focal landscapes; two in the Western Study Region ("Western Minnesota" and "Eastern Minnesota") and two in the Eastern Study Region ("Central Pennsylvania" and "Eastern Pennsylvania"). We selected these four focal landscapes based on the availability of GWWA breeding productivity data (McNeil, 2019; Streby et al., 2019), availability of restoration sites, and differences in habitat conditions and GWWA population dynamics within each (described in detail below). We defined the centroid of each focal landscape using the centroid of each landscape's available nest and fledgling monitoring data (see "Nest and fledgling monitoring sites" section, below). We defined the spatial extent of a focal landscape using a 35 km radius circle because this distance represents the typical natal dispersal distance for species like the GWWA (Tittler et al., 2009). Finally, as analyses progressed, we quickly noticed that a 35 km buffer appeared inappropriate for our Central- and Eastern Pennsylvania focal landscapes as the vast majority of GWWA detections (92% in Central Pennsylvania and 98% in Eastern Pennsylvania) occurred within 15 km of the centroids. Sites 15–35 km from these two focal landscapes' centroids were mostly vacant, hosting naïve occupancy = 4% (3/77 samples; Central Pennsylvania) and 5% (3/66 samples; Eastern Pennsylvania). In contrast, site occupancy was homogenous across our focal landscapes in Minnesota (see McNeil, 2019). To account for potential differences in local population extent, we refined our occupancy buffers in the two Pennsylvania focal landscapes to include both 15 and 35 km radii scales and report the results of both analyses.

Our Eastern Pennsylvania Focal Landscape was within the heavily forested Pocono Mountains region of northeastern Pennsylvania (Shultz, 1999). This region is characterized by rolling hills (300–600 m) with many naturally occurring wetlands (Davis, 1993) where GWWA often nest (McNeil et al., 2018). The Pocono Mountains support abundant secondary mature deciduous forests with oak, maple, and eastern hemlock (*Tsuga canadensis*) among the most abundant species (McCaskill et al., 2009). Unlike most GWWA populations in the Appalachian Mountains, abundance within the Poconos landscape appears robust (Larkin and Bakermans, 2012) and the population is known to respond well to local habitat restoration projects (McNeil et al., 2018). A more detailed description of the Eastern Pennsylvania focal landscape can be found within McNeil et al. (2018) and Fiss (2018). The Central Pennsylvania focal landscape was within the Appalachian Plateau of the northcentral Appalachian Mountains. This focal landscape featured a series of ridges (500–750 m) along the Allegheny Front (Shultz, 1999) that are, like the eastern Pennsylvania focal landscape, dominated by secondary deciduous forest (McCaskill et al., 2009). Unlike the eastern Pennsylvania focal landscape, the Central Pennsylvania focal landscape has very few natural wetlands (Davis, 1993; Shultz, 1999) and nesting GWWA are largely restricted to upland habitats (e.g., regenerating wildfire burns). The GWWA population in the Central Pennsylvania Focal Landscape, like many of the disjunct populations of Appalachian GWWA, is relatively small (Sauer et al., 2017) and unstable (Larkin and

Bakermans, 2012). See Fiss (2018) for a more detailed description of the Central Pennsylvania Focal Landscape.

Our Eastern Minnesota focal landscape was within the Northern Lakes and Forests region of eastern Minnesota (Shultz, 1999). This landscape is characterized by abundant natural shrublands, wetlands, and forest communities at 300–600 m, all potentially supporting nesting GWWA (Confer et al., 2011; Peterson, 2014). This portion of eastern Minnesota has widespread secondary mature deciduous forests with aspen, oak, and maple among the most abundant taxa. Although GWWAs remain abundant across this focal landscape, eastern Minnesota GWWA populations appear to be in decline (Sauer et al., 2017). Our Western Minnesota focal landscape was along the Prairie-Hardwood Transition Zone in western Minnesota at 300–600 m in elevation (Shultz, 1999). This region is characterized by diverse forest communities (both upland and wetland) as well as a mosaic of natural shrublands, bogs, and other communities within which GWWAs are known to nest (Confer et al., 2011; Peterson, 2014). Like the Eastern Minnesota focal landscape, our Western Minnesota focal landscape hosted abundant secondary forests with aspen, birch, and eastern larch (*Larix laricina*) among the most common species. Breeding GWWA remain abundant in western Minnesota and, unlike eastern Minnesota, this local population appears to be growing (Sauer et al., 2017). See Peterson (2014) for a more detailed description of both Minnesota focal landscapes.

2.3.3. Sites

We defined a site as the boundary within which BMPs were applied. To select sites for monitoring, we obtained ArcGIS shapefiles (ESRI, 2011) from NRCS conservation planners delineating privately owned restored habitats from 2012 to 15. These shapefiles included all restoration sites treated with region- and habitat-specific BMPs through NRCS conservation programs through 2015. All NRCS sites in both study regions monitored were treated using silviculture practices (0–5 years, post-treatment; Fig. 1). Additionally, we included a comparable sample of sites managed using GWWA BMPs on nearby public lands in each study region (Roth et al., 2012; McNeil et al., 2017). All public land sites in the Eastern Study Region were treated using silvicultural practices (0–9 years, post-treatment) and all those in the Western Study Region were treated using shrub management practices (0–3 years, post-treatment; Fig. 1). Although sites treated with shrub management may support GWWAs prior to implementation, this treatment is intended to enhance GWWA abundance (Roth et al., 2012). Silvicultural practices, in contrast, are applied to mature forest sites wherein GWWAs do not breed (Bakermans et al., 2011; Roth et al., 2012).

2.4. Surveys of singing males

We counted male GWWAs using standard point count surveys within restoration sites across study regions and focal landscapes (see Study area section, below). Our point placement and GWWA survey protocol were identical to those described by McNeil et al. (2018). Briefly, we conducted standard point count surveys for GWWAs at 1–2 locations within each restoration site (Ralph et al., 1995). Survey locations were placed randomly within each restoration patch > 80 m from the untreated habitat edge and > 250 m from the nearest neighboring point location (McNeil et al., 2018). Point counts were sampled twice per breeding season by a single observer using a combined passive/playback sampling protocol understood to maximize GWWA detection probability and visual identification (Kubel and Yahner 2007, McNeil et al., 2014, Aldinger and Wood, 2015). We counted males from mid-May through June 2015–18 (Eastern Study Region: 15 May–15 June; Western Study Region: 25 May–25 June) during fair weather and from 0.5 h pre-sunrise to 4.5 h post-sunrise. At the beginning of each survey, we recorded Beaufort wind index (0–5), sky condition (% cloud cover), time, and date. We removed all GWWA records for males
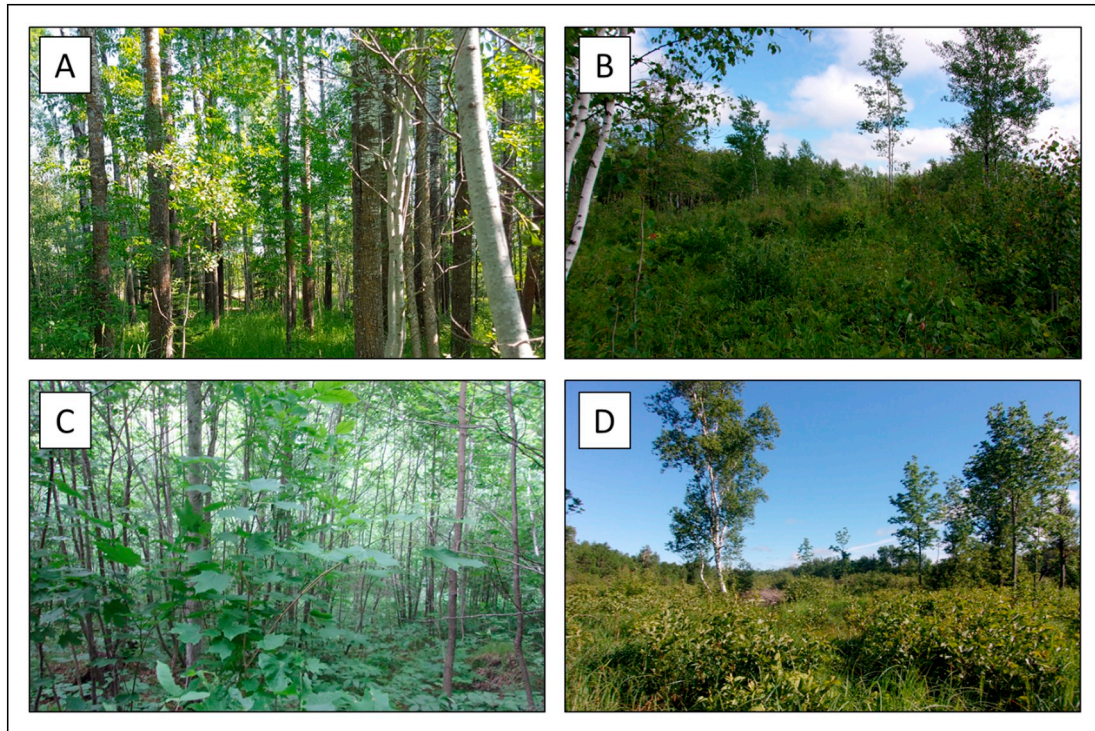
Fig. 1. Examples of Golden-winged Warbler habitat management: timber harvest (A–B) and shrub management (C–D). Timber harvest involves cutting mature forest (A) such that the subsequent regenerating stand (B) provides ephemeral nesting habitat for birds like Golden-winged Warblers. Shrub management is a method of habitat restoration/enhancement in which mature stands of woody stems (e.g., *Alnus* spp., *Salix* spp., etc.; C) are cut to allow regenerating woody vegetation (D) to serve as nesting habitat.

observed outside the boundaries of managed sites. We also visually identified the plumage phenotype for each bird to avoid false positive identifications based on *Vermivora* song mismatch (Ficken and Ficken 1969, Highsmith, 1989). Confirming the plumage phenotype of *Vermivora* spp. was important in our study because, although Blue-winged Warblers and hybrids were rare (< 7% of all locations; McNeil, 2019), false positives would violate a major assumption of occupancy models (MacKenzie et al., 2006).

2.4.1. Perennial and annual point count sites

We visited 514 independent point count sites from 2015 to 18 where GWWA BMPs had been recently implemented. A subset of our sites was monitored every year from 2015 to 17 (hereafter, "perennial point count sites"). This included 430 sites with 275 across our Eastern Study Region and 155 over our Western Study Region (Fig. 2). The remainder of our sites (hereafter, "annual point count sites") were monitored for < 3 years (between 2015 and 2018) and occurred within the bounds of our four focal landscapes (Fig. 2). The annual point count dataset included of 84 independent sites with 34 sites across our Minnesota focal landscapes (western MN: 14, eastern MN: 20) and 50 sites in our Pennsylvania focal landscapes (central PA: 22, eastern PA: 28). See Appendix A for a more detailed summary of sample sizes within each spatial extent for both perennial and annual point counts.

2.5. Nest and fledgling monitoring

We considered nest and fledgling survival data from multiple focal landscapes within each study region. Nest and fledgling survival data within the Western Study Region were collected during 2011–12 (Peterson, 2014; Streby et al., 2019; DOI: https://doi.org/10.7717/peerj.4319/supp-2). To compliment Western Study Region data, our study contributes analogous nest and fledgling data from two focal landscapes in the Eastern Study Region: Central Pennsylvania (2016–17) and Eastern Pennsylvania (2014–15). Across these

landscapes, we searched for GWWA nests using standard nest searching and monitoring methods (Martin and Geupel, 1993). This included following females with nesting material, adults provisioning young, and, to a lesser extent, systematic searching. We monitored nests every 1–3 days and until either failure or success (i.e., at least one nestling fledged the nest; Williams and Wood, 2002, Streby and Andersen, 2013). As nestlings approached fledging (~7–8 days old), we randomly removed 1–3 from each nest to tag with radio-transmitters (Rappole and Tipton 1991). Our fledgling survival monitoring approach was identical to protocols described by Peterson (2014) and is detailed by Fiss (2018). Briefly, we randomly marked two brood-mates from each GWWA brood with radio transmitters either shortly before fledging (7–8 days old) or immediately after fledging (9 days old). We attached transmitters using a figure-eight style harness (Rappole and Tipton 1991) and the combined mass of transmitter and harness together did not exceed 5% of each fledgling's mass. We tracked each fledgling daily using the homing method and recorded survival/mortality.

2.5.1. Nest and fledgling monitoring sites

Within the Eastern Pennsylvania focal landscape, we sampled nests and fledglings within six regenerating timber harvests across a large tract of public land: Delaware State Forest of Pike and Monroe Counties, Pennsylvania. Our Central Pennsylvania sampling occurred across 11 timber harvests across Sproul State Forest and Pennsylvania State Game Lands 100 of Centre and Clinton Counties, Pennsylvania. Within the Western Minnesota focal landscape, Peterson (2014) collected data across Minnesota's Tamarac National Wildlife Refuge of Becker County, Minnesota. Within the Eastern Minnesota focal landscape, data were collected data across Rice Lake National Wildlife Refuge of Aitkin County, Minnesota.
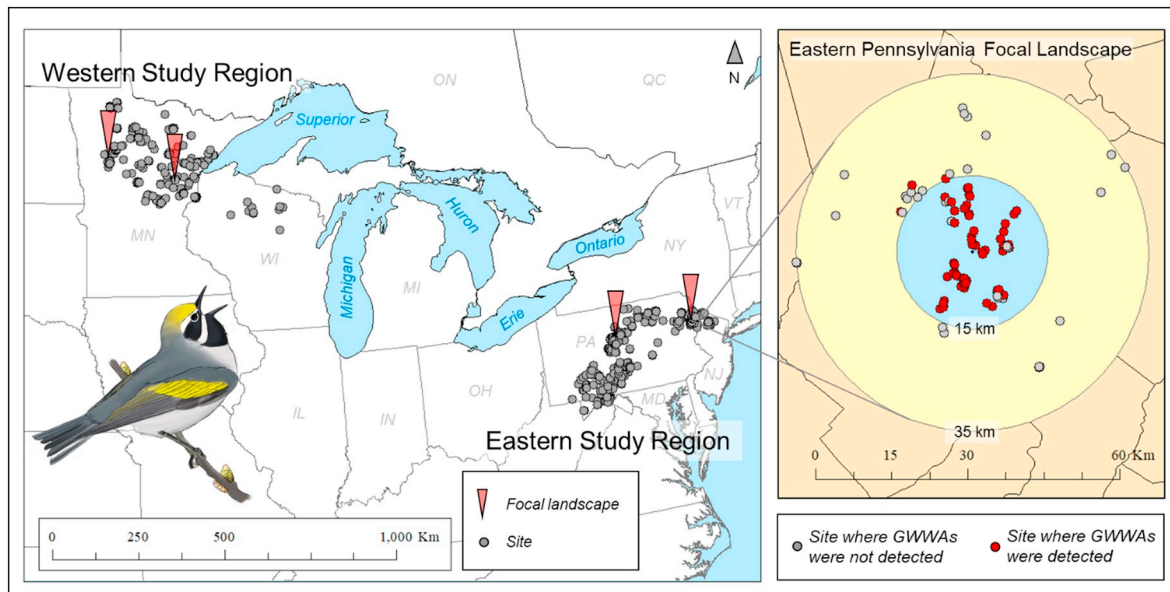
Fig. 2. Point count locations (dark gray circles) where we monitored occupancy response of Golden-winged Warblers (GWWA) to habitat restoration efforts across the Western and Eastern portions of the species' breeding range (left map). Also noted are four focal landscapes where full-season productivity (FSP) estimates were made and compared with rates of focal landscape occupancy (red arrows); West-to-East: Tamarac National Wildlife Refuge (Western Minnesota; Peterson et al. 2016), Rice Lake National Wildlife Refuge (Eastern Minnesota; Peterson et al. 2016), Sproul State Forest/State Game Lands 100 (Central Pennsylvania; this study) and Delaware State Forest (Eastern Pennsylvania; this study). The rightmost map depicts sites across one of our four focal landscapes (Eastern Pennsylvania). In both Pennsylvania focal landscapes, we assessed occupancy at two spatial scales: 35 km radius (yellow buffer) and 15 km radius (blue buffer) from our FSP sites. Most sites in Pennsylvania surveyed beyond 15 km hosted no GWWA detections (red circles) but this pattern was not true in Minnesota. We therefore only assessed focal landscape occupancy at the 35 km radius in our two Minnesota focal landscapes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.6. Statistical analyses

2.6.1. Occupancy modeling

We used GWWA detections to fit occupancy models using the un-marked package in R (Fiske and Chandler, 2011; R Core Team, 2018). This package allows the user to fit linear models within a maximum likelihood framework and can be combined with an Information Theoretic approach (Anderson, 2007) for model selection (e.g., using Akaike's Information Criterion; AIC; Burnham and Anderson, 2002). We conducted two occupancy analyses: A study region comparison (Eastern vs. Western; each modeled separately) and a focal landscape comparison (Western Minnesota vs. Eastern Minnesota vs. Central Pennsylvania vs. Eastern Pennsylvania). We conducted our study region comparison using a multi-season ('dynamic') occupancy model with the standard parameterization ('detection probability (p), initial occupancy (Ψ_1), colonization (γ), and local extinction (ε)', MacKenzie et al., 2006). We modeled variation in occupancy and related parameters through a set of survey- and site-specific covariates. Specifically, we varied detection probability as a function of all possible combinations (0–4) of our survey covariates (i. minutes since sunrise (mssr), ii. ordinal date, iii. modified Beaufort wind index and iv. cloud cover [%]; Appendix B). A more detailed description of our detection modeling procedure can be found in McNeil (2019). We modeled our three state variables (Ψ_1, γ, and ε) using all possible combinations of two covariates (i. management type (Western Study Region only; shrub management/timber harvest) and ii. site age [number of growing seasons post-management]). Although the effects of management type and site age were not the focus of our study, we included them in our models to account for major sources of variation for our state variables. We also considered models that included full time dependency to account for potential inter-annual variation (i.e., a 'year' effect) in our two dynamic variables (γ, and ε; Appendix B). To create a set of candidate dynamic occupancy models, we created all possible combinations of detection- and state models using our most parameterized (global) model: 'p (mssr + ordinal

date + wind + cloud cover), Ψ_1 (site age + management type), γ/ε (site age + survey year + management type)' using the *dredge* function in the R package MuMIn (Barton, 2018; R Core Team, 2018). Our study region comparison used only the perennial point count dataset (Appendix A).

We followed a similar approach for our focal landscape comparison except each landscape was modeled separately and we used static occupancy models with a stacked dataset because sub-regional datasets were smaller samples and dynamic parameters (i.e., γ, and ε) were not essential to this second analysis (McClure and Hill, 2012, Fogg et al. 2014). Our global model for this analysis was: 'p (mssr + ordinal date + wind + cloud cover), Ψ (site age + management type + survey year)'. Our focal landscape comparison used all perennial point count sites that fell within focal landscape boundaries and annual point count sites and each sample consisted of a unique point count-by-year combination (Appendix A).

2.6.2. Full season productivity

To estimate productivity of juveniles within restored habitats, we multiplied estimated rates of nest productivity (NP) and fledgling survival (FS) to calculate full-season productivity (FSP; Peterson, 2014). Nest productivity was the product of fledglings per successful nest (fledgling productivity) and nest success rate (NS; % nests that fledged young). GWWA pairs attempt to rear a single brood of young each season but will re-nest at least once in response to early nest failures (Confer et al., 2011). We calculated NS using nest daily survival rate (DSR) over a 25-day nesting cycle and accounting for two nesting attempts using the formula: $(1 - [1 - DSR^{25}]^2)$ (Aldinger, 2018). We propagated error using the delta method (Powell, 2007). We generated estimates of DSR using logistic exposure models in program MARK (Dinsmore and Dinsmore, 2007). Fledgling productivity was the local mean output of fledglings for nests that successfully fledged young. Both focal landscapes in Minnesota had mean fledgling productivity = 4.00, however, no error was reported (Peterson, 2014), so

we used the largest observed variance between the two Pennsylvania focal landscapes to conservatively incorporate uncertainty. Fledgling survival was the fraction of fledglings that survived from fledging (day 1 post-fledging) to independence from parental care (~day 30 post-fledging).

3. Results

3.1. Occupancy of restored habitats

We detected GWWAs at 173 of 430 points (naïve occupancy = 0.40) across our Western Study Region (naïve occupancy = 0.75) and Eastern Study Region (naïve occupancy = 0.20) over three years. Most detections in the Eastern Study Region were concentrated around either central Pennsylvania (i.e., Centre, Clinton Counties) or eastern Pennsylvania (i.e., Pike, Monroe Counties) while the species was nearly homogeneous across our Western Study Region. We created a candidate set of 4096 and 512 dynamic occupancy models for our Western Study Region and Eastern Study Region, respectively (Appendix C). Occupancy was best explained by 'time since management' in both the Eastern- and Western Study Regions. Similarly, local extinction (but not colonization) in the Eastern Study Region was explained by 'time since management' while this was not true in the Western Study Region. After accounting for the effects of detection probability, site age, and management type, occupancy ($\widehat{\psi_1}$ = 0.78; 95% CI: 0.71–0.85) and colonization ($\hat{\gamma}$ = 0.56; 95% CI: 0.41–0.70) were both higher in the Western Study Region than in the Eastern Study Region ($\widehat{\psi_1}$ = 0.23; 95% CI: 0.17–0.31; $\hat{\gamma}$ = 0.07; 95% CI: 0.04–0.11; Fig. 2A). In contrast, Eastern Study Region sites were more likely to experience local extinction events ($\hat{\varepsilon}$ = 0.21; 95% CI: 0.12–0.34) than sites in the Western Study Region ($\hat{\varepsilon}$ = 0.04; 95% CI: 0.02–0.09).

Across our four focal landscapes, we collected 628 site × year samples at the 35 km radius scale: 107 (37 independent sites) in Western Minnesota, 76 (31 independent sites) in Eastern Minnesota, 193 (73 independent sites) in Central Pennsylvania, and 252 (95 independent sites) in Eastern Pennsylvania (Appendix A). We created 128 candidate models for each Minnesota focal landscape and 64 candidate models for each of our Pennsylvania focal landscapes (Appendix D). Occupancy rates in restored habitats in Western Minnesota (timber harvests $\hat{\psi}$ = 0.86; 95% CI: 0.55–0.97, shrub management $\hat{\psi}$ = 0.98; 95% CI: 0.92–1.00), Eastern Minnesota ($\hat{\psi}$ = 0.97; 95% CI: 0.88–0.99), and Central Pennsylvania ($\hat{\psi}$ = 0.31; 95% CI: 0.16–0.53) landscapes resembled broader patterns of occupancy at the Study Region scale (Figs. 3–4; Appendix D). In contrast, occupancy rates of restored habitats in Eastern Pennsylvania were high ($\hat{\psi}$ = 0.86; 95% CI: 0.76–0.93) and more closely resembled occupancy rates observed in the Western

Study Region than the Study Region within which this Landscape occurred (Fig. 4; Appendix D).

3.2. Full-season productivity

We monitored 77 nests in the Eastern Pennsylvania focal landscape (2014–15) and 79 nests in the Central Pennsylvania focal landscape (2016–17; Appendix E). During the 2017 nesting season, a highly localized hail storm within Central Pennsylvania resulted in 100% nest failure at one site (n = 11 nests; Fiss et al., 2019), so we excluded those nests from our analyses. Sixty percent (46/77) and 34% (23/68) of nests fledged young in the Eastern and Central Pennsylvania focal landscapes, respectively. Daily survival rates were similar between Eastern Pennsylvania (DSR: 0.97; 95% CI: 0.96–0.98) and Central Pennsylvania (DSR: 0.95; 95% CI: 0.94–0.97). Successful nests in Eastern Pennsylvania produced more fledglings (4.28/successful nest, 95% CI: 3.91–4.65) than those in the Central Pennsylvania (3.17/successful nest, 95% CI: 2.67–3.67). When we accounted for re-nesting attempts, nest productivity was 4.19 fledglings/pair/year (95% CI: 4.07–4.30) in Eastern Pennsylvania and 2.28 fledglings/pair/year (95% CI: 2.20–2.38) in Central Pennsylvania. From successful nests, we marked 64 and 63 fledglings in the Eastern and Central Pennsylvania focal landscapes, respectively (Appendix E). A higher number of fledglings from Eastern Pennsylvania (n = 47; 73%, 95%CI: 63–84%) survived to independence (30 days post-fledging) as compared to fledglings from Central Pennsylvania (n = 30; 48%, 95% CI: 35–60%). These values combined to yield FSP values of 3.07 (95% CI: 2.62–3.53) juveniles/pair/year in Eastern Pennsylvania and 1.08 (95% CI: 0.80–1.37) juveniles/pair/year in Central Pennsylvania (Fig. 4).

We analyzed data from 58 nests and 42 fledglings in Eastern Minnesota (2011−12) and 138 nests and 89 fledglings in Central Minnesota (2011–12; Appendix E). Daily survival rates for nests were similar between Eastern (DSR: 0.96; 95% CI: 0.94–0.97) and Western Minnesota (DSR: 0.95; 95% CI: 0.94–0.96). When we accounted for re-nesting attempts, nest productivity was 3.48 fledglings/pair/year (95% CI: 3.33–3.63) and 3.09 fledglings/pair/year (95% CI: 3.00–3.17) in Eastern and Western Minnesota, respectively. A higher number of fledglings from Western Minnesota (53/89; 60%, 95% CI: 49–70%) survived to independence as compared to fledglings from Central Minnesota (19/42; 45%, 95% CI: 30–60%; Appendix E). These values combined to yield FSP values of 1.84 (95% CI: 1.52–2.16) juveniles/pair/year in Western Minnesota and 1.57 (95% CI: 1.05–2.10) juveniles/pair/year in Eastern Minnesota (Fig. 4).
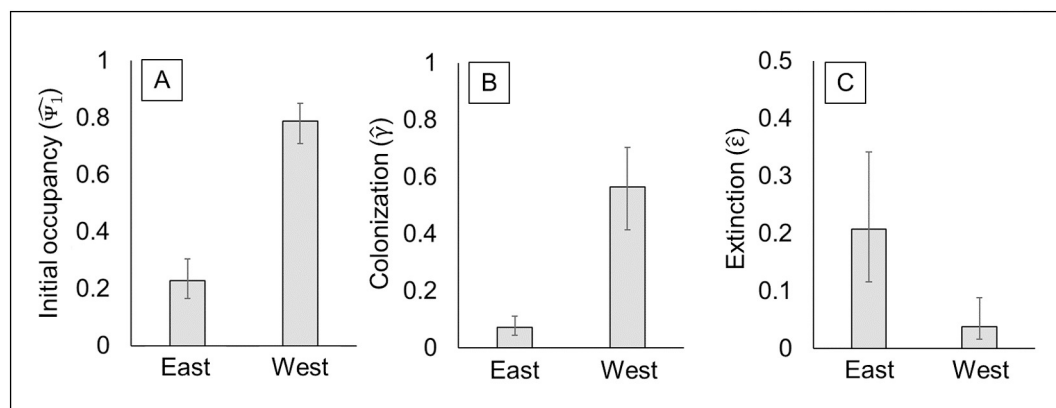
Fig. 3. Parameter estimates (gray bars) associated with Golden-winged Warbler use of managed early-successional communities across two distinct regions of the species' breeding range: Eastern Study Region ("East") and Western Study Region ("West"). Shown are Study Region-specific differences in initial occupancy ($\widehat{\psi_1}$; A), colonization ($\hat{\gamma}$; B), and local extinction ($\hat{\varepsilon}$; C). Error bars represent 95% confidence intervals.
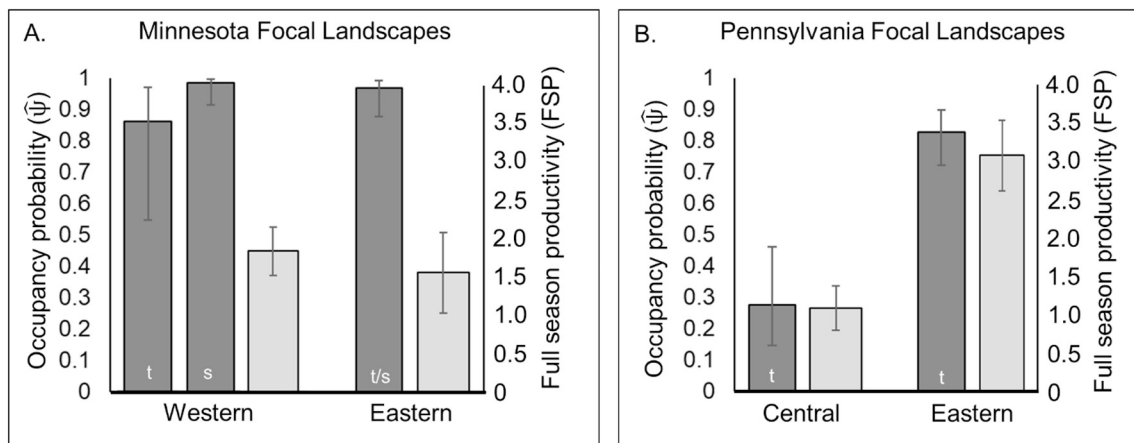
Fig. 4. Occupancy ($\hat{\psi}$; dark gray bars, left vertical axis) of habitats managed for Golden-winged Warblers across focal landscapes ($n = 4$) in Minnesota (A) and Pennsylvania (B). Focal landscapes were chosen based on the availability of full season productivity data (FSP; light gray bars, right vertical axis). Habitats managed in Pennsylvania were solely timber harvests (t) whereas both timber harvests and shrub management (s) were monitored in Minnesota. Our best-supported model for Western Minnesota suggested timber harvests and shrub management sites hosted different rates of occupancy while this was not true for Eastern Minnesota. Error bars represent 95% confidence intervals.

4. Conclusions

As large-scale habitat restorations efforts become increasingly common (Suding, 2011), we face an imperative to better monitor species response and understand drivers of successful outcomes (Brudvig, 2011; Menz et al., 2013), particularly at ecologically meaningful scales (McIntosh et al., 2018). Our results provide only mixed support for the Field of Dreams hypothesis (i.e., "if you build it, they will come"), thereby indicating that habitat restoration does not guarantee colonization by a focal species, even within landscapes where habitat is limited. This is somewhat surprising given that GWWAs are a disturbance-dependent species and such species are expected to respond rapidly to restoration efforts (Cahall et al. 2013). Instead, occupancy of restored habitats was three times higher and colonization eight times greater in regions with abundant (i.e., Western Study Region) versus rare GWWAs (i.e., Eastern Study Region). Likewise, local extinction of restored sites was seven times more likely in the low-abundance region. Thus, habitat restoration efforts are most likely to achieve goals in regions with source populations to accelerate colonization and occupancy.

Not only did regional abundance (e.g., Sauer et al., 2017) explain restoration outcomes, but we also found compelling evidence that occupancy of restored habitats is related to breeding productivity (i.e., FSP), even within a region of overall population decline. This result highlights the importance of pairing records of singing males (e.g., occupancy/abundance) with data on reproductive success. Indeed, data on breeding output are an essential component of habitat quality assessment (Pulliam, 1988) as presence, alone, may be a misleading metric of restoration success (Van Horne, 1983). A positive association between occupancy and local breeding productivity makes sense as landscapes with high FSP necessarily export more dispersing juveniles than those with low FSP (Greenwood and Harvey, 1982). Still, even this pattern varied by study region; while FSP and occupancy were linked in the Eastern Study Region, both landscapes in the Western Study Region exhibited intermediate FSP paired with high occupancy (Fig. 4). Although understanding the factors that drive regional variation in this pattern requires further study, it seems likely that regional abundance plays an important role here, as well. Across the Appalachian Mountains, GWWAs have become rare and patchily distributed while the species remains common in the western Great Lakes (Roth et al., 2012; McNeil, 2019; Bakermans et al. 2015). Restored sites in the eastern portion of the GWWA's breeding range therefore rely upon one of only a small handful of sub-populations to produce dispersing colonists while

those in the western portion may be colonized by juveniles produced nearly anywhere across the entire region (Sauer et al., 2017). Hatch-year Blackpoll Warblers (*Setophaga striata*) in Canada spend the post-breeding period prospecting the landscapes around their natal territories while adults, in contrast, began southward travel immediately after breeding (Brown and Taylor, 2015). Post-breeding prospecting behaviors may explain why many songbird species establish breeding territories within a few kilometers of their natal home range (Payne, 1991; McKim-Louder et al., 2013; Perlut and Strong, 2016). To this end, success of private lands programs like WLFW and RCPP and similar efforts on public lands may require patience in regions where GWWAs have become rare due to persistent breeding habitat loss over the past century (Rosenberg et al., 2016).

Less clear is why FSP (and associated capacity to colonize new habitats) was elevated in Eastern Pennsylvania and both Minnesota landscapes but low in central Pennsylvania. GWWA pairs replaced themselves (with independent juveniles) *every* year in Eastern Pennsylvania while pairs appeared to require two years to do so in Central Pennsylvania. Although it remains unknown why Eastern Pennsylvania continues to support high output of young while other areas have lost this capacity, one contributor may be the regionally unique abundance of natural wetlands (McNeil et al., 2018). While many formerly occupied landscapes across the eastern portion of the GWWA range have seen local extirpation of this species (Larkin and Bakermans, 2012; Rosenberg et al., 2016), those with abundant natural shrub-wetlands (like the Western Study Region and Eastern Pennsylvania Focal Landscape) have retained GWWA populations within these habitats (Confer et al., 2011, Peterson et al. 2016, McNeil et al., 2018). A recent study from another eastern landscape lacking shrub wetlands, eastern Tennessee, found low FSP within anthropogenic habitats (FSP = 0.66; Lehman, 2017), even lower than those we observed in Central Pennsylvania (FSP = 1.08). While our study did not assess the occupancy of restoration sites in Tennessee, our results suggest that implementation would be unlikely to yield high rates of successful colonization in the state. Indeed, it seems possible that robust GWWA response to management like we observed in Eastern Pennsylvania and both Minnesota focal landscapes would require FSP rate to exceed a threshold that may fall between > 1.08 (that of Central Pennsylvania) and 1.57 juveniles/pair/year (that of Western Minnesota). Alternatively, it may be that the magnitude of population stressors varies among regions and thus require different FSP threshold values to achieve similarly high occupancy rates (Rushing et al., 2016).

Regardless of where implementation occurs, early-successional

habitat management requires expenditure of limited conservation funds (Cullinane et al., 2016; WLFW, 2016a, 2016b). Maximization of restoration success is therefore critical for ensuring that scarce resources provide maximum benefit to imperiled species (Scott et al., 2001). Our finding that GWWAs in the eastern portion of their breeding range were largely concentrated within a few small portions of the region suggests that regional habitat restoration efforts should be focused near existing populations. Moreover, the observation of very few detections beyond 15 km of each sub-region's core suggests that GWWAs rarely make long-distance dispersals in the Appalachian Mountains either due to limited dispersal capacities (e.g., Aldinger, 2018) or lack of need due to vacant habitat near natal home ranges. Studies of simulated data have suggested that habitat management is most successful when focused near population centers (Huxel and Hastings, 1999), however, few have tested this idea at meaningful spatial scales (McIntosh et al., 2018). Our results support this idea and suggests that restoration efforts in the eastern portion of the GWWA breeding range (i.e., Appalachian Mountains) implemented > 15 km from population centers are less likely to be colonized by GWWAs, at least until these populations grow and spread beyond what we observed in our study.

Migratory species like GWWA present an inherent challenge to conservation because such organisms encounter myriad threats across different portions of the lifecycle (Martin et al., 2007; Hostetler et al., 2015). Long-distance migratory species, in particular, constitute an exceptional challenge because disparate breeding- and non-breeding areas frequently span wide political and ecological boundaries (Marra et al., 2011), yet effective conservation requires protection of both (Rosenberg et al., 2016; Bennett et al., 2016). With this in mind, the value of breeding grounds conservation to GWWA populations has been challenged recently (Kramer et al., 2018). Despite stark differences in their capacity to occupy restored habitats, geolocator studies tracking individual GWWAs breeding in Central- and Eastern Pennsylvania reveal that males from both landscapes winter together in northern South America (Kramer et al., 2017). This suggests that, while preservation of non-breeding habitat is important to the long-term survival of migratory species like the GWWA, restoring and maintaining breeding habitat with high reproductive output is critical for species recovery (Aldinger, 2018).

While our findings constitute a promising exploration of how species response to habitat restoration varies with respect to local abundance and reproductive output, our results are not without limitation. Measurements of FSP, while an improvement over nest-only analyses (Cox et al. 2014), do not account for overwinter survival of hatch-year birds and therefore are not analogous to 'recruitment'. Still, unless overwinter survival rates vary greatly for individuals born in different regions, we expect recruitment patterns in each region to be consistent with patterns of FSP. Given that apparent survival rates for adult GWWAs are constant across even large geographic extents (Peterson et al., 2015), such a disparity in overwinter survival seems unlikely. We also recognize that our proxy for habitat quality, time-since-management, is imperfect. Future work incorporating detailed habitat data (e.g., within-stand vegetation, landscape composition, etc.) would be very useful for informing adaptive habitat management for this species. Indeed, GWWA occupancy probability is only expected to increase as sites age because many of the sites monitored here were only a few years post-management (Roth et al., 2012). With this in mind, we do not believe a systematic bias in habitat quality to be present within the context of our sites and other studies have reported site age to be a suitable proxy for GWWA site quality (e.g., Otto and Roloff, 2012; Aldinger, 2018). Although our study is not a comprehensive assessment of how species respond to habitat restoration, our work provides new insights into factors driving the colonization of restored habitats by an imperiled species, especially with respect to local abundance and reproductive output.

Author contributions

DJM, ADR, CJF, KVR, VRG, AAD, and JLL conceived the ideas and designed the study. DJM, CJF, JLL, and SP collected the data. DJM, OJR, VRG, and KRA analyzed the data. JLL and ADR secured funding for the study. All authors wrote and edited the paper and gave final approval for publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Role of the funding source

Appendix A. Samples sizes for analyses of GWWA occupancy for both the study region ("Region") and focal landscape ("Landscape") extents. Focal landscapes were assessed at both 35 km (both Pennsylvania [PA] and Minnesota [MN]) and 15 km (PA only) radii. Regional analyses were modeled with dynamic occupancy model types whereas all focal landscapes were analyzed using static occupancy model types. Also shown are "Years" (years during which sampling occurred), "# Sites" (total number of independent sites in each category), "N Per." (number of sites in the 'perennial' category), "N Ann.", (number of sites in the 'annual' category), "N. T.H." (number of sites managed with 'timber harvest'), "N. S.M." (number of sites managed with 'shrub management'), and "N SxY." (number of site x year combinations in each category). In our analyses, sample size was # Sites for dynamic occupancy analyses whereas sample size was N SxY for each static occupancy analysis

Extent	Location	Model type	Years	# Sites	N Per.	N Ann.	N T.H.	N. S.M.	N SxY
Region	Western	Dynamic	2015–17	155	155	*NA*	80	75	*NA*
Region	Eastern	Dynamic	2015–17	275	275	*NA*	275	0	*NA*
Landscape - 35 km	Western MN	Static	2015–18	37	23	14	7	30	107
Landscape - 35 km	Eastern MN	Static	2015–18	31	11	20	17	14	76
Landscape - 35 km	Central PA	Static	2015–17	73	51	22	73	0	193
Landscape - 15 km	Central PA	Static	2015–17	44	30	14	44	0	116
Landscape - 35 km	Eastern PA	Static	2015–17	95	67	28	95	0	252
Landscape - 15 km	Eastern PA	Static	2015–17	67	53	14	67	0	186

Appendix B. Variables considered in our Golden-winged Warbler (GWWA) occupancy analyses. We considered four survey covariates (ordinal date, cloud cover, minutes since sunrise, and wind index) on detection probability in both static- and dynamic occupancy analyses and both were used to model only detection probability (p). Although our study was focused on assessing regional- and landscape-specific patterns of restoration success, it was important to account for major factors associated with variation in state parameters: management type ('mgmt', shrub management vs. timber harvest; Western Study Region only), time since management ('tsm'), and sampling year ('year'). We modeled all state parameters (occupancy probability [Ψ; static occupancy], initial occupancy probability [Ψ_1; dynamic occupancy], colonization probability [γ; dynamic occupancy] and, local extinction probability [ε; dynamic occupancy]) using 'mgmt' and 'tsm' but only included 'year' in models of Ψ, γ and ε because Ψ_1 is only estimated in the first season (i.e., year 2015)

Predictor	Predictor abv.	Parameter	Description
Ordinal date	date	p	A continuous survey covariate representing the date of each GWWA survey.
Cloud cover	cloud	p	A continuous survey covariate representing percent cloud cover at the time of survey.
Minutes since sunrise	mssr	p	A continuous survey covariate representing number of minutes elapsed since sunrise at the time of each GWWA survey.
Wind index	wind	p	A binary survey covariate representing an index of windiness derived from the Beaufort wind index (values < 2 = "low wind"; values > 2 = "high wind").
Management type	mgmt	Ψ, Ψ_1, γ, ε	A binary site covariate representing the type of management implemented at each site: shrub management vs. timber harvest. Western Study Region only.
Time since management	tsm	Ψ, Ψ_1, γ, ε	A continuous site covariate representing number of growing seasons elapsed since management implementation at each site.
Sampling year	year	Ψ, γ, ε	A categorical site covariate representing the year in which sampling was conducted

Appendix C. Dynamic occupancy models for Golden-winged Warblers within restored habitats across the Eastern Study Region (top) and Western Study Region (bottom). Models are ranked in descending order of Akaike's Information Criterion adjusted for small sample size (AIC$_c$). All four model components (detection probability [p], initial occupancy [Ψ_1], colonization [γ], and local extinction [ε]) were modeled using all possible subsets of model parameters. We allowed detection probability to vary as a function of four survey covariates: i) minutes since sunrise ('mssr'), ii) cloud cover ('cloud'), iii) ordinal date ('date'), and Beaufort wind index ('wind'). State variables were modeled using covariates for management type ('mgmt', Western Study Region only; shrub management/timber harvest), time since management ('tsm', # growing seasons), and survey year ('year'; 2015–17). We only report detection models < 4.0 ΔAICc. For each model, we report number of model parameters (k), ΔAIC$_c$, and AIC$_c$ weight (w)

Eastern study region

p (detection)				Ψ_1 (initial occupancy)		γ (local colonization)			ε (local extinction)			k	ΔAIC$_c$	w
cloud	date	mssr	wind	mgmt	tsm	mgmt	tsm	year	mgmt	tsm	year			
pos	neg	neg	neg	–	pos	–			–	neg		10	0.00	0.09
	neg	neg	neg	–	pos	–			–	neg		9	0.04	0.09
	neg	neg	neg	–	pos	–	pos		–	neg		10	0.51	0.07
	neg	neg	neg	–	pos	–			–	neg		10	0.52	0.07
pos	neg	neg	neg	–	pos	–			–	neg		11	0.66	0.07
pos	neg	neg	neg	–	pos	–	pos		–	neg		11	0.88	0.06
	neg	neg	neg	–	pos	–	pos		–	neg	yes	11	1.07	0.05
	neg	neg	neg	–	pos	–		yes	–	neg		10	1.27	0.05
pos	neg	neg	neg	–	pos	–		yes	–	neg		11	1.34	0.05
pos	neg	neg	neg	–	pos	–	pos		–	neg	yes	12	1.59	0.04
	neg	neg	neg	–	pos	–		yes	–	neg	yes	11	1.61	0.04
pos	neg	neg	neg	–	pos	–		yes	–	neg	yes	12	1.87	0.04
	neg	neg	neg	–	pos	–	pos	yes	–	neg		11	2.07	0.03
pos	neg	neg	neg	–	pos	–	pos	yes	–	neg		12	2.48	0.03
	neg	neg	neg	–	pos	–	pos	yes	–	neg	yes	12	2.53	0.03

cloud	date	mssr	wind	mgmt	tsm	mgmt	tsm	year	mgmt	tsm	year	k	ΔAIC$_c$	w
pos	neg	neg	neg	–	pos	–	pos	yes	–	neg	yes	13	3.10	0.02
pos	neg	neg	neg	–	pos	–			–			9	3.44	0.02
	neg	neg	neg	–	pos	–	pos		–			9	3.51	0.02
pos	neg	neg	neg	–	pos	–	pos		–			10	3.73	0.01
	neg	neg	neg	–	pos	–			–			8	3.84	0.01
pos	neg	neg	neg	–	pos	–			–		yes	10	3.91	0.01

Western study region

p (detection)				ψ_1 (initial occupancy)		γ (local colonization)			ε (local extinction)			k	ΔAIC$_c$	w
cloud	date	mssr	wind	mgmt	tsm	mgmt	tsm	year	mgmt	tsm	year			
	neg		neg	yes		yes						8	0.00	0.05
	neg		neg	yes		yes	neg					9	0.85	0.03
	neg		neg	yes								7	1.62	0.02
	neg		neg	yes	pos	yes						9	1.63	0.02
	neg	pos	neg	yes		yes						9	1.93	0.02
	neg		neg	yes		yes					yes	9	2.16	0.02
pos	neg		neg	yes		yes						9	2.16	0.02
	neg		neg	yes		yes				pos		9	2.17	0.02
	neg		neg	yes		yes			yes			9	2.21	0.02
	neg		neg	yes		yes					yes	9	2.24	0.02
	neg		neg	yes	pos	yes	neg					10	2.60	0.01
	neg	pos	neg	yes		yes	neg					10	2.82	0.01
	neg		neg	yes			neg					8	2.84	0.01
	neg		neg	yes		yes	neg				yes	10	3.05	0.01
pos	neg		neg	yes		yes	neg					10	3.05	0.01
	neg		neg	yes		yes	neg			pos		10	3.08	0.01
	neg		neg	yes		yes	neg		yes			10	3.09	0.01
	neg		neg	yes		yes	neg	yes				10	3.14	0.01
	neg		neg	yes	pos							8	3.28	0.01
	neg		neg	yes					yes			8	3.55	0.01
	neg	pos	neg	yes								8	3.57	0.01
	neg	pos	neg	yes	pos	yes						10	3.61	0.01
neg	neg		neg	yes								8	3.69	0.01
	neg		neg	yes						pos		8	3.80	0.01
	neg		neg	yes	pos	yes				pos		10	3.81	0.01
	neg		neg	yes	pos	yes					yes	10	3.81	0.01
	neg		neg	yes							yes	8	3.82	0.01
	neg		neg	yes				yes				8	3.83	0.01
neg	neg		neg	yes	pos	yes						10	3.86	0.01
	neg		neg	yes	pos	yes			yes			10	3.88	0.01
	neg		neg	yes	pos	yes	yes					10	3.90	0.01

Appendix D. Static occupancy models for Golden-winged Warblers within restored habitats across the four focal landscapes: Western Minnesota, Eastern Minnesota, Central Pennsylvania, and Eastern Pennsylvania. Models are ranked in descending order of Akaike's Information Criterion adjusted for small sample size (AIC$_c$). We considered all possible combinations of survey covariates ordinal date ('date'), cloud cover (%), minutes since sunrise ('mssr'), and Beaufort wind index ('wind') and three site covariates: management type ('mgmt'; Minnesota only), time since management ('tsm', # growing seasons), and survey year ('year'; 2015–18). Shown are only the top-ranked models for each focal landscape. We modeled each focal landscape separately and assessed two spatial scales for our two Pennsylvania landscapes (15 and 35 km radius). For each model set, we report number of model parameters (k), ΔAIC$_c$, and AIC$_c$ weight (*w*). Only models with ΔAICc < 4.0 are shown for each analysis for conciseness

p (detection)				ψ (occupancy)			k	ΔAICc	w
date	cloud	mssr	wind	mgmt	tsm	year			
Eastern Pennsylvania, 35 km radius									
neg			yes	–	pos	yes	7	0.00	0.19
			yes	–	pos	yes	6	0.44	0.16
neg	neg		yes	–	pos	yes	8	1.12	0.11
	neg		yes	–	pos	yes	7	1.35	0.10
neg		neg	yes	–	pos	yes	8	2.09	0.07
		neg	yes	–	pos	yes	7	2.47	0.06
neg	neg	neg	yes	–	pos	yes	9	3.24	0.04
neg			yes	–	pos		5	3.33	0.04
	neg	neg	yes	–	pos	yes	8	3.42	0.04
			yes	–	pos		4	3.70	0.03
Eastern Pennsylvania, 15 km radius									
neg			yes	–	pos		4	0.00	0.20
			yes	–	pos		5	0.96	0.12
			yes	–	pos	yes	6	1.77	0.08
	neg		yes	–	pos		5	1.95	0.08
		neg	yes	–	pos		5	2.06	0.07

| p (detection) | | | | Ψ (occupancy) | | | K | ΔAICc | w |
date	cloud	mssr	wind	mgmt	tsm	year			
neg			yes	–	pos	yes	7	2.68	0.05
neg	neg		yes	–	pos		6	2.97	0.05
neg		neg	yes	–	pos		6	3.06	0.04
				–	pos		3	3.17	0.04
	neg		yes	–	pos	yes	7	3.74	0.03
		neg	yes	–	pos	yes	7	3.85	0.03
Central Pennsylvania, 35 km radius									
		neg		–	pos		4	0.00	0.22
				–	pos		3	1.11	0.13
pos		neg		–	pos		5	1.99	0.08
		neg	yes	–	pos		5	2.05	0.08
	neg	neg		–	pos		5	2.10	0.08
			yes	–	pos		4	2.71	0.06
	neg			–	pos		4	3.14	0.05
				–	pos		4	3.15	0.05
Central Pennsylvania, 15 km radius									
		neg		–	pos		4	0.00	0.32
		neg	yes	–	pos		5	1.94	0.12
pos		neg		–	pos		5	2.16	0.11
	pos	neg		–	pos		5	2.17	0.11
Eastern Minnesota, 35 km radius									
neg			yes				4	0.00	0.181
neg			yes		pos		5	0.94	0.113
neg			yes	yes			5	1.77	0.075
neg		pos	yes				5	2.24	0.059
neg	neg		yes				5	2.27	0.058
neg			yes	yes	pos		6	2.62	0.049
neg	neg		yes		pos		6	3.25	0.036
neg		pos	yes		pos		6	3.26	0.036
Western Minnesota, 35 km radius									
		pos	yes	yes	pos		6	0.00	0.213
			yes	yes	pos		5	0.25	0.188
pos		pos	yes	yes	pos		7	2.10	0.075
	pos	pos	yes	yes	pos		7	2.14	0.073
pos			yes	yes	pos		6	2.39	0.065
		pos	yes	yes	pos		6	2.45	0.063

Appendix E. Vital rates for Golden-winged Warbler populations in Eastern Pennsylvania, Central Pennsylvania, Eastern Minnesota, and Western Minnesota. Shown for nests are sample size ('N'), nest survival ('NS'), and nest productivity (# fledglings/pair/yr; parentheses indicate 95% confidence intervals). Shown for fledglings are sample size ('N') and fledgling survival ('FS'). Finally, we also include estimates of full season productivity ('FSP') for each focal landscape (# independent juveniles/pair/yr; parentheses indicate 95% confidence intervals). Vital rate data from Minnesota were re-analyzed from Streby et al. (2019) and data from Pennsylvania are newly presenter in this study

| Focal landscape | Nests | | | Fledglings | | FSP |
	N	NS	NP	N	FS	
Eastern Pennsylvania	77	46 (60%)	4.19 (4.07–4.30)	64	47 (74%)	3.07 (2.62–3.53)
Central Pennsylvania	68	23 (34%)	2.28 (2.20–2.38)	63	30 (38%)	1.08 (0.80–1.37)
Eastern Minnesota	58	33 (57%)	3.48 (3.33–3.63)	42	19 (45%)	1.57 (1.05–2.10)
Western Minnesota	138	60 (47%)	3.08 (3.00–3.17)	89	53 (60%)	1.84 (1.52–2.16)

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