

Population trends in *Vermivora* warblers are linked to strong migratory connectivity

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Edited by Robert E. Ricklefs, University of Missouri–St. Louis, St. Louis, MO, and approved January 30, 2018 (received for review October 31, 2017)

Migratory species can experience limiting factors at different locations and during different periods of their annual cycle. In migratory birds, these factors may even occur in different hemispheres. Therefore, identifying the distribution of populations throughout their annual cycle (i.e., migratory connectivity) can reveal the complex ecological and evolutionary relationships that link species and ecosystems across the globe and illuminate where and how limiting factors influence population trends. A growing body of literature continues to identify species that exhibit weak connectivity wherein individuals from distinct breeding areas co-occur during the nonbreeding period. A detailed account of a broadly distributed species exhibiting strong migratory connectivity in which nonbreeding isolation of populations is associated with differential population trends remains undescribed. Here, we present a range-wide assessment of the nonbreeding distribution and migratory connectivity of two broadly dispersed Nearctic–Neotropical migratory songbirds. We used geolocators to track the movements of 70 *Vermivora* warblers from sites spanning their breeding distribution in eastern North America and identified links between breeding populations and nonbreeding areas. Unlike blue-winged warblers (*Vermivora cyanoptera*), breeding populations of golden-winged warblers (*Vermivora chrysoptera*) exhibited strong migratory connectivity, which was associated with historical trends in breeding populations: stable for populations that winter in Central America and declining for those that winter in northern South America.

animal tracking | conservation | geocator | limiting factor | migration

Populations of migratory species can be limited by factors throughout their annual cycle. The degree to which spatially isolated breeding populations use geographically distinct areas during the nonbreeding period (i.e., migratory connectivity) affects the potential for regionally specific factors to influence population trends (1–3). Tracking migratory animals to link breeding populations with nonbreeding areas has primarily focused on the migratory behaviors of large mammals and large birds, which have been studied for decades, and even centuries (4–9). However, following recent technological advances, it is now possible to track all but the smallest migratory species across time and space (10–12). The value of tracking species throughout the annual cycle is manifold. Identifying the migratory pathways by which animal populations navigate between breeding and nonbreeding areas can reveal population-level differences in route or space use that may explain differential breeding population trends (13) or signal tradeoffs in life-history strategies (14–16). In migratory birds, the distribution of breeding populations during the nonbreeding period has the potential to be the primary driver of population trends as many long-distance migrant species spend more time on nonbreeding sites than in any

other location during the annual cycle (17). Furthermore, environmental conditions experienced during the nonbreeding period can have both direct (18) and indirect effects (19) on individuals, and can consequently influence population trends. As such, describing the spatial structure and level of dispersion of a migratory species during the nonbreeding period can identify potential areas that may limit some populations but not others (20–22), provide insight into the evolutionary history of migratory species (23–25), and aid in the identification of important areas that may be targeted for conservation (18, 21, 26–30).

Despite a growing body of information on the behaviors and connectivity of migratory birds, detailed range-wide studies investigating the nonbreeding distribution and migratory connectivity of entire species remain rare (20, 21). Weak migratory connectivity is most commonly reported in studies of long-distance migratory bird species worldwide (31–35). Weak connectivity results in nonbreeding areas that are inhabited by

Significance

Identifying drivers of population trends in migratory animals is difficult due to their reliance on different geographic regions throughout the annual cycle. Populations of Nearctic–Neotropical migratory birds are often thought to be limited by spatial variation in factors affecting reproduction and survival during the breeding season. We tracked individual songbirds from a two-species complex of New World warblers and discovered unequivocal evidence of a system in which strong associations between breeding areas and nonbreeding areas (i.e., migratory connectivity) is concordant with breeding population trends. The strong migratory connectivity we documented is associated with differential rates of land-use change in population-specific nonbreeding areas. Our results suggest that other migratory species with similar population trends may also exhibit strong migratory connectivity.

Author contributions: G.R.K., D.E.A., D.A.B., P.B.W., and H.M.S. designed research; G.R.K., D.E.A., D.A.B., S.M.P., J.A.L., K.R.A., L.P.B., J.A.J., J.P.L., C.S., R.V., and H.M.S. performed research; G.R.K., D.E.A., and H.M.S. analyzed data; and G.R.K., D.E.A., D.A.B., P.B.W., S.M.P., J.A.L., K.R.A., L.P.B., S.H., J.A.J., J.P.L., C.S., R.V., and H.M.S. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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Data deposition: Data used for this study are freely and publicly available on the Data Repository for the University of Minnesota (<https://conservancy.umn.edu/handle/11299/193202>).

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1718985115/-DCSupplemental.

individuals from multiple, widely dispersed breeding populations. Strong migratory connectivity, resulting in geographic isolation during the nonbreeding period, is required for differential population trends of geographically distinct breeding populations to be driven by factors away from the breeding grounds. Although the theoretical implications of strong connectivity have been addressed and discussed (2), rarely are species' breeding population trends decisively linked to individual populations' occurrence at isolated nonbreeding areas, and this information can be particularly important for the conservation of declining and threatened species. Identifying species with populations that might be independently limited by factors outside of the breeding period will contribute to the understanding of the ecological and evolutionary implications of strong migratory connectivity, and why it appears to be uncommon among migratory birds.

We investigated the migratory connectivity of *Vermivora* wood-warblers (Parulidae), a species complex composed of two extant species of obligate Nearctic-Neotropical migrant warblers that are extremely closely related (36). Golden-winged warblers (*Vermivora chrysoptera*) and blue-winged warblers (*Vermivora cyanoptera*) breed and migrate throughout deciduous forests of eastern North America and occur throughout Central America, with golden-winged warblers also occurring in northern South America during the nonbreeding period, and recent evidence suggests golden-winged warblers may exhibit strong, range-wide migratory connectivity (29, 37). On the breeding grounds, golden-winged warblers and blue-winged warblers have overlapping distributions and regularly hybridize to produce viable young (38). Recent genomic evidence suggests overlap and hybridization has occurred for >1,000 y and that these two species may constitute a single, polymorphic species with differences in their genomes primarily associated with different plumage traits (36). That said, detailed information on the genetic structure of *Vermivora* populations is lacking (36, 39). Furthermore, there is little evidence of costs to producing hybrid young in this system (38, 40). Both species of *Vermivora* and two recognized hybrid phenotypes breed in a similar habitat, often with overlapping territories; sing songs with overlapping characteristics; and exhibit nearly identical foraging and reproductive strategies (41, 42).

Despite remarkable genetic, behavioral, and natural history similarities, regional populations of *Vermivora* have experienced starkly contrasting population trajectories since standardized monitoring began in 1966 (43, 44). Golden-winged warblers breeding throughout the Great Lakes region have maintained historical abundances, whereas golden-winged warblers breeding throughout the Appalachian Mountains region have declined steadily (44) (Fig. 1 *C* and *D*). To date, declines in the Appalachian Mountains have amounted to a loss of 98% of historical abundance and resulted in regional extirpations from many areas where golden-winged warblers were once common (41). Hypotheses about the cause of these declines have focused on breeding-grounds factors, namely, habitat loss and hybridization (i.e., genetic swamping), as the primary drivers of declines in Appalachian Mountains populations of golden-winged warblers (41). However, habitat loss and hybridization fail to parsimoniously explain the stationary population trends of Great Lakes populations of golden-winged warblers and the stationary population trends of blue-winged warblers throughout their distribution, including in the Appalachian Mountains, where they co-occur with historically declined populations of golden-winged warblers (42). Previous investigations into the migratory connectivity of *Vermivora* warblers have focused exclusively on golden-winged warblers and are equivocal. Assessments of stable isotopes in feathers of golden-winged warblers collected during the nonbreeding period showed a possible overlap between Appalachian and Great Lakes populations in Central America (46), whereas a smaller scale, light-level geolocator study found no evidence of nonbreeding population overlap between golden-winged warblers at Great Lakes

and Appalachian breeding sites (29). Populations of blue-winged warblers, including those breeding sympatrically with declining golden-winged warblers in the Appalachian Mountains region, have remained numerically stable (44) (Fig. 1 *E–G*). This suggests that the limiting factor primarily driving declines of Appalachian golden-winged warblers is likely experienced somewhere outside the breeding period at a time or location that exclusively affects golden-winged warblers that breed in the Appalachian Mountains.

Here, we present the results of a large, range-wide study (Fig. S1) tracking individual songbirds and describe the migratory connectivity of two hybridizing migratory species. We used light-level geolocators (hereafter, geolocators; *Materials and Methods* and *SI Materials and Methods*) to track individual *Vermivora* warblers throughout their annual cycle and determine links between breeding and nonbreeding areas. Based on differences in breeding population trends (Fig. 1) that are not explained by breeding-grounds factors, we predicted that golden-winged warblers would exhibit strong migratory connectivity, with declining populations occurring disparately from numerically stable populations. If there is strong migratory connectivity and isolation among populations during the nonbreeding period, we further predicted that nonbreeding areas used by historically declining populations will have experienced disproportionate rates of forest loss that coincide with population trends. We discuss the implications of the observed migratory connectivity of *Vermivora* warblers in ecological and evolutionary frameworks. Lastly, we identify species that share similar nonbreeding distributions with *Vermivora* and exhibit varied regional population trajectories akin to those seen in golden-winged warblers that we hypothesize may have similarly strong migratory connectivity driving those species' regional population trends.

Results and Discussion

Geolocator-marked golden-winged warblers ($n = 41$) occurred at sites from Guatemala and southern Mexico to northern Venezuela during the nonbreeding period (Fig. 2*A*). Individuals from historically stable Great Lakes breeding populations [bird conservation region (BCR) S12: Boreal Hardwood Transition; *Materials and Methods* and Fig. 1] were dispersed broadly and almost exclusively throughout Central America during the nonbreeding period [28 of 29 (97%); Fig. 2 *B* and *C*], although one individual from a breeding site in central Ontario, Canada, occurred in northern South America (Fig. 2*A*). Golden-winged warblers from historically declining breeding populations in the Appalachian Mountains (BCR S28: Appalachian Mountains, $n = 12$) occurred at sites exclusively in northern South America, primarily in northern Venezuela (Fig. 2 *D* and *E*), during the nonbreeding period. Blue-winged warblers ($n = 25$), which exhibit historically stable population trends throughout their breeding distribution (BCRs S23, S24, and S28: Prairie Hardwood Transition, Central Hardwoods, and Appalachian Mountains, respectively; Fig. 1), occurred almost exclusively in Central America during the nonbreeding period [24 of 25 (96%); Fig. 2*F*]. Only one blue-winged warbler from a northern Appalachian Mountains breeding population occurred in northern South America. Phenotypic hybrids ($n = 4$) from breeding populations in the Great Lakes region ($n = 2$) occurred in northern Central America during the nonbreeding period (Fig. 3*B*), whereas hybrids from breeding populations in the Appalachian Mountains ($n = 2$) occurred in northern South America (Fig. 3*C*). Golden-winged warblers from Great Lakes breeding populations and blue-winged warblers overlapped extensively in Central America during the nonbreeding period (Fig. 2 *B*, *C*, and *G–J* and Fig. S3). However, historically declining Appalachian Mountains populations of golden-winged warblers were isolated from historically stable populations of both golden-winged warblers and blue-winged warblers during the nonbreeding period (Fig. S2).

Regional breeding populations of blue-winged warblers (i.e., populations identified by their BCRs) did not occur in isolation

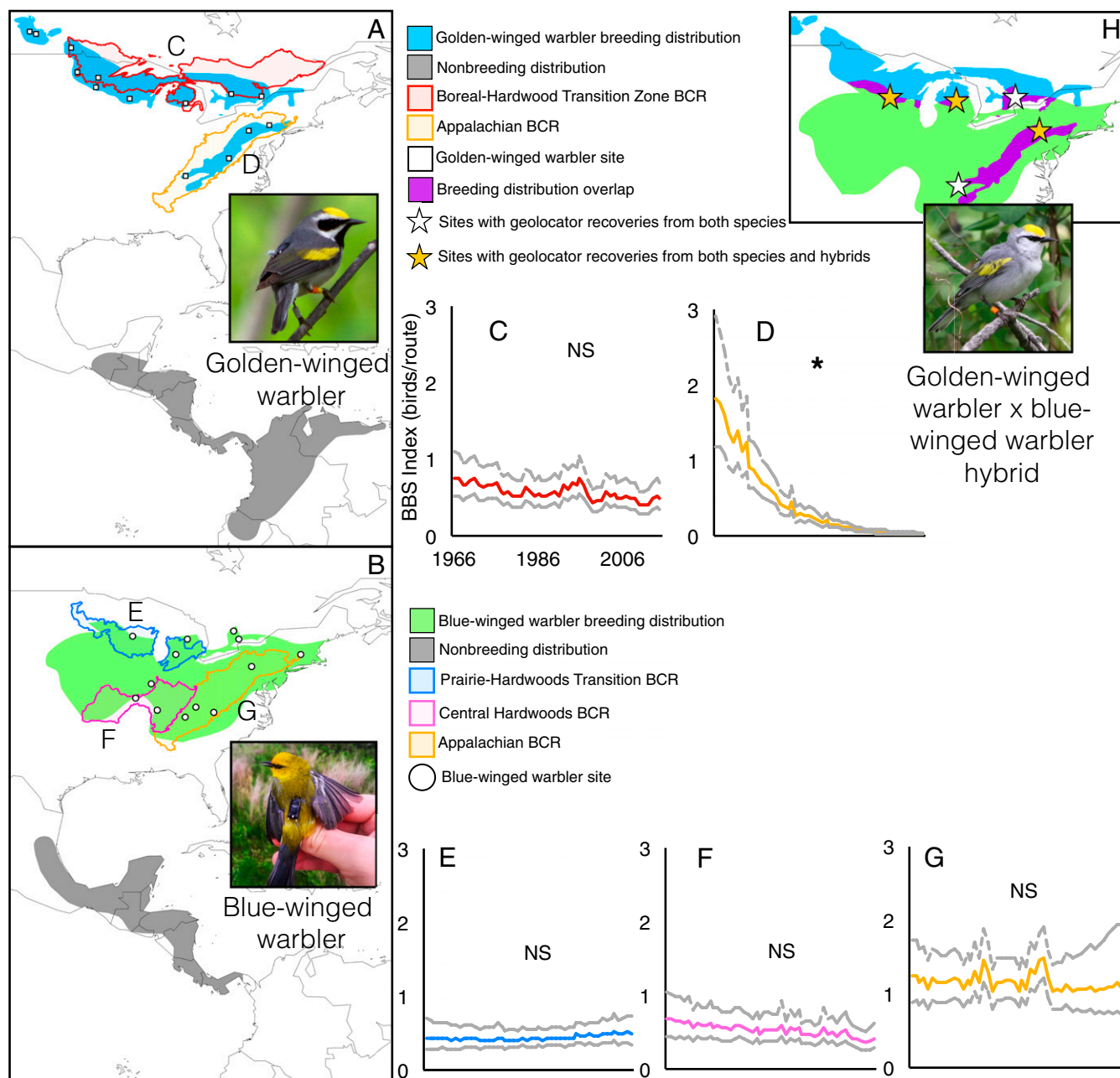


Fig. 1. Breeding and nonbreeding distributions of golden-winged warblers (A) and blue-winged warblers (B) with relevant BCRs outlined and study sites identified (keys are provided for details). Historical population trends of each species are provided for each relevant BCR from 1966 to 2015 [Breeding Bird Survey (44)]. In trend graphs, solid-colored lines represent annual indices of golden-winged warblers (C and D) and blue-winged warblers (E–G) (44) derived from hierarchical model analysis. Dashed gray lines represent 95% credible intervals around annual indices. Populations are noted as exhibiting nonsignificant trends [i.e., numerically stable (NS)] or significant trends [increasing or declining (*)] depending on whether the 95% credible interval around the trend estimate (from 1966 to 2015) includes zero. Note that all trend graphs have the same axis scales. (H) Breeding distribution overlap between golden-winged warblers and blue-winged warblers is presented. Range map information is adapted from BirdLife International (45), and nonbreeding ranges are buffered by 100 km.

from one another during the nonbreeding period (one-way ANOVA: $F = 1.3$; $df = 3, 20$; $P = 0.3$; Fig. S3). However, individual blue-winged warblers that spent the nonbreeding period in Central America exhibited a pattern such that individuals from more easterly breeding longitudes tended to occur farther east during the nonbreeding period (Fig. S3). Conversely, regionally isolated breeding populations of golden-winged warblers maintained their separation during the nonbreeding period, with the Great Lakes population of golden-winged warblers occurring farther west during the nonbreeding period, on average, than

Appalachian Mountains breeding populations ($F = 213.4$; $df = 1, 39$; $P < 0.0001$; Figs. S2 and S3). Unsurprisingly, this pattern remained when we considered the relationship between individual breeding longitude and nonbreeding longitude within and between populations of golden-winged warblers (Fig. S4).

We found strong evidence to support our hypothesis that population trends of *Vermivora* warblers were associated with the distribution and isolation of historically stable and declining populations during the nonbreeding period. Historically stable populations of golden-winged warblers from breeding sites in the

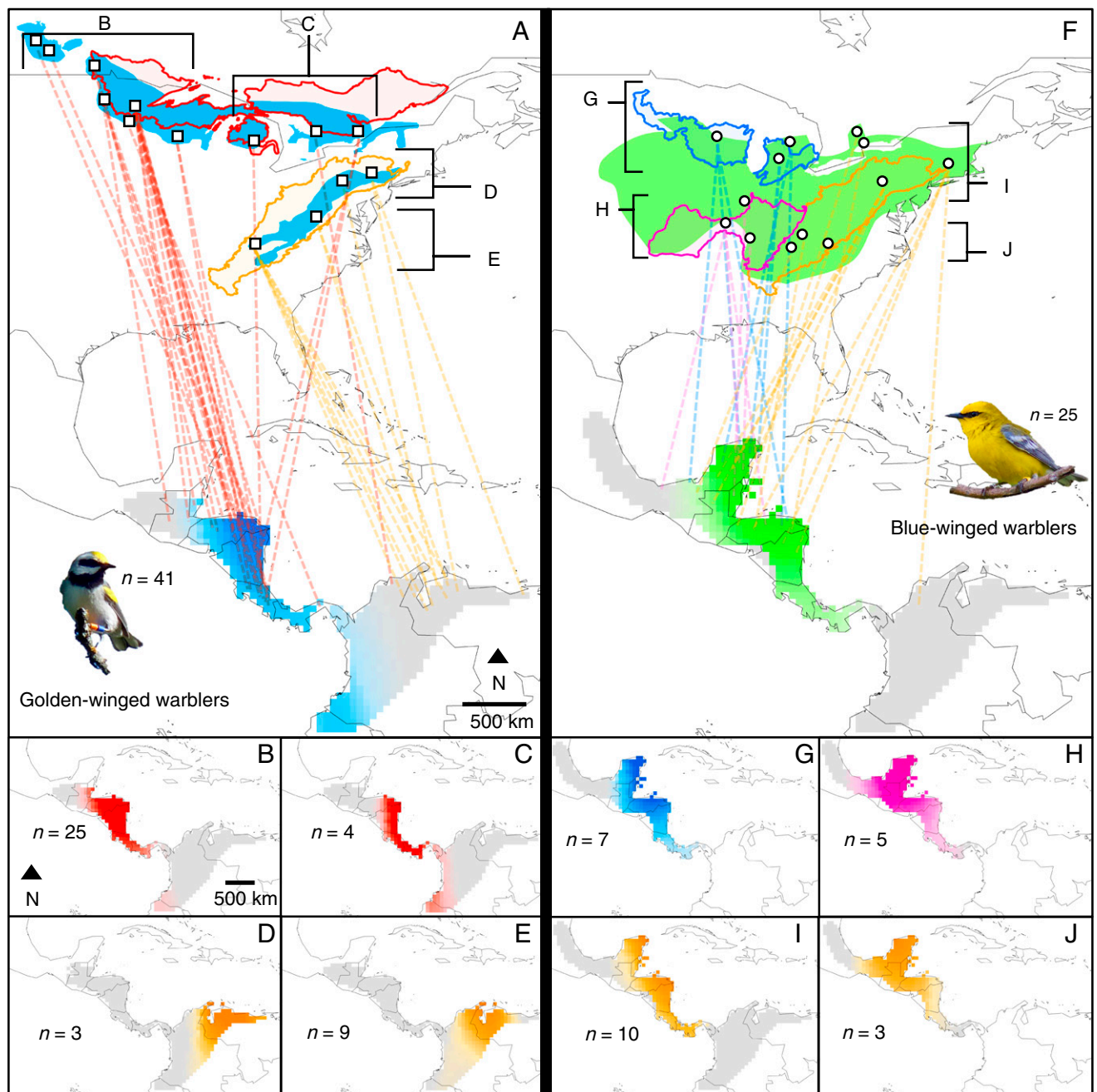


Fig. 2. Species-level average nonbreeding probability density function of golden-winged warblers (A) and blue-winged warblers (F). Dashed lines link individual warblers from breeding sites to their highest probability nonbreeding area. Colors correspond to BCRs in Fig. 1. Lines do not represent migration routes. Brackets define sites used to create population-level average probability density functions of golden-winged warblers (B–E) and blue-winged warblers (G–J). In all probability density functions, darker colors correspond to higher probability of use and the bottom 50% of probabilities are shown in gray to aid in visualization of core use areas. Range maps are adapted from BirdLife International (45). A description of BCRs is provided in Fig. 1.

Great Lakes region occurred throughout Central America during the nonbreeding period, whereas historically declining populations from breeding sites in the Appalachian Mountains region occurred in northern South America. Notably, blue-winged warblers from breeding sites in the Appalachian Mountains region (i.e., the same region in which golden-winged warblers are declining) occurred in Central America during the nonbreeding period alongside historically stable Great Lakes populations of golden-winged warblers. The remarkable similarities between these two species on the breeding grounds (e.g., nearly identical

habitat use, phenology, life-history) and co-occurrence in geographical space suggest that the differential population trends observed between populations of golden-winged warblers and blue-winged warblers breeding in the Appalachian Mountains region are likely driven by factors outside of the breeding period.

Intraspecific migratory connectivity between populations of golden-winged warblers was strong (i.e., individuals from distinct breeding populations used different areas during the nonbreeding period), and we are not aware of any other report of similarly strong connectivity from a range-wide study of distinct breeding

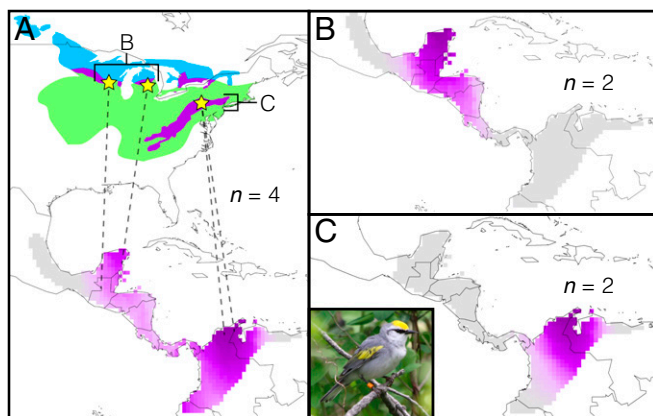


Fig. 3. Average nonbreeding probability density function of all phenotypic *Vermivora* hybrids ($n = 4$; A) and average nonbreeding probability density functions of hybrids from distinct breeding regions in the Great Lakes (B) and Appalachian Mountains (C) regions. Darker colors correspond to higher probability of use, and probabilities $<50\%$ of the maximum shown in gray to aid in visualization of core use areas. Lines represent links between individuals' breeding sites and areas of most probable nonbreeding sites but do not represent migration routes. Range maps are adapted from BirdLife International (45).

populations in another species of migratory songbird. Blue-winged warbler populations exhibited weak connectivity (i.e., individuals from distinct and isolated breeding areas co-occurred during the nonbreeding period) and occurred throughout Central America alongside golden-winged warblers from Great Lakes populations. We found weak connectivity (or high levels of dispersion) within Great Lakes golden-winged warblers and blue-winged warblers range-wide. For example, individual golden-winged warblers from breeding sites in Minnesota, where $\sim 50\%$ of the global population of golden-winged warblers breed (41), were dispersed throughout Central America, occurring from southern Mexico to Panama (maximum distance between two individuals was $>1,500$ km) during the nonbreeding period. Similarly, blue-winged warblers from breeding sites in Massachusetts were dispersed during the nonbreeding period from the Yucatan Peninsula, Mexico, to northern Colombia (maximum distance between two individuals was $\sim 2,000$ km). Without considering the individual that migrated to Colombia, Massachusetts blue-winged warblers were still broadly dispersed (maximum distance between two individuals was $\sim 1,000$ km). Conversely, populations of golden-winged warblers from breeding sites throughout the Appalachian Mountains were more concentrated in a relatively small area in northeastern Colombia and northwestern Venezuela during the nonbreeding period (maximum distance between two individuals from the same breeding site was ~ 600 km).

European migratory bird species that disperse broadly during the nonbreeding period are less likely to be declining than species with restricted distributions during the nonbreeding period compared with their breeding distributions (47, 48). We observed this trend at the population level, with greater nonbreeding dispersion among numerically stable populations (i.e., golden-winged warblers breeding in the Great Lakes and all populations of blue-winged warblers) compared with declining breeding populations (e.g., golden-winged warblers breeding in the Appalachian Mountains), suggesting that migratory diversity (i.e., within-population variation in migratory routes and/or destinations) may be linked to population trends at both species and population levels. Tracking additional individuals may uncover greater dispersion, but golden-winged warblers from Appalachian Mountains breeding populations were overrepresented in our sample based on estimated population size [29% of golden-winged warbler sample but only $\sim 5\%$ of the global population (41)];

therefore, we believe additional sampling will likely confirm low dispersion in this population.

The differential population trends observed in *Vermivora* warblers using Central American vs. South American nonbreeding areas may be caused by a variety of factors. The complexity of the ecological relationships and resource requirements that exist throughout the annual cycle of a migratory species makes it unlikely that there is a single driver of these trends. However, the identification of spatial isolation between these populations of *Vermivora* warblers suggests that the drivers of historical declines in populations of Appalachian Mountains-breeding golden-winged warblers are linked to their nonbreeding distribution in northern South America or the migratory pathways they use between breeding and nonbreeding locations. The cause of the precipitous declines of golden-winged warblers that use this region during the nonbreeding period need not be tied to a single factor, but may be the result of a reliance on a region that has experienced extensive anthropogenic exploitation and changes in land use over the past century (49–52).

Aerial photographs and/or satellite imagery covering the entire nonbreeding distribution of *Vermivora* are not available for the period when Appalachian Mountains populations of golden-winged warblers experienced their steepest declines [~ 1970 –1980 (44)]. Furthermore, it is unlikely that golden-winged warblers in the Appalachian Mountains region began declining in 1966, the first year of the Breeding Bird Survey (41). Therefore, clearly identifying a mechanism related to these declines is challenging. Using modeled estimates of historical land-use and land-cover change (HYDE 3.1) (53–55) (*SI Materials and Methods*, in which a detailed description of the analysis is provided, and Fig. S5) for the region, we found that forest-dominated landscapes at appropriate elevations for golden-winged warblers [i.e., 200–2,400 m above sea level (41)] were converted to other, nonforest land uses in northern South America at a disproportionate rate compared with Central America (53–55) (Fig. 4). The loss of the forest-dominated landscape within the appropriate elevation envelope for golden-winged warblers in northern South America began in the early- to mid-1940s and continued through 1980 (Fig. 4). Based on our description of the migratory connectivity of *Vermivora*, these dramatic regional shifts in land use would likely affect primarily golden-winged warblers from Appalachian Mountains breeding populations (Fig. 2). Simple linear regressions reveal that these predicted changes in the amount of forest-dominated land in population-specific nonbreeding ranges explain significant variation in the breeding population trends of all three groups [(i) blue-winged warblers range-wide, 1966–2010: $F = 16.3$; $df = 1, 8$; $P = 0.004$; (ii) Great Lakes populations of golden-winged warblers, 1966–2010: $F = 13.5$; $df = 1, 8$; $P = 0.006$; and (iii) Appalachian Mountains populations of golden-winged warblers, 1966–1990: $F = 77.7$; $df = 1, 4$; $P = 0.0009$] (Fig. 4). This evidence provides a parsimonious and temporally synchronized explanation for the observed differences in breeding population trends among these three groups of *Vermivora* warblers.

Certainly, the loss of appropriate humid mid-elevation tropical forest cover types caused by changes in land use, or other consequences of human activities, may have direct effects on the survival of nonbreeding golden-winged warblers (56). However, habitat fragmentation, reduced habitat quality, and habitat loss may have nonlethal effects that lead to lower reproductive success and survival of individuals that return to North America to breed (19, 57). Additionally, golden-winged warblers migrating to northern South America from northern Appalachian Mountains breeding sites travel $>5,000$ km farther than golden-winged warblers migrating between Central America and Great Lakes breeding sites each year (29). Therefore, northern Appalachian breeding populations of golden-winged warblers may be more sensitive to declines in available food resources, phenology mismatches during migration, and/or higher risk of encountering

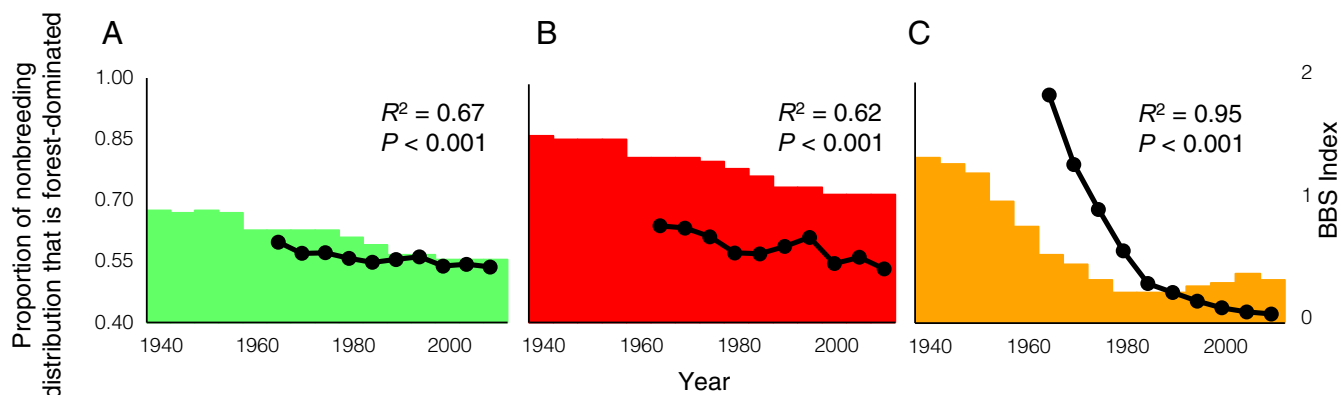


Fig. 4. Bar charts showing the modeled proportion of forest-dominated land cover at 200–2,400 m above sea level in the nonbreeding distribution of blue-winged warblers (A; Central America, southern Mexico), Great Lakes breeding populations of golden-winged warblers (B; Central America), and Appalachian Mountains breeding populations of golden-winged warblers (C; northern South America). Overlaid lines show breeding population trends (44) of each group over the same time scale. Axes for the proportion of forest (left y axis) and the Breeding Bird Survey (BBS) index (right y axis) are the same for all respective plots. Summary statistics of simple linear relationships of BBS index as a function of the proportion of forest-dominated land cover are presented. Regressions in blue-winged warblers (A) and Great Lakes breeding populations of golden-winged warblers (B) use all available years. The regression for Appalachian Mountains breeding populations of golden-winged warblers used the period 1966 to 1990 during the steepest decline and before the population was effectively reduced to near zero. Land-use data are from the HYDE 3.1 database (53–55).

predators or other obstacles during migration (16, 17, 57–59). Conversely, *Vermivora* that occur in Central America during the nonbreeding period migrate shorter distances to nonbreeding sites and are more widely dispersed during the nonbreeding period such that the effects of potentially limiting factors are not likely to be experienced by all individuals of a population. A future productive research focus may be identifying potential limiting factors during migration so as to assess the impact of differential migration strategies on population trends of *Vermivora* warblers.

We did not observe intermediate nonbreeding site affinity in probable first-generation hybrids [identified based on plumage characteristics (60)]. Hybrids with intermediate migratory traits have been described in other species (61), but the hybrids we monitored did not occur in areas that we could differentiate from one of the parental types (e.g., hybrids from the Appalachian Mountains did not occur in Panama). However, if hybrids and parental types used nonbreeding areas separated by short distances (i.e., <250 km), we would be unlikely to differentiate those sites due to the spatial resolution of geolocator data. Future research with higher resolution technology (i.e., satellite-enabled markers, global positioning system-enabled markers) may be useful in determining if hybrids exhibit intermediate phenotypes in nonbreeding site affinity that are unable to be identified with geolocators. It is challenging to identify meaningful patterns in the nonbreeding distribution of two hybrids captured in the Great Lakes portion of the breeding distribution as there is little differentiation in the nonbreeding ranges of blue-winged warblers and golden-winged warblers breeding in that region. However, the two phenotypic hybrids we tracked from the Appalachian Mountains wintered in northern South America, where golden-winged warblers from the Appalachian Mountains occur during the nonbreeding period. We note, however, that our sample of hybrids may be influenced by ascertainment bias in that we only captured and attached geolocators to hybrids that returned to breeding areas after successfully migrating to and from nonbreeding locations, reducing any opportunity to identify migration to poor-quality or inappropriate nonbreeding locations that negatively influenced survival or breeding propensity (13). It is likely that the hybrid individuals we captured and tracked originated from interspecific pairings or extrapair copulations between parental species in the Appalachian Mountains region. Given the results of this study, the hybrid offspring of these pairings likely received genetic information from a blue-winged warbler that wintered in Central America and a golden-winged warbler that wintered in

northern South America. If a subset of hybrid individuals produced in the Appalachian Mountains with a genetic predisposition to migrate to Central American nonbreeding areas does not survive (possibly due to a multitude of reasons, including a recombination of alleles that results in maladaptive migratory orientation or another postzygotic barrier), disperses to breeding areas that are outside the Appalachian Mountains (i.e., nonbreeding site affinity and breeding site affinity are genetically linked), or does not exhibit breeding behavior, our sample of hybrids would likely be biased. Further research is required to fully account for the behaviors of hybrid *Vermivora* warblers during their first migration and winter and to identify specific genomic regions associated with different migratory phenotypes (62).

It is unlikely that golden-winged warblers are the only broadly dispersed Nearctic-Neotropical migrant songbird species that exhibits strong migratory connectivity and shows population trends consistent with being limited by nonbreeding factors. Our results confirm that migratory connectivity and the nonbreeding distribution of species can be linked to breeding population trends. However, range-wide geolocator studies are expensive and logistically challenging, and being able to identify potential candidate species that may exhibit these similar relationships without mounting a continent-wide study would be valuable. We therefore identified 25 species of Nearctic-Neotropical migrant passerines that have similar nonbreeding distributions to *Vermivora* warblers and broadly dispersed breeding distributions (*Materials and Methods*, Fig. S6, and Table S2). Of those 25 species, we identified 16 (64%) that showed structured differences in regional breeding population trajectories that could be caused by nonbreeding factors (Table S2). Six of those species showed similar patterns in range-wide population trends as golden-winged warblers (declines from 1966 to 1990, followed by stable trends from ~1990 to 2015). Without detailed knowledge of the factors affecting population trends of these species, we predict their regionally distinct breeding population trends may be linked to migratory connectivity and nonbreeding distribution similar to what we observed in golden-winged warblers. The Kentucky warbler (*Geothlypis formosa*) stands out as one of the most likely candidates to exhibit strong migratory connectivity based on these assumptions (Fig. S6 and Table S2). Kentucky warblers exhibit a dichotomous north-south pattern in their breeding population trends and occur in the same regions as golden-winged warblers during the nonbreeding period. In addition, range-wide declines starting in 1966 have leveled off and

global population trends have been stable since ~1990, similar to golden-winged warblers. Kentucky warblers may be another species that exhibits strong migratory connectivity, and like golden-winged warblers, signals of strong connectivity (e.g., coinciding population declines) may be shared among species that occupy similar regions and are affected by similar limiting factors during the annual cycle.

More complex scenarios may explain the patterns in population trends exhibited by Kentucky warblers and the other species we have promoted as potential candidates to exhibit strong migratory connectivity. There also are factors (e.g., regionally specific breeding-ground factors) that could obfuscate or mask the purported signals that we used to identify species that may exhibit strong migratory connectivity. Identifying species with strong connectivity and understanding the implications of such strong connectivity are timely and important (63). If anthropogenic changes in land-use patterns in northern South America are identified as a key factor driving population declines of golden-winged warblers occurring in that region during the nonbreeding period, then the strong migratory connectivity we observed in golden-winged warblers may constitute an evolutionary trap (64). In this case, anthropogenic factors that are limiting populations may be occurring over a relatively short period and outpacing the natural ability of these populations to adapt. Understanding the implications (65, 66) and diversity (67–69) of patterns in the distribution of migratory species throughout the annual cycle will aid in predicting the effects of continuously changing anthropogenic factors on migratory species globally (70).

Conclusion

We provide details on the distribution and migratory connectivity of two closely related, Nearctic-Neotropical migrant songbird species, which recent genetic evidence suggests may be plumage morphs of a single-species complex. More importantly, we show through a thorough sampling of populations throughout these species' breeding ranges that strong connectivity leading to the isolation and segregation of populations during the nonbreeding period may be associated with patterns in breeding population trends. Unlike blue-winged warblers, golden-winged warblers exhibited strong migratory connectivity, with declining populations occurring exclusively in northern South America. Identifying the factors that led to the severe declines and local extirpation of golden-winged warblers in the Appalachian Mountains region will be critical for their long-term conservation. Our observations of migratory connectivity in *Vermivora* warblers represent a major advance in understanding the unique drivers shaping migration strategies; the distribution of populations throughout the annual cycle; and, ultimately, the evolutionary trajectories of migrants in the rapidly changing Anthropocene. Studies like ours may benefit future research focused on identifying genomic regions associated with specific migratory behaviors. Our findings highlight the value of collecting information about the annual movements of species across their distribution, and studies like ours can aid in the conservation of migratory species, such as *Vermivora* warblers, in the future.

Materials and Methods

Study Area and General Procedures. We studied golden-winged warblers, blue-winged warblers, and their hybrids across their breeding distributions in eastern North America from 2013 to 2017. A small portion of these results include a reanalysis of geolocator data (<https://conservancy.umn.edu/handle/11299/183086>) reported by Kramer et al. (29). Study areas were chosen based upon location (i.e., representing the greatest geographic distribution), density of *Vermivora* warblers, and ease of access. *Vermivora* warblers are diverse-forest species that are often associated with young, regenerating forest surrounded by a larger matrix of mature forest, and our study sites reflected the full range of land-cover types used by these species (71). We captured all warblers in mist nets using conspecific call and song broadcasts. Upon initial capture, we determined age and sex, assigned a phenotypic

species (i.e., typical golden-winged warbler, typical blue-winged warbler, hybrid) based on plumage traits (60), and weighed and banded each individual with a US Geological Survey/Canadian Wildlife Service aluminum band and one to three plastic color leg bands to aid in future identification. We attached geolocators (model ML6240, 2-min light-sampling regime; Biotrack Ltd.) to male *Vermivora* warblers that we determined to exhibit territorial or breeding behaviors (i.e., resident, nonmigratory behaviors) using an adapted leg-loop harness that was developed and tested on this species complex without any known negative effects (72–74). All birds were released after processing, and we monitored geolocator-marked birds for signs of stress during a brief (~1–15 min) acclimation period.

The year following deployment, we returned to the sites where we marked warblers with geolocators and attempted to recapture all marked birds that returned. *Vermivora* warblers exhibit high site fidelity when their breeding habitat is not altered or removed and often return to the same territories year after year (73, 75). Thus, we began searches for returning geolocator-marked birds at the site where they were marked the previous year. We expanded our search radius to include appropriate breeding cover types within ~1–3 km of the deployment site depending on the site and the surrounding landscape. We used the same methods as described above to lure returning geolocator-marked individuals into mist nets. We then removed the geolocator and released the warbler at its capture location. We attached new geolocators to a subset of individuals that successfully carried a geolocator in 2013 or 2014 in an attempt to understand whether individuals use different nonbreeding areas in different years (a discussion of how we treated individuals with multiple years of data is provided in the next section).

We captured and marked birds following Protocol 561, approved by the University of Tennessee Institutional Animal Care and Use Committee; Protocol 104A80575, approved by the University of Minnesota Institutional Animal Care and Use Committee; Virginia Commonwealth University Institutional Animal Care and Use Committee Proposal 10230; and Protocols 07-0303 and 10-0201 approved by the West Virginia University Institutional Animal Care and Use Committee.

Geolocator Data Analysis. We downloaded and decompressed raw light-level data from geolocators using BASTrack software (Bastrack Ltd.). All additional processing and analyses were conducted in R (76). Briefly, we followed the methods described by Kramer et al. (29) to derive nonbreeding probability density functions for each individual during the tropical dry season (i.e., January 1–February 28). This period represents the nonbreeding period when we assumed individuals were residing on nonbreeding territories and were exposed to the least environmental shading. We used FLIGHTR (77) to estimate spatially explicit likelihood surfaces (~0.5° cell size) for each transition period (i.e., sunrise, sunset) from January 1 to February 28. We used a subset of data or data from a different portion of the nonbreeding period if data were unavailable from January 1 to February 28 (due to geolocator failure or occlusion of the light sensor; Table S1). We then averaged all transition-derived likelihood surfaces for each individual to produce an average probability density function showing the most probable regions used by that individual during the nonbreeding period. We transformed individual nonbreeding likelihood surfaces into probability density functions by dividing each likelihood surface by the sum of its surface. We averaged nonbreeding probability density functions of individuals from the same breeding populations to achieve a population-level probability density function representing areas most likely used by an individual warbler from each population during the nonbreeding period.

Because that portion of the Neotropics used during the nonbreeding period by *Vermivora* warblers extends primarily from west to east, we used longitude as a proxy for individual nonbreeding site location in our calculations and estimations of overlap. Longitude is more accurate than latitude in geolocator analyses and can be useful for determining movement and location (78), especially in terrestrial organisms that are constrained to land during the period of interest but travel through regions that are bounded to the north and south by expansive water (e.g., Central America). To estimate nonbreeding site longitude, we extracted the longitude of the highest probability cell in the probability density function for each individual. We averaged the nonbreeding probability density functions for warblers for which we collected 2 y of data ($n = 6$) so that those individuals did not bias estimates of average nonbreeding distribution of populations.

Statistical Analysis. We evaluated differences between the nonbreeding distributions of populations using linear regression and one-way ANOVA and post hoc Tukey honest significance difference tests in R unless otherwise noted. Results of all tests were considered significant at $\alpha = 0.05$. We investigated the level of migratory connectivity in populations of *Vermivora*

warblers based on BCRs for which annual population-level sampling is conducted and reported by the Breeding Bird Survey (44). Golden-winged warbler populations are largely contained within two BCRs: Boreal Hardwood Transition BCR (S12; i.e., Great Lakes population) and Appalachian Mountains BCR (S28; i.e., Appalachian Mountains population). Blue-winged warblers are more widespread, but our study sites fell primarily in three BCRs: Prairie Hardwood Transition BCR (S23), Central Hardwoods BCR (S24), and Appalachian Mountains BCR (S28). For both blue-winged warblers and golden-winged warblers, we split the Appalachian Mountains BCR into northern and southern halves (separated at ~39° N) to investigate potential differences in the nonbreeding distributions of these groups of *Vermivora*. For golden-winged warblers, we also split the Great Lakes population (BCR 12) into eastern and western portions (~85° W) for the same purpose.

Predicting Other Species with Nonbreeding Population Structure. We used range data from BirdLife International (45) to visually inspect the nonbreeding distributions of Nearctic-Neotropical migrant songbird species. We identified species that occurred in both Central America and South America during the nonbreeding period, as observed in golden-winged warblers (Table S2). We then visually inspected breeding period trend maps from the Breeding Bird Survey (44) and identified species that showed structured, regional variation in population trends. Finally, we visually inspected the survey-wide population trends for those species and noted their general population trends from 1966 to 1990 and 1991 to 2015. From 1966 to ~1985, the range-wide population trend of golden-winged warblers declined as a result of the loss of individuals from the Appalachian Mountains breeding population. Following that decline, the range-wide population trend stabilized between 1985 and 1990. If other species had strong migratory connectivity similar to that which we observed in golden-winged warblers (i.e., isolated breeding populations occurring separately in Central America and South America during the nonbreeding period), one might expect to see a similar trend over the same period if limiting factors (e.g., deforestation, fragmentation; Fig. 4) were also affecting other Nearctic-Neotropical migrant populations. For example, yellow-throated vireos (*Vireo flavifrons*) are broadly dispersed throughout eastern North America during the breeding period and occur in both Central America and northern South America during the nonbreeding period. Eastern populations of yellow-throated vireos tend

to be declining more than western populations. However, survey-wide trends of yellow-throated vireos revealed a stationary trend from 1966 to 1985, switching to increasing population trends from 1986 to 2010 (44). This suggests that the factors limiting yellow-throated vireos are different from those limiting golden-winged warblers; therefore, we predict that it is unlikely that yellow-throated vireos have similar nonbreeding population distribution and migratory connectivity as golden-winged warblers.

Data Accessibility

Data used for this study are freely and publicly available [data conservation provided by the Data Repository for the University of Minnesota (<https://conservancy.umn.edu/handle/11299/193202>)]. All other data used in this study were retrieved from publicly accessible databases.

ACKNOWLEDGMENTS. We thank M. Barber, M. Barnes, J. Bell, J. Chancey, L. Coe-Starr, C. Colley, E. Davis, J. Dodson, K. Eckert, R. Eckstein, R. Fenty, C. Fiss, M. Gallagher, B. Gray, A. Grupenhoff, C. Henderson, L. Hendrixson, N. Henke, E. Hess, L. Hoehn, J. Kawlewski, B. Keinath, J. Koberdahl, L. Loegering, S. McLaughlin, S. Midthune, L. Mielke, D. Miles, M. Morin, N. Moy, J. Nelson, A. Pesano, S. Prevost, J. Reubensam, M. Schilling, N. Seeger, L. Schofield, A. Tomcho, S. Wallace, J. Warmbold, J. Wessels, A. Worm, B. Yliniemi, and others for assistance in the field. We are especially grateful to N. Hill, K. Maley, D. McNeil, R. Pagel, P. Rodrigues, K. Stein, and C. Ziegler for their commitment to the project, and to W. Ford, W. Bringer, A. Hewitt, D. King, J. Larkin, and H. Saloka for providing logistical support. We thank D. Toews and two anonymous reviewers for comments improving earlier drafts of this manuscript. These data were collected during a project funded by the US Fish and Wildlife Service and the US Geological Survey through Research Work Order 98 at the US Geological Survey, Minnesota Cooperative Fish and Wildlife Research Unit, and by the National Science Foundation through Postdoctoral Research Fellowship 1202729 (to H.M.S.). Additional funding was provided by the Virginia Department of Game and Inland Fisheries and the Grace Jones Richardson Trust. None of our funders had any influence on the content of the submitted or published manuscript, and only the US Geological Survey required approval of the final manuscript prior to publication as required in their Fundamental Sciences Practices protocols. Use of trade names does not imply endorsement by the US Geological Survey or any other institutions affiliated with this study.

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Supporting Information

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SI Materials and Methods

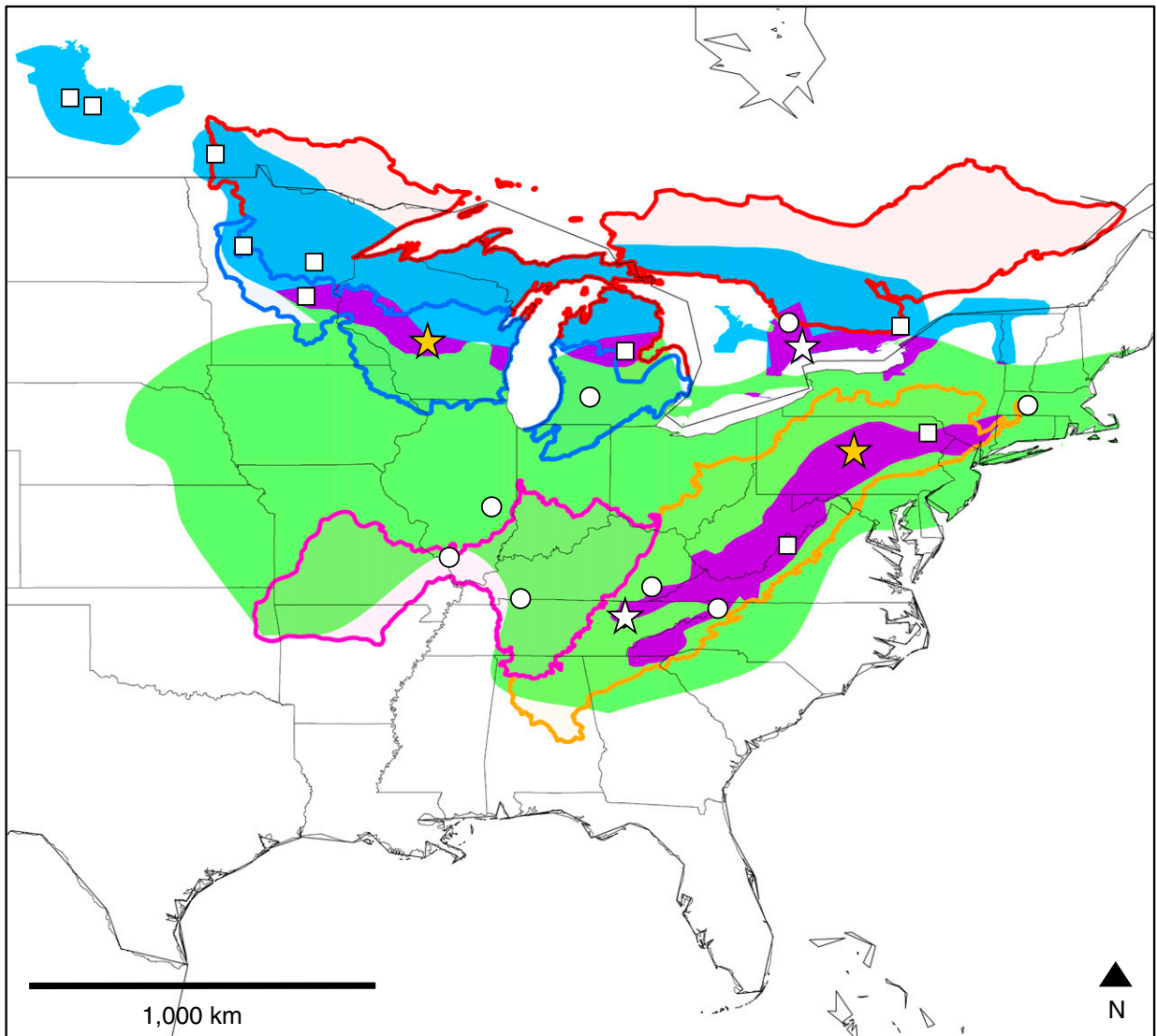
Basic Background on Light-Level Geolocators. Light-level geolocators (geolocators) are a simple yet powerful tool used to estimate location based on seasonal and locational differences in the timing of day and night. Simply, geolocators record the amount of ambient light using a light sensor at a regular interval throughout the life of the unit. A measure of the amount of light is stored with a time stamp such that the full light regime experienced by a geocator can be recreated upon its recovery. Two primary methods exist for analyzing geocator data: the threshold method and the template-fit method. Both methods have been used to identify movements of migratory species, and both methods have their advantages (11, 29). The threshold method is simpler, uses less information, and has been shown to be less accurate when compared directly with the template-fit method (68). The template-fit method uses the entire curve of light intensity during twilight periods (i.e., dawn, dusk) to estimate a likelihood surface that can be combined with other likelihood surfaces from previous or subsequent twilights to provide a location estimate (67). The template-fit method also provides the user with an understanding of variability or error around the location estimate as it produces a spatially explicit likelihood surface where the likelihood of the geocator being in any given cell is relative to the likelihood of it being in the rest of the cells. We chose to use the template-fit method because it allowed us to create spatially explicit estimates of nonbreeding location that we could standardize for each individual and compare across individuals and populations. Further details are provided by Kramer et al. (29).

Assigning Species Status to Individuals. The plumage of typical, phenotypically pure golden-winged warblers and blue-winged warblers is strikingly different and easily differentiable. Golden-winged warblers are mostly gray with a gold crown, gold patch on the wing (wing-bar), and black mask and throat patch (Figs. 1A and 2A). Blue-winged warblers are mostly yellow, often with separate white wing-bars and a black eye-line without any black mask or throat patch (Figs. 1B and 2F). Hybrids occur in two recognized phenotypes representing crosses between pure parental types [i.e., first-generation hybrid (F1), “Brewster’s warbler”; Fig. 1H] and the rare homozygous-recessive offspring produced from an F1-cross (i.e., “Lawrence’s warbler”). Intermediate phenotypes with combinations of plumage traits commonly occur in individuals with complex ancestral lineages. We assigned species status in the field following capture and took standardized, diagnostic photographs of each individual for confirmation. Upon capture, we classified individuals as hybrids or phenotypically pure species based on their plumage. We classified individuals with at least one obviously incongruous plumage

character (i.e., mostly blue-winged warbler characters: yellow body plumage, no throat patch, and eye-stripe, but with one yellow wing-bar instead of two white wing-bars) as hybrids. All hybrids referenced in this study possessed plumage characters typical of F1 hybrids (i.e., gray body plumage, black eye-line, no black throat patch).

Methods for Interpreting Changes in Historical Land-Use Data. We generally quantified the modeled changes in land use across broad geographical regions that corresponded to three groups of *Vermivora* warblers based on their nonbreeding distributions. We used the HYDE 3.1 database (53–55) to quantify modeled changes in land use in cells ($0.5^\circ \times 0.5^\circ$) containing land from 200 to 2,400 m above sea level. This elevational range generally contains the humid, mid-elevation forests that *Vermivora* warblers occupy during the nonbreeding period (41, 56). The HYDE 3.1 database provides model-generated estimates of historical land use based on a variety of factors (53–55). Although it provides estimates of the area of different land-cover types, due to the coarseness and uncertainty of the models, we chose to measure the proportion of forest-dominated cells that fell in our population masks for each group (i.e., southern Mexico, Central America, northern South America). As such, we did not attempt to measure the true amount of any land-cover types; instead, we only measured the number of cells for which native forest was the dominant land-cover type (i.e., >50%). In this way, our data accomplish the goal of providing large-scale, regional, and general information about the predicted changes in land-use patterns in the northern Neotropics from 1940 to 2010.

Observations of Site-Level Differences in Population Trends Explained by Nonbreeding Site Affinity. We found additional evidence for this relationship at the site level. The only golden-winged warbler from the historically stable Great Lakes breeding population that occurred in northern South America during the nonbreeding period was from a site in western Ontario, Canada, which has experienced declines at a rate of greater than -2.5% per year (43) similar to populations in the Appalachian Mountains. Populations of golden-winged warblers to the east and west of this historically declining population are numerically stable or increasing (44) (Fig. S7), and individuals we tracked from these populations occurred exclusively in Central America during the nonbreeding period (Fig. 2 and Fig. S7). Despite our limited sample size in this portion of the breeding distribution, this finding highlights the importance of defining conservation strategies based on biologically meaningful populations instead of relying solely on arbitrary boundaries (e.g., state lines) or general ecoregions (e.g., BCRs), especially in migratory species.



- Golden-winged warbler breeding distribution
- Blue-winged warbler breeding distribution
- Breeding distribution overlap
- Boreal-Hardwood Transition Zone BCR
- Appalachian BCR
- Prairie-Hardwoods Transition BCR
- Central Hardwoods BCR
- Golden-winged warbler site
- Blue-winged warbler site
- ☆ Sites with geolocator recoveries from both species
- ★ Sites with geolocator recoveries from both species and hybrids

Fig. S1. Detailed map of study sites in relation to BCRs and breeding distributions of *Vermivora* warblers. Distribution data are adapted from BirdLife International (45).

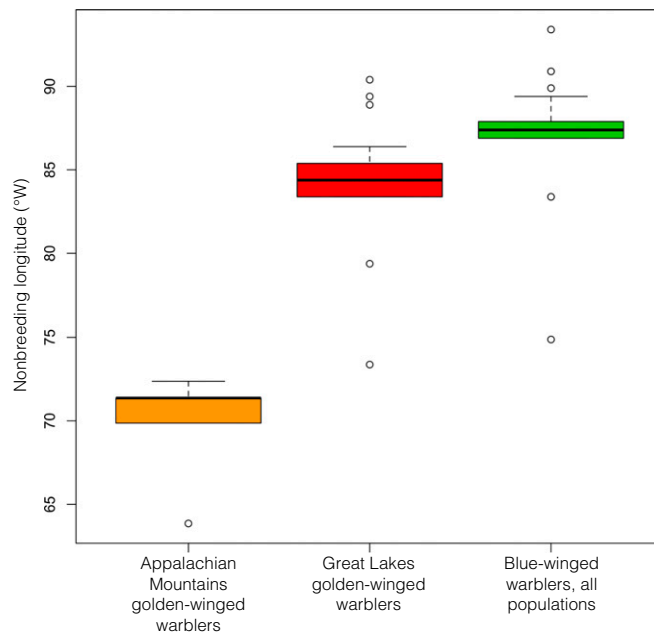


Fig. S2. Box plot of nonbreeding longitude in golden-winged warblers from Appalachian Mountains (orange) and Great Lakes (red) breeding sites and blue-winged warblers from throughout their breeding range (green). Blue-winged warblers and golden-winged warblers breeding in the Great Lakes region exhibit historically stable population trends, whereas golden-winged warblers in the Appalachian Mountains region have experienced declines.

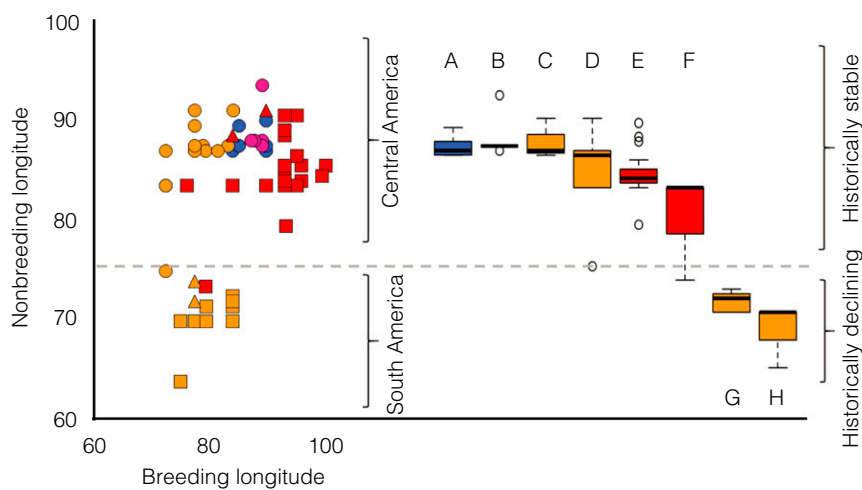


Fig. S3. Nonbreeding longitude as a function of breeding longitude between individual blue-winged warblers, golden-winged warblers, and hybrids (*Left*) and average nonbreeding longitude by population (*Right*). Individuals are identified as golden-winged warblers (squares), blue-winged warblers (circles), or hybrids (triangles) from breeding sites in BCRs identified in Fig. 1 [colors correspond to those in Fig. 1; orange, Appalachian Mountains BCR (C and D and G–H); blue, Prairie-Hardwoods Transition BCR (A); pink, Central Hardwoods BCR (B); red, Boreal-Hardwoods Transition BCR (E and F)]. The box plot shows average nonbreeding longitude of blue-winged warbler populations (A–D) and golden-winged warbler populations (E–H), with the dashed gray line representing the longitude separating Central America and South America (75° W). We considered southern and northern Appalachian Mountains populations of blue-winged warblers (C, southern and D, northern) and golden-winged warblers (G, southern and H, northern) separately. We also considered western and eastern populations of Great Lakes golden-winged warblers separately (E, western and F, eastern).

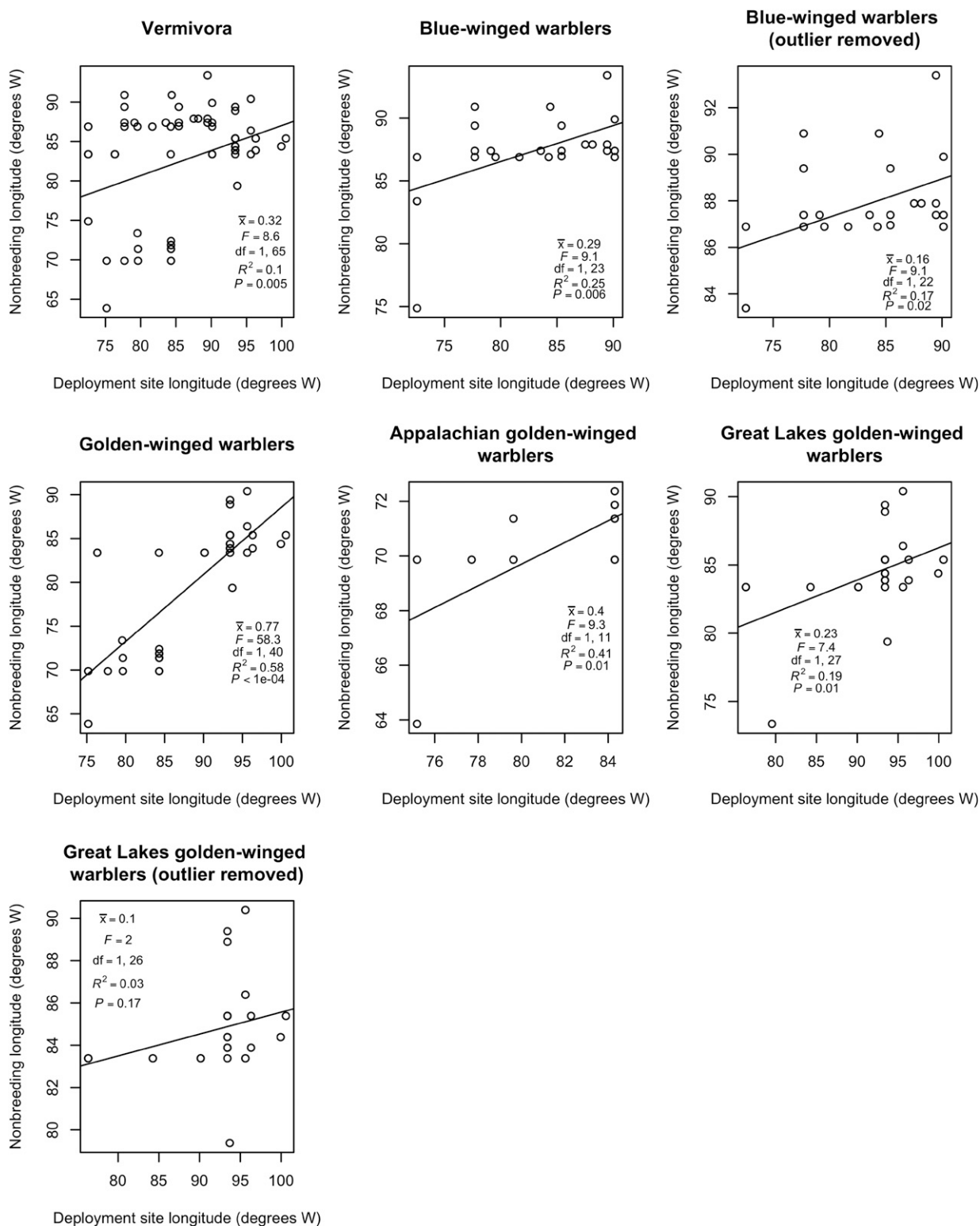


Fig. 54. Relationships between deployment site longitude ($^{\circ}$ W) and nonbreeding longitude ($^{\circ}$ W) derived from the longitude of the highest probability cell in the nonbreeding probability density functions of individual *Vermivora* warblers (phenotypic hybrids not included). Descriptions of populations are provided in *Materials and Methods* and Fig. 1. W, west.

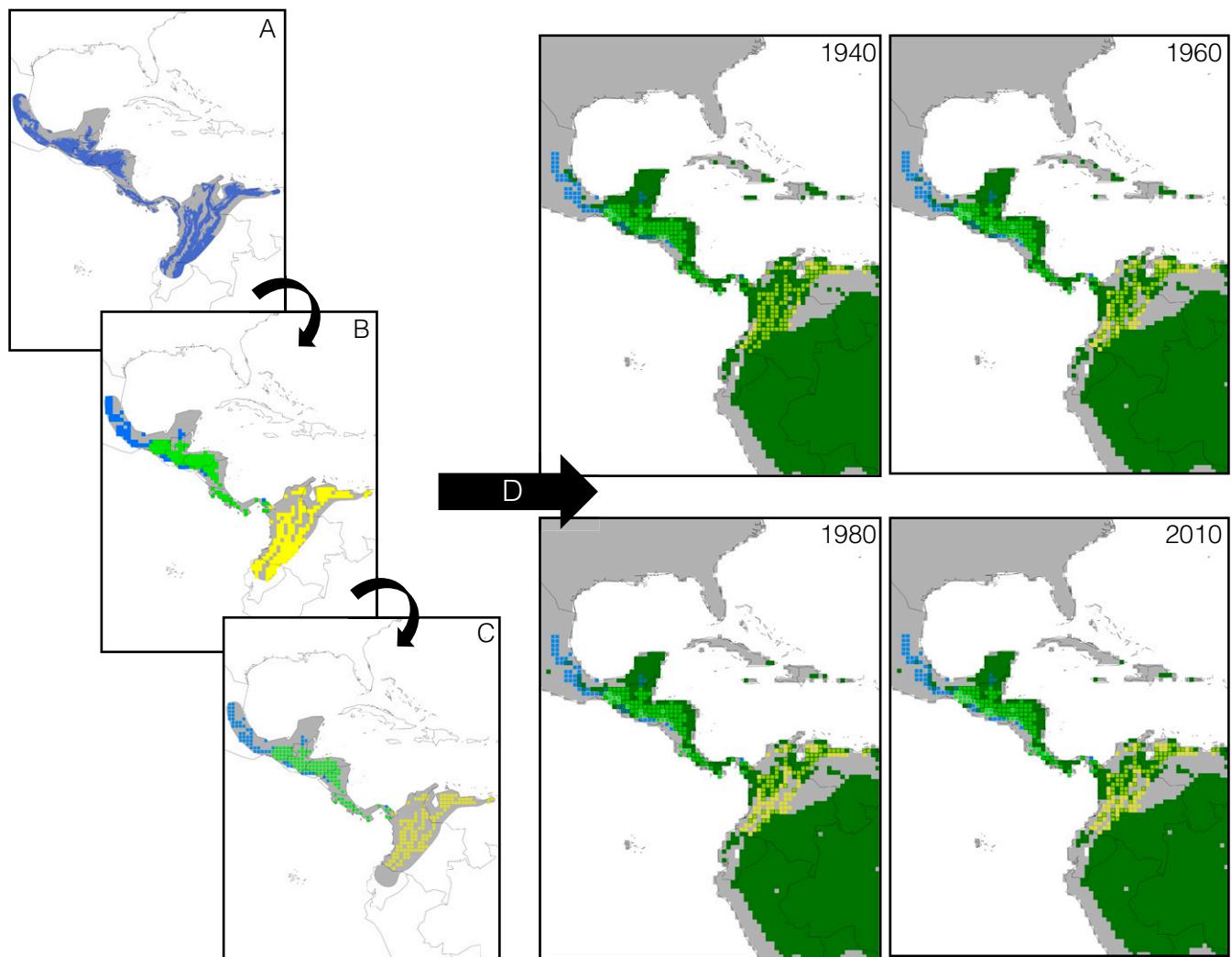


Fig. S5. Conceptual model of estimating changes in land-use patterns using the HYDE 3.1 database (53–55). (A) First, we identified cells ($0.5^\circ \times 0.5^\circ$) in the nonbreeding distribution of *Vermivora* warblers containing land 200–2,400 m above sea level. (B) We then characterized cells based on their geographic location and our understanding of the nonbreeding distribution of *Vermivora* warblers as being likely to affect blue-winged warblers (blue cells + lime green cells), Great Lakes breeding populations of golden-winged warblers (lime green cells), or Appalachian Mountains breeding populations of golden-winged warblers (yellow cells). (C) We then eliminated cells that were outside the known historical nonbreeding distribution of *Vermivora* (41). Finally, we extracted modeled land-use characteristics from each cell that overlapped with our mask (C) in 5-y increments from 1940 to 2010 (D). Here, we show only forest-dominated cells (dark green cells) in 1940, 1960, 1980, and 2010 (D) overlaid with a partially transparent mask (C) representing the nonbreeding distribution of different groups of *Vermivora* warblers.

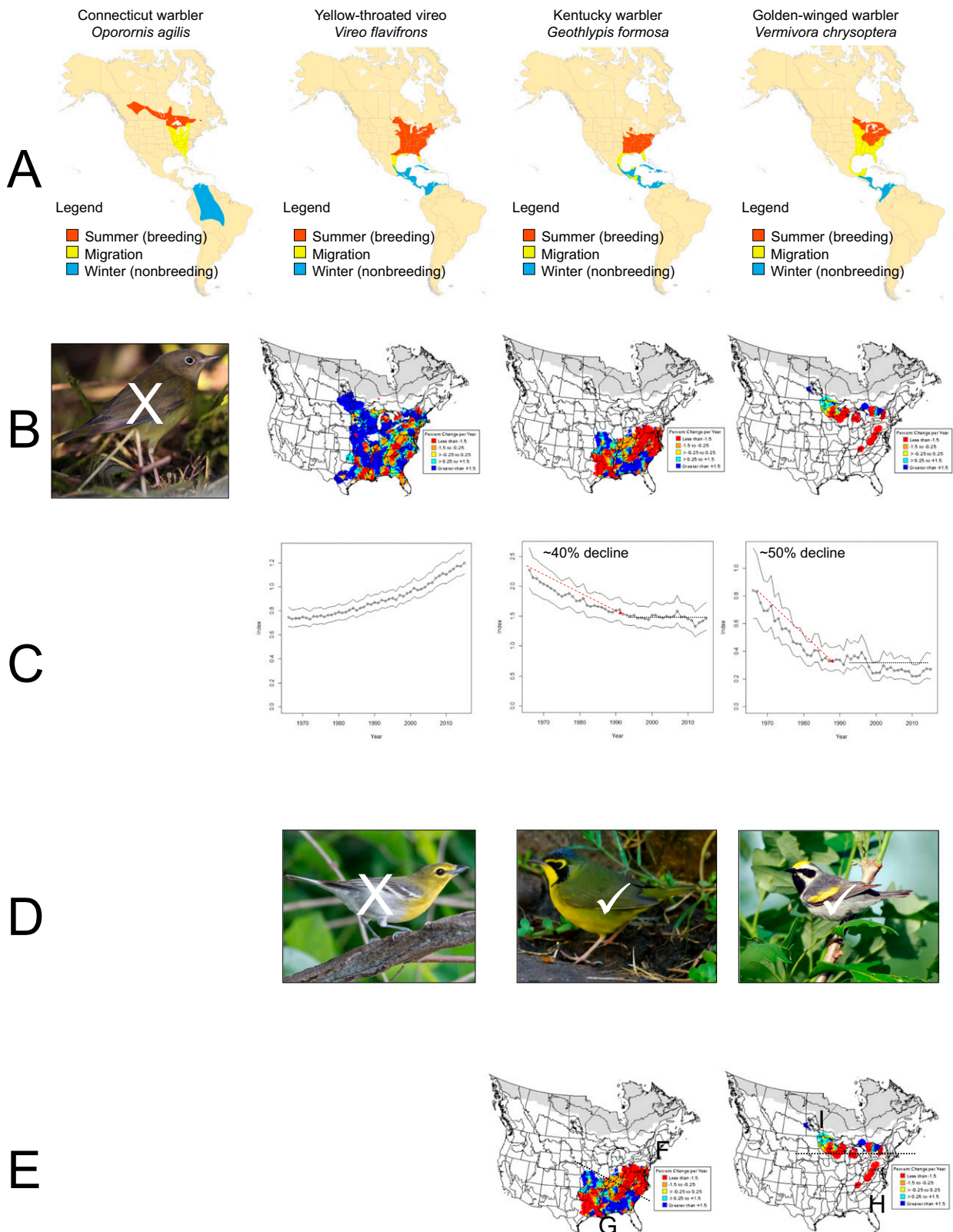


Fig. S6. Conceptual model used to identify other species (Table S2) that may experience similar limiting factors as golden-winged warblers due to strong migratory connectivity. (A) We visually inspected the annual distribution of Nearctic-Neotropical migrant songbird species and identified those that had relatively broadly dispersed breeding distributions and nonbreeding distributions in Central America and South America (similar to golden-winged warblers). (B) We visually inspected the Breeding Bird Survey trend maps (44) for the species meeting the criteria in A and selected species that exhibited regionally specific population trends. (C) Using the survey-wide population trends (44) estimated by the Breeding Bird Survey, we identified species that showed declines from the beginning of monitoring (~1966) to ~1990 before stabilizing (similar to golden-winged warblers). In this example, Connecticut warblers (*Oporornis agilis*) did not occur in Central America during the nonbreeding period, so they were eliminated from consideration as a species that may exhibit similar nonbreeding population structure and migratory connectivity as golden-winged warblers. Yellow-throated vireos (*Vireo flavifrons*) wintered in both Central America and South America and exhibited regional patterns in breeding population trends, but were eliminated from consideration as a species that we would predict to have strong migratory connectivity similar to golden-winged warblers because the range-wide population trend was stable until ~1985, when it began to increase. Kentucky warblers (*Geothlypis formosa*) wintered in both Central America and South America, exhibited regional patterns in breeding population trends, and showed range-wide patterns of declines from 1966 to 1990 with stable trends thereafter. (D) Kentucky warblers show many of the same signals of strong migratory connectivity as golden-winged warblers. (E) Therefore, we predict a migratory divide in Kentucky warblers, with individuals in declining, northeastern populations (F) occurring in South America and stable or increasing southwestern populations (G) occurring in Central America during the nonbreeding period reflecting the nonbreeding structure of declining (H) and numerically stable (I) populations of golden-winged warblers. Range maps are adapted from BirdLife International (45). Photo of Connecticut warbler courtesy of Flickr/Aaron Maizlish. Photo of yellow-throated vireo courtesy Flickr/Matt Stratmoen. Photo of Kentucky warbler courtesy of Flickr/Andy Reago and Chrissy McClarren.

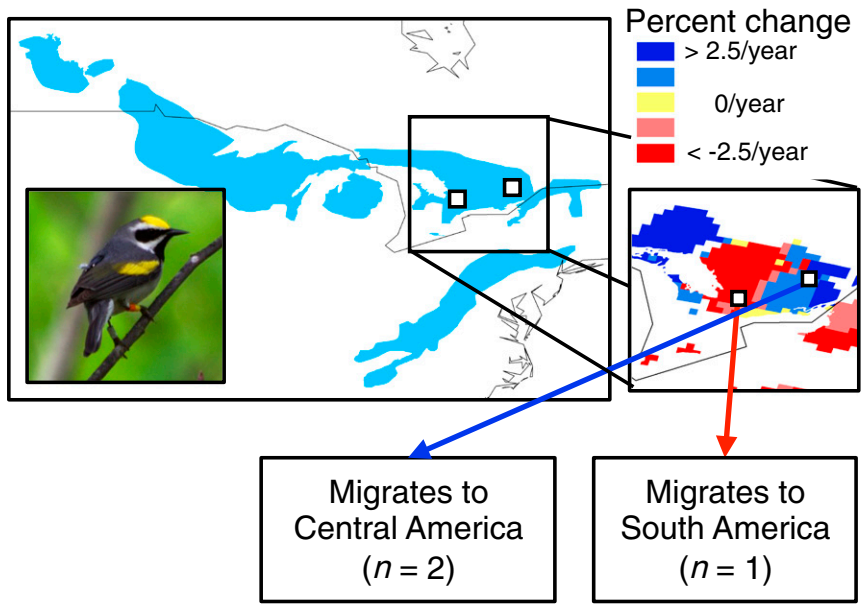


Fig. S7. Breeding distribution of golden-winged warblers (blue) with details of the eastern portion of the Great Lakes (BCR 12) population (*Inset*) showing more detailed population trends. Sites where we deployed geolocators are denoted with white squares. Range maps adapted from BirdLife International (45).

Table S1. Transition windows and total numbers of transitions (i.e., sunrises, sunsets) used to create nonbreeding probability density functions for *Vermivora* warblers

Bird ID	Deployment year	Transitions span	Total no. of transitions used	Full track?	Species	Deployment site latitude	Deployment site longitude	Nonbreeding latitude	Nonbreeding longitude	Probability
DMG03	2015	Dec 1 to Jan 15	82	N	GW	51.535	-100.581	15.9893	-85.386	0.005575
ILB04	2015	Jan 1 to Feb 29	110	Y	BW	37.816	-89.463	21.4972	-87.8896	0.005323
ILB06	2015	Jan 1 to Feb 29	110	Y	BW	37.816	-89.463	21.4972	-87.3889	0.005114
ILB08	2015	Jan 1 to Feb 29	114	Y	BW	37.816	-89.463	17.9922	-93.3976	0.006060
ILB18	2015	Jan 1 to Feb 29	115	Y	BW	39.407	-88.161	21.4972	-87.8896	0.005246
KYB14	2015	Sep 20 to Oct 23	65	N	BW	36.913	-83.562	20.9965	-87.3889	0.004951
MAB05	2015	Jan 1 to Feb 29	112	Y	BW	42.343	-72.568	10.4814	-74.8709	0.004974
MAB06	2015	Jan 1 to Feb 29	114	Y	BW	42.343	-72.568	14.9879	-83.3831	0.009560
MAB09	2015	Jan 1 to Feb 29	117	Y	BW	42.343	-72.568	20.9965	-86.8882	0.006007
MAB12	2015	Jan 1 to Feb 29	116	Y	BW	42.343	-72.568	14.9879	-83.3831	0.008518
MIB02	2015	Jan 1 to Feb 29	112	Y	BW	43.948	-84.267	20.9965	-86.8882	0.006974
MIB05	2015	Feb 11 to Mar 18	70	N	BW	42.615	-85.41	21.1235	-86.9527	0.005591
MIB12	2015	Jan 1 to Feb 29	110	Y	BW	42.615	-85.41	21.4972	-87.3889	0.006442
MIB14	2015	Jan 1 to Feb 29	96	Y	BW	42.615	-85.41	20.9965	-89.3918	0.005409
MIG01	2015	Jan 1 to Feb 29	105	Y	GW	43.948	-84.267	14.9879	-83.3831	0.005125
MIH02	2015	Jan 1 to Feb 29	113	Y	H	43.948	-84.267	20.9965	-88.3904	0.004580
MN03*	2013	Sep 14 to Sep 28	28	Y	GW	46.533	-93.407	14.4871	-85.386	0.004360
MN05*	2013	Jan 1 to Feb 28	110	Y	GW	46.533	-93.407	15.4886	-84.3846	0.004582
MN06*	2013	Jan 1 to Feb 28	107	Y	GW	46.533	-93.407	15.4886	-84.3846	0.003474
MN11*	2013	Jan 1 to Feb 28	103	Y	GW	46.533	-93.407	15.9893	-85.386	0.007540
MN12*	2013	Jan 1 to Feb 28	109	Y	GW	46.533	-93.407	16.9907	-88.8911	0.005720
MN14*	2013	Jan 1 to Feb 26	94	Y	GW	46.533	-93.407	14.9879	-83.3831	0.005082
MN14	2015	Nov 6 to Jan 10	122	Y	GW	46.533	-93.407	15.4886	-84.3846	0.004282
MN15*	2013	Dec 27 to Jan 6	20	N	GW	46.533	-93.407	15.9893	-85.3860	0.003221
MN16*	2013	Jan 1 to Feb 28	100	Y	GW	46.533	-93.407	14.9879	-83.8839	0.005006
MN20*	2013	Jan 1 to Feb 28	109	Y	GW	46.533	-93.407	15.9893	-85.3860	0.006177
MN25*	2014	Jan 1 to Feb 28	133	Y	GW	46.533	-93.407	15.4886	-84.3846	0.005637
MN29*	2014	Jan 1 to Feb 28	112	Y	GW	46.533	-93.407	14.9879	-83.3831	0.005051
MN29	2015	Nov 1 to Dec 28	113	N	GW	46.533	-93.407	14.9879	-83.3831	0.004626
MN36*	2014	Jan 1 to Feb 28	115	Y	GW	46.533	-93.407	17.4915	-90.3932	0.008099
MN36	2015	Jan 1 to Feb 29	118	Y	GW	46.533	-93.407	16.9907	-88.3904	0.005714
NCB01	2015	Jan 1 to Feb 29	115	Y	BW	36.412	-81.655	20.9965	-86.8882	0.005368
ONB02	2015	Jan 1 to Feb 29	104	Y	BW	44.003	-79.123	21.4972	-87.3889	0.006879
ONB05	2015	Jan 1 to Feb 29	117	Y	BW	44.7	-79.545	20.9965	-86.8882	0.006027
ONG03	2015	Jan 1 to Feb 29	107	Y	GW	44.641	-76.343	14.9879	-83.3831	0.007138
ONG05	2015	Jan 1 to Feb 29	112	Y	GW	44.641	-76.343	14.9879	-83.3831	0.006794
ONG10	2015	Jan 1 to Feb 29	105	Y	GW	44.7	-79.545	10.9821	-73.3687	0.004923
PA05*	2014	Jan 1 to Feb 28	108	Y	GW	41.38	-75.18	11.9835	-69.8637	0.005327
PA11*	2014	Jan 1 to Feb 28	115	Y	GW	41.38	-75.18	9.9806	-63.8550	0.006809
PAB01	2015	Jan 1 to Feb 29	118	Y	BW	40.995	-77.701	20.9965	-89.3918	0.005524
PAB03	2015	Jan 1 to Feb 29	115	Y	BW	40.995	-77.701	20.9965	-86.8882	0.006134
PAB05	2015	Jan 1 to Feb 29	111	Y	BW	40.995	-77.701	21.4972	-87.3889	0.005295

Table S1. Cont.

Bird ID	Deployment year	Transitions span	Total no. of transitions used	Full track?	Species	Deployment site latitude	Deployment site longitude	Nonbreeding latitude	Nonbreeding longitude	Probability
PAB07	2015	Jan 1 to Feb 29	111	Y	BW	40.995	-77.701	18.9936	-90.8940	0.005835
PAG12	2015	Jan 1 to Feb 29	105	Y	GW	40.995	-77.701	11.9835	-69.8637	0.005171
PAH01	2015	Jan 1 to Feb 29	119	Y	H	40.995	-77.701	10.9821	-73.8694	0.004082
PAH06	2015	Jan 1 to Feb 29	110	Y	H	40.995	-77.701	11.9835	-71.8665	0.004909
RLG16	2015	Jan 1 to Feb 11	80	N	GW	46.533	-93.407	15.9893	-85.3860	0.002996
RLG23	2015	Jan 1 to Feb 29	112	Y	GW	46.533	-93.407	15.9893	-85.3860	0.004066
RLGF15 [†]	2015	Jan 1 to Feb 29	112	Y	GW	46.533	-93.407	14.4871	-83.8839	0.006869
RMG02	2015	Jan 1 to Feb 29	111	Y	GW	51.024	-99.941	15.4886	-84.3846	0.005192
SHG07	2015	Jan 1 to Feb 29	117	Y	GW	45.517	-93.699	9.4799	-79.3774	0.004460
SLG12	2015	Jan 1 to Feb 29	114	Y	GW	49.624	-96.307	15.9893	-85.3860	0.005836
SLG18	2015	Jan 1 to Feb 29	108	Y	GW	49.624	-96.307	14.9879	-83.8839	0.006849
TAG07	2015	Jan 1 to Feb 29	114	Y	GW	46.987	-95.611	17.4915	-90.3932	0.006745
TAG09	2015	Jan 1 to Feb 29	113	Y	GW	46.987	-95.611	15.4886	-86.3875	0.004290
TAG14	2015	Jan 1 to Feb 29	115	Y	GW	46.987	-95.611	14.9879	-83.3831	0.004864
TN05*	2013	Jan 1 to Feb 28	116	Y	GW	36.291	-84.302	11.4828	-72.3673	0.005868
TN06*	2013	Jan 1 to Feb 28	115	Y	GW	36.291	-84.302	15.9893	-85.3860	0.005575
TN09*	2013	Jan 1 to Feb 28	113	Y	GW	36.291	-84.302	11.9835	-69.8637	0.005270
TN10*	2013	Jan 1 to Feb 28	105	Y	GW	36.291	-84.302	11.9835	-71.3658	0.004930
TN13*	2014	Jan 1 to Feb 28	111	Y	GW	36.291	-84.302	11.9835	-71.3658	0.005333
TN16*	2013	Jan 1 to Feb 28	116	Y	GW	36.291	-84.302	11.9835	-71.8665	0.005747
TNB03	2015	Jan 1 to Feb 29	111	Y	BW	35.927	-84.404	18.9936	-90.894	0.004836
TNB09	2015	Jan 1 to Feb 29	111	Y	BW	36.62	-87.515	21.4972	-87.8896	0.006032
TNG13	2015	Jan 1 to Feb 29	107	Y	GW	36.291	-84.302	11.9835	-71.3658	0.005063
VAG01	2015	Jan 1 to Feb 29	117	Y	GW	38.26	-79.627	11.9835	-71.3658	0.005735
VAG02	2015	Jan 1 to Feb 29	113	Y	GW	38.26	-79.627	11.9835	-69.8637	0.005708
WIB05	2015	Jan 1 to Feb 29	113	Y	BW	44.319	-90.131	20.9965	-86.8882	0.006157
WIB11	2015	Feb 2 to Feb 24	40	Y	BW	44.319	-90.131	20.9965	-89.8925	0.004362
WIB19	2016	Jan 1 to Feb 28	91	Y	BW	44.319	-90.131	18.4929	-92.3961	0.004500
WIB19	2016	Jan 30 to Mar 9	70	Y	BW	44.319	-90.131	21.4972	-87.3889	0.005115
WIG01	2015	Jan 1 to Feb 29	119	Y	GW	44.319	-90.131	14.9879	-83.3831	0.005170
WIG02	2015	Jan 1 to Feb 29	114	Y	GW	44.319	-90.131	14.9879	-83.3832	0.006351
WIH03	2015	Jan 1 to Feb 29	87	Y	H	44.319	-90.131	18.9936	-90.8940	0.003502
WIH03	2016	Jan 1 to Feb 28	111	Y	H	44.319	-90.131	15.9893	-85.3860	0.005575

Deployment year is the year the specific geolocator was attached to an individual. Some tags failed before recovery, and we were therefore unable to recover a full track of those individuals. Species reference the apparent species (based on plumage phenotype), with "GW" representing the golden-winged warbler, "BW" representing the blue-winged warbler, and "H" representing a phenotypic hybrid (based on plumage characteristics). The longitude and latitude where individuals were marked with geolocators is provided, along with the extracted longitude and latitude of the highest probability cell in the nonbreeding probability density function. The highest probability of the nonbreeding probability density function is presented, and values may be compared for a relative measure of error around latitude and longitude estimates. Briefly, higher probabilities are associated with spatially constrained (i.e., tighter) probability density functions. All individuals are males unless otherwise noted. N, no; Y, yes.

*Data reanalyzed from Kramer et al. (ref. 29; <https://conservancy.umn.edu/handle/11299/183086>).

[†]Female golden-winged warbler.

Table S2. Common name, species name, and distribution and trend data for Nearctic-Neotropical migratory bird species (Passeriformes)

Species name (common)	Species name (Latin)	Nonbreeding range includes South America	Nonbreeding range includes Central America	Nonbreeding range includes North America and South America	Regional variation in breeding population trends?	Survey-wide trend 1966–1990	Survey-wide trend 1991–2015
Olive-sided flycatcher	<i>Contopus cooperi</i>	X	X	X	No	Declining	Stable after 2000
Western wood-pewee	<i>Contopus sordidulus</i>	X	X	X	Yes; N declining, S increasing	Declining	Declining
Eastern wood-pewee	<i>Contopus virens</i>	X	X	X	Yes; E declining, W increasing	Declining	
Yellow-bellied flycatcher	<i>Empidonax flaviventris</i>	X	X	X	Yes; E declining, W, increasing	Stable	Stable
Acadian flycatcher	<i>Empidonax virens</i>	X	X	X			
Willow flycatcher	<i>Empidonax traillii</i>	X	X	X			
Alder flycatcher	<i>Empidonax alhorum</i>	X	X	X			
Least flycatcher	<i>Empidonax minimus</i>	X	X	X			
Hammond's flycatcher	<i>Empidonax hammondi</i>	X	X	X			
Gray flycatcher	<i>Empidonax wrightii</i>	X	X	X			
Dusky flycatcher	<i>Empidonax oberholseri</i>	X	X	X			
Pacific-slope flycatcher	<i>Empidonax occident</i>	X	X	X			
Cordilleran flycatcher	<i>Empidonax difficilis</i>	X	X	X			
Ash-throated flycatcher	<i>Myiarchus cinerascens</i>	X	X	X			
Great-crested flycatcher	<i>Myiarchus crinitus</i>	X	X	X	Complicated; E stable, W declining, but smaller scale differences	Stable	Stable
Western kingbird	<i>Tyrannus verticalis</i>	X	X	X			
Eastern kingbird	<i>Tyrannus tyrannus</i>	X	X	X			
Scissor-tailed flycatcher	<i>Tyrannus forficatus</i>	X	X	X			
Black-capped vireo	<i>Vireo atricapilla</i>	X	X	X			
White-eyed vireo	<i>Vireo griseus</i>	X	X	X			
Bell's vireo	<i>Vireo bellii</i>	X	X	X			
Gray vireo	<i>Vireo vicinior</i>	X	X	X			
Yellow-throated vireo	<i>Vireo flavifrons</i>	X	X	X	Yes; E declining, W increasing	Increasing	Increasing
Cassin's vireo	<i>Vireo cassinii</i>	X	X	X			
Blue-headed vireo	<i>Vireo solitarius</i>	X	X	X			
Plumbeous vireo	<i>Vireo plumbeus</i>	X	X	X			
Philadelphia vireo	<i>Vireo philadelphicus</i>	X	X	X			
Warbling vireo	<i>Vireo gilvus</i>	X	X	X			
Red-eyed vireo	<i>Vireo olivaceus</i>	X	X	X			
Northern rough-winged swallow	<i>Stelgidopteryx serripennis</i>	X	X	X			
Purple martin	<i>Progne subis</i>	X	X	X			
Tree swallow	<i>Tachycineta bicolor</i>	X	X	X			
Violet-green swallow	<i>Tachycineta thalassina</i>	X	X	X			
Barn swallow	<i>Hirundo rustica</i>	X	X	X			
Bank swallow	<i>Riparia riparia</i>	X	X	X			
Cliff Swallow	<i>Petrochelidon pyrrhonota</i>	X	X	X			
Veery	<i>Catharus fuscescens</i>	X	X	X			
Gray-cheeked thrush	<i>Catharus minimus</i>	X	X	X			
Swainson's thrush	<i>Catharus ustulatus</i>	X	X	X	Whole range not accounted for; complex; NW declining, central increasing, NE declining	Declining	Stable

Table S2. Cont.

Species name (common)	Species name (Latin)	Nonbreeding range includes South America	Nonbreeding range includes Central America and South America	Nonbreeding range includes breeding population trends?	Survey-wide trend 1966–1990	Survey-wide trend 1991–2015
Hermit thrush	<i>Catharus guttatus</i>	X				
Wood thrush	<i>Hyloichla mustelina</i>	X				
Gray catbird	<i>Dumetella carolinensis</i>	X				
Ovenbird	<i>Seiurus aurocapilla</i>	X				
Worm-eating warbler	<i>Helminthos vermivorum</i>	X	X	Yes; E decreasing, W increasing Full range not accounted for	Stable	Increasing
Louisiana waterthrush	<i>Parkesia motacilla</i>	X	X		Stable	Increasing
Northern waterthrush	<i>Parkesia noveboracensis</i>	X	X	Yes; E declining, W increasing	Declining	Stable
Golden-winged warbler	<i>Vermivora chrysoptera</i>	X	X			
Blue-winged warbler	<i>Vermivora cyanoptera</i>	X	X			
Black-and-white warbler	<i>Mniotilta varia</i>	X	X	Yes; E declining, W increasing/stable	Declining	Declining
Prothonotary warbler	<i>Protonotaria citrea</i>	X	X	Complex; declining SW and SE, increasing N and central	Declining	Stable
Swainson's warbler	<i>Limnithlypis swainsonii</i>	X				
Tennessee warbler	<i>Oreothlypis peregrina</i>	X	X		Stable	Stable
Orange-crowned warbler	<i>Oreothlypis celata</i>	X		Full range not accounted for		
Lucy's warbler	<i>Oreothlypis luciae</i>	X				
Nashville warbler	<i>Oreothlypis ruficapilla</i>	X				
Virginia's warbler	<i>Oreothlypis virginiae</i>	X				
Connecticut warbler	<i>Oporornis agilis</i>	X				
MacGillivray's warbler	<i>Geothlypis tolmiei</i>	X				
Mourning warbler	<i>Geothlypis philadelphia</i>	X	X	Complex; S increasing, N declining	Declining	Stable after 2000
Kentucky warbler	<i>Geothlypis formosa</i>	X	X	Yes; NE declines, S increases	Declining	Stable
Common yellowthroat	<i>Geothlypis trichas</i>	X				
Hooded warbler	<i>Setophaga citrina</i>	X				
American redstart	<i>Setophaga ruticilla</i>	X	X	Complex; central stable/increasing, E and W declining	Declining	Stable after 2000
Cape May warbler	<i>Setophaga tigrina</i>	X				
Cerulean warbler	<i>Setophaga cerulean</i>	X				
Northern parula	<i>Setophaga americana</i>	X				
Magnolia warbler	<i>Setophaga magnolia</i>	X	X	Range not fully accounted for	Stable	Stable
Bay-breasted warbler	<i>Setophaga castanea</i>	X	X	Yes; S declines, N increasing	Stable	Increasing
Blackburnian warbler	<i>Setophaga fusca</i>	X	X	Complex; declining E and W, stable central	Declining	Declining
Yellow warbler	<i>Setophaga petechia</i>	X	X			
Chestnut-sided warbler	<i>Setophaga pensylvanica</i>	X				
Blackpoll warbler	<i>Setophaga striata</i>	X				
Black-throated blue warbler	<i>Setophaga caerulescens</i>	X				
Palm warbler	<i>Setophaga palmarum</i>	X				
Audubon's warbler	<i>Setophaga coronata auduboni</i>	X				
Myrtle's warbler	<i>Setophaga coronata coronata</i>	X				
Yellow-throated warbler	<i>Setophaga dominica</i>	X				
Prairie warbler	<i>Setophaga discolor</i>	X				
Black-throated gray warbler	<i>Setophaga nigrescens</i>	X				
Townsend's warbler	<i>Setophaga townsendi</i>	X				

Table S2. Cont.

Species name (common)	Species name (Latin)	Nonbreeding range includes South America	Nonbreeding range includes Central America	Nonbreeding range includes Central and South America	Regional variation in breeding population trends?	Survey-wide trend 1966–1990	Survey-wide trend 1991–2015
Hermit warbler	<i>Setophaga occidentalis</i>		X				
Golden-cheeked warbler	<i>Setophaga chrysoparia</i>		X				
Black-throated green warbler	<i>Setophaga virens</i>	X		X	No		
Canada warbler	<i>Cardellina canadensis</i>	X					
Wilson's warbler	<i>Cardellina pusilla</i>		X				
Yellow-breasted chat	<i>Icteria virens</i>	X					
Summer tanager	<i>Piranga rubra</i>	X		X	No		
Scarlet tanager	<i>Piranga olivacea</i>	X					
Western tanager	<i>Piranga ludoviciana</i>		X				
Rose-breasted grosbeak	<i>Pheucticus ludovicianus</i>	X	X	X	Yes; E declining, W stable	Declining	Stable
Black-headed grosbeak	<i>Pheucticus melanocephalus</i>		X				
Blue grosbeak	<i>Passerina caerulea</i>		X				
Lazuli bunting	<i>Passerina amoena</i>		X				
Indigo bunting	<i>Passerina cyanea</i>		X				
Painted bunting	<i>Passerina ciris</i>		X				
Dickcissel	<i>Spiza Americana</i>	X		X	No		
Bobolink	<i>Dolichonyx oryzivorus</i>	X					
Orchard oriole	<i>Icterus spurius</i>	X	X	X	Yes; N stable/increasing, S declining	Declining	Stable
Bulluck's oriole	<i>Icterus bullockii</i>		X				
Baltimore oriole	<i>Icterus galbula</i>	X		X	Yes; S stable, N declining	Declining	Declining

Information on nonbreeding distribution was gathered from BirdLife International (45). Trend data were retrieved from the Breeding Bird Survey database (43, 44). Orange-highlighted entries represent species we predict may exhibit strong migratory connectivity as described in golden-winged warblers in this study based on characteristics of population trends and geographical distributions described in detail in *Materials and Methods*. E, east; N, north; S, south; W, west.