TITLE: Exposure to risk factors experienced during migration is not associated with recent *Vermivora* warbler population trends

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STRUCTURED ABSTRACT—

Context: Understanding the factors limiting populations of animals is critical for effective conservation. Determining which factors limit populations of migratory species can be especially challenging because of their reliance on multiple, often geographically distant regions during their annual cycles.

Objectives: We investigated whether distribution-wide variation in recent breeding population trends was more strongly associated with exposure to risk factors experienced during migration (i.e., natural and anthropogenic threats often associated with increased mortality or carry-over effects) or factors associated with breeding and nonbreeding areas in golden-winged warblers (*Vermivora chrysoptera*) and blue-winged warblers (*V. cyanoptera*), two Nearctic-Neotropical migrants experiencing regionally variable population trends.

Methods: We used geolocator data from 85 *Vermivora* warblers ($n = 90$ geolocator tracks) tracked from North American breeding locations and Central American nonbreeding locations from 2013–2017 to determine variation in space use among populations. We assessed whether differences in space use among populations of *Vermivora* warblers during migration were associated with exposure to migration risk-factors and whether increased relative exposure to migration risk factors was associated with population declines at regional and subregional scales.

Results: Regional and subregional populations of *Vermivora* warblers exhibited variation in space use and exposure to anthropogenic and natural risk-factors. However, we found no evidence that recent variation in population trends of *Vermivora* warblers was associated with risk-factors experienced by different populations during migration. Instead, factors associated with land cover-types in breeding and nonbreeding areas were more strongly associated with recent population trends.

Conclusions: Understanding how populations of migratory birds are affected by factors experienced during migration is critical for their conservation. We did not find evidence that variation in exposure to migration risk-factors is associated with recent regional or subregional variation in *Vermivora* warbler population trends. Consequently, our results suggest that efforts to reverse ongoing population declines of *Vermivora* warblers may be more effective if directed toward conservation actions targeting limiting factors within the breeding and nonbreeding periods versus those directed at conditions encountered during migration. We caution that geographic variation in projected land-use change may differentially affect areas used by different populations of *Vermivora* warblers during migration, posing a potential threat to these species in the future.

Keywords: annual cycle, bird migration, geolocators, limiting factors

INTRODUCTION—

Migratory animals face an array of threats throughout their annual cycle that may affect their survival and productivity. Identifying which factors contribute to regulating populations of migratory animals is inherently challenging because of their reliance on multiple, often geographically distant regions (Webster et al. 2002, Newton 2006, Sherry

2018). Populations of migratory species can be limited both directly and indirectly by any number of factors affecting the survival of adults or production and survival of young at breeding sites (Milner-Gulland et al. 2003, Flockhart et al. 2015), the survival of individuals at nonbreeding sites (Mihoub et al. 2010, Kramer et al. 2018a), and the survival of individuals along migration routes between breeding and nonbreeding areas (Berger 2004, Hewson et al. 2016). However, quantifying the relative importance of limiting factors experienced throughout the annual cycle on the abundance or trends of many populations of migratory species remains a challenge due to the often-limited ability to monitor individuals throughout the annual cycle (McKinnon and Love 2018). Moreover, identifying whether distinct populations are regulated by the same or population-specific factors is critical for directing limited resources to implement effective conservation strategies (Hewson et al. 2016, Studds et al. 2017, Kramer et al. 2018a, Wilson et al. 2018).

In many species, limiting factors occur during breeding or nonbreeding seasons when individuals are relatively sedentary and where individuals are reproducing and/or resident for a period usually longer than the migratory portions of their annual cycle (Probst 1986, Milner-Gulland et al. 2003, Flockhart et al. 2015, Heinsohn et al. 2015). However, migration is thought to be an exceptionally challenging portion of the annual cycle for many migratory species and a period with elevated mortality rate relative to sedentary periods of the annual cycle (Nicholson et al. 1997, Sillett and Holmes 2002). Relatively greater rates of mortality during migration are associated with population declines in some migratory species (e.g., Hewson et al. 2016). Severe weather events (Newton 2007, Dionne et al. 2008, O'Shea et al.

2016, Yang et al. 2021) and collisions with communications towers, buildings, and wind turbines are known to cause mortality in migrating birds (Loss et al. 2015). Estimated mortality of migratory birds colliding with buildings (372–1,030 million birds in the US and Canada, annually; Machtans et al. 2013, Loss et al. 2014), communications towers (~7 million birds in the US; Longcore et al. 2013), and wind turbines (< 1 million birds in the US, annually; Smallwood 2013, Loss et al. 2013) vary by orders of magnitude and are staggering. However, the effects of natural and anthropogenic mortality on the overall population trends of many migratory bird species are poorly understood and an area of rapidly developing research (e.g., Buchnan et al. 2022).

Identifying variation in the cumulative exposure of individuals or populations to different migration risk-factors (i.e., those experienced away from areas of prolonged residency) has historically been challenging for many species (Marra et al. 2015). Advancements in tracking technology (e.g., light-level geolocators, Global Positioning System [GPS] tags, and satellite/cellular tags) recently have made it possible to collect large geographic-scale movement data from many smaller species (e.g., songbirds and insects; Stutchbury et al. 2009, Knight et al. 2019). These advances provide novel opportunities to identify factors limiting populations of some of the smallest migratory vertebrate and invertebrate species and potentially improve conservation strategies.

We assessed whether variation in exposure to documented migration risk-factors associated with increased mortality rate (i.e., direct effects) and/or decreased future survival or productivity (i.e., indirect, carry-over effects wherein conditions experienced by an individual during one period of the annual cycle affect their fitness in another period; e.g., Legagneux et al. 2012) in migratory birds was associated with regional population trends in *Vermivora* wood-warblers (Parulidae). The genus *Vermivora* comprises a complex of two extant Nearctic-Neotropical migrant warbler species (golden-winged warblers [*Vermivora chrysoptera*] and blue-winged warblers [*V. cyanoptera*]) that are extremely closely related and exhibit a range of shared phenotypes (Toews et al. 2016, Kramer et al. 2020). These small (~9 g) songbirds breed and migrate throughout the deciduous forests of eastern North America (Fig. 1; Rosenberg et al. 2016, Kramer et al. 2017) and during the nonbreeding period, golden-winged warblers occur in Central America and northern South America whereas blue-winged warblers primarily occur in Central America (Kramer et al. 2017, 2018a; Fig. 1).

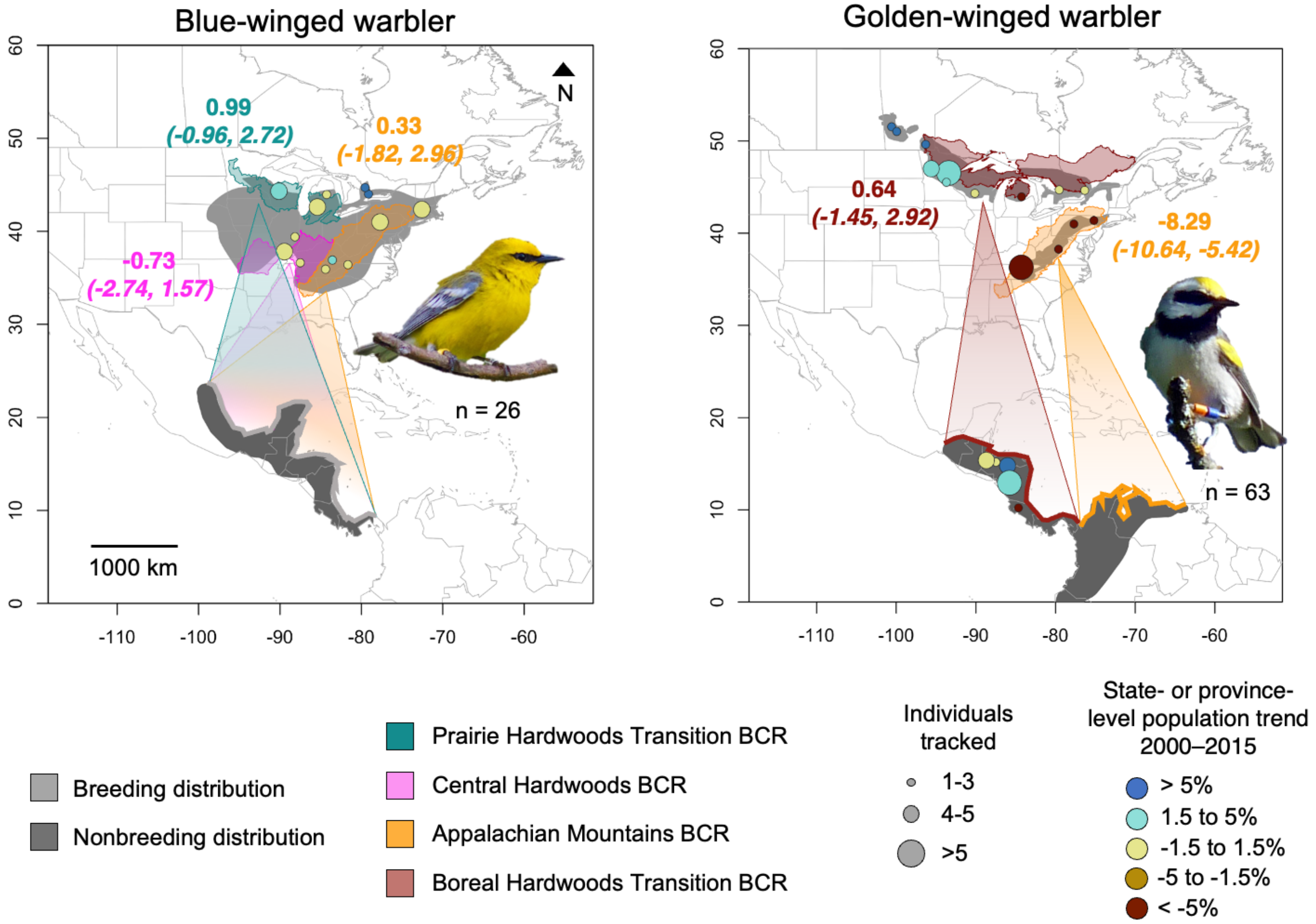

Figure 1. Breeding (light gray) and nonbreeding (dark gray) distributions of blue-winged warblers (*Vermivora cyanoptera*; left) and golden-winged warblers (*V. chrysoptera*; right). Sites where geolocators were deployed and recovered from *Vermivora* warblers are denoted by colored circles. The size of circles corresponds to the number of individuals tracked from that site. The color of circles indicates the state- or province- level population trend from 2000–2015 at breeding distribution sites or the average state- or province-level breeding population trend from 2000–2015 of individuals marked at nonbreeding distribution sites based on Breeding Bird Survey data (BBS; BBS Regional Trend Analysis Form). Shaded polygons delineate Bird Conservation Regions (BCRs) that we used to aggregate sites into regional populations. Shaded areas linking breeding and nonbreeding regions indicate the general migratory connectivity of populations but do not represent migratory routes. Geolocators from deployment sites in Central America are from Bennett et al. (2019b). Geolocators from deployment sites in the US and Canada are from Kramer et al. (2018b)

On the breeding grounds, these two species have overlapping distributions where they hybridize and produce viable young (Vallender et al. 2007a, Baiz et al. 2020, Toews et al. 2021). Populations of blue-winged warblers exhibit relatively weak migratory connectivity in which individuals from across the breeding distribution co-occur throughout Central America during the nonbreeding period (Kramer et al. 2018a). Conversely, golden-winged warblers exhibit strong migratory connectivity in which populations breeding throughout the Great Lakes region occur almost exclusively in Central America during the nonbreeding period whereas populations breeding in the Appalachian Mountains occur almost exclusively in northern South America (Kramer et al. 2018a; Fig. 1). Standardized annual surveys of breeding bird abundance across North America (i.e., Breeding Bird Survey [BBS]) suggest blue-winged warbler population trends have remained stationary (i.e., numerically stable) since the 1960s with little variation in population trends across their breeding distribution (1966–2016; Sauer et al. 2017, Kramer et al. 2018a). Conversely, golden-winged warbler populations declined since the 1960s (when BBS monitoring began; Sauer et al. 2017) until ~1990–2000. These declines resulted in a ~50% reduction in the abundance of golden-winged warblers over that period (Rosenberg et al. 2016). These historical declines were driven by the near extirpation of golden-winged warblers breeding in the Appalachian Mountains (Rosenberg et al. 2016) and were facilitated by extensive habitat loss in population-specific nonbreeding areas (Kramer et al. 2018a). However, the broad-scale conversion of forest to other cover types in regions of northern South America inhabited by golden-winged warblers during the sedentary nonbreeding period has stabilized since ~1990 relative to historical rates (i.e., since ~1940; Goldewijk et al. 2011). Yet, populations of golden-winged warblers continue to decline in the Appalachian Mountains (Fig. 1). Notably, blue-winged warblers across their distribution and golden-winged warblers breeding in the Great Lakes region have maintained stationary population trends. These differences in regional population trends suggest that the factors limiting blue-winged warbler populations and golden-winged warblers breeding in the Great Lakes region likely differ from those limiting golden-winged warblers breeding in the Appalachian Mountains. Population trends of *Vermivora* warblers also vary within broadly defined regional populations (i.e., at the scale of states and provinces) suggesting that the type of limiting factor and/or their intensity may differentially affect populations of *Vermivora* warblers at a subregional scale.

Golden-winged warblers in the Great Lakes region have relatively high rates of apparent reproductive success (Streby et al. 2016, 2018). Rates of reproductive success for golden-winged warblers breeding in the Appalachian Mountains vary among sites but golden-winged warblers at some sites reproduce at rates apparently sufficient to maintain populations or experience population growth (Lehman 2017, Aldinger 2018, McNeil 2019). If declining populations are adequately productive and wintering habitat loss has slowed or reversed in recent decades, then ongoing variation in regional and subregional population trends of *Vermivora* warblers might be linked to factors experienced during migration. Determining if factors during migration are associated with variable population trends requires identifying whether declining populations migrate through areas that could disproportionately affect survival or carry-over effects (Newton 2006). Relatively little is known about the movements of individual *Vermivora* warblers during seasonal migration (Bennett et al. 2017, Kramer et al. 2017, Bennett et al. 2019b), although preliminary evidence suggests populations of golden-winged warblers exhibit variation in space use during both autumn and spring migrations (i.e., strong migratory connectivity during migration; Kramer et al. 2017). The magnitude of variation in space use during migration among populations of *Vermivora* warblers and whether variation in space use is associated with differential exposure to migration risk-factors remains unknown.

Here, we used light-level geolocator (hereafter, geolocator) data to identify terrestrial areas where *Vermivora* warblers occurred during migration (i.e., stopover regions). We addressed four questions to assess the strength of association between migration risk-factors and past and future population trends of *Vermivora* warblers (Table 1). First, we assessed whether patterns of space use during migration differed among regional populations (defined by Bird Conservation Region [BCR]) and whether variation in space use during migration was associated with differential exposure to a suite of natural and anthropogenic migration risk-factors that could explain differences in regional population trends. Second, we quantified the relative importance of migration risk-factors versus breeding and nonbreeding period factors in models explaining variation in recent subregional *Vermivora* warbler population trends (i.e., 2000–2015). Third, we assessed whether migration risk-factors experienced within seasonal stopover regions bordering the Gulf of Mexico were important relative to breeding and nonbreeding factors in models describing recent variation in subregional population trends of *Vermivora* warblers. Migration risk-factors experienced by individuals immediately prior to navigating the Gulf of Mexico could have a disproportionate effect on populations if those risk-factors reduce the probability of individuals successfully navigating this barrier. Last, we investigated whether anthropogenic developmental potential differed between areas used by stationary or increasing versus declining populations of *Vermivora* warblers to characterize potential threats to these populations in the future (i.e., by 2030). We predicted that *Vermivora* warblers would exhibit both inter- and intraspecific variation in space use during migration and that variation in space use would lead to differential exposure to migration risk-factors between species and among populations. We predicted that populations of blue-winged warblers and stationary populations of golden-winged warblers would use similar areas during migration and be exposed to lower levels of migration risk-factors compared to declining populations of golden-winged warblers breeding in the Appalachian Mountains. We also expected projected future anthropogenic development to differentially affect populations of *Vermivora* warblers.

Table 1. Modeling approaches, response variables, and explanatory variables used to address primary research questions in this study. The variable "overall" was calculated by summing standardized individual migration risk-factor rasters (*n* = 8; assigning equal weight to all risk factors).

Research question	Modeling approach	Response variable(s)	Explanatory variable(s)
1. Do regional populations of *Vermivora* warblers (defined by Bird Conservation Region [BCR]) exhibit variation in exposure to different anthropogenic and natural migration risk-factors?	One-way analysis of variance (ANOVA) and *post hoc* Tukey test	Annual relative exposure to migration risk-factors (*n* = 9) within individuals' 25th percentile core-use areas (*n* = 81): forest and shrub cover, net change in forest cover 2000–2010, agricultural cover, human footprint, wind energy, communications towers, tornados, hurricanes, overall.	Species and Bird Conservation Region (BCR): blue-winged warblers (*n* = 3 BCRs; Prairie Hardwood Transition BCR [BW PHT], Central Hardwoods BCR [BW CH], Appalachian Mountains BCR [BW AM]); golden-winged warblers (*n* = 2 BCRs; Boreal Hardwood Transition BCR [GW BHT], Appalachian Mountains BCR [GW AM]).
2. Are migration risk-factors, or breeding and nonbreeding factors more strongly	Partial least squares (PLS) regression	Individuals' subregional (state- or province-level) Breeding Bird	Breeding factors (*n* = 3): forest and shrub cover, net change in forest cover

	associated with recent subregional population trends of *Vermivora* warblers?		Survey population trend ($n = 81$ individuals; $n = 15$ subregional populations; 2000–2015).	2000–2010, human footprint. Nonbreeding factors ($n = 3$): forest and shrub cover, net change in forest cover 2000–2010, human footprint. Annual relative exposure to migration risk-factors ($n = 8$): forest and shrub cover, net change in forest cover 2000–2010, agricultural cover, human footprint, wind energy, communications towers, tornados, hurricanes.
3.	Does seasonal relative exposure to migration risk-factors in stopover regions (adjacent to the Gulf of Mexico) explain additional variation in recent state- and province-level population trends of *Vermivora* warblers after controlling for breeding and nonbreeding factors?	Partial least squares (PLS) regression	Individuals' estimated state- or province-level Breeding Bird Survey population trend ($n = 81$ individuals; $n = 15$ subregional populations; 2000–2015).	Breeding factors ($n = 3$): forest and shrub cover, net change in forest cover 2000–2010, human footprint. Nonbreeding factors ($n = 3$): forest and shrub cover, net change in forest cover

			2000–2010, human footprint. Seasonal relative exposure to migration risk-factors ($n = 9$) prior to crossing the Gulf of Mexico: forest and shrub cover, net change in forest cover 2000–2010, agricultural cover, human footprint, wind energy, communications towers, tornados, hurricanes, overall.
4. Are there differences in the developmental suitability of areas used during migration by *Vermivora* warbler populations that are stationary or increasing versus populations that are declining?	Simple linear regression (*t*-tests)	Relative exposure to landscapes suitable for future conversion to anthropogenic land-use types ($n = 6$): solar energy, urban cover, agricultural cover, wind energy, biofuel, and mining.	Groups ($n = 2$) based on classification of individuals' estimated state- or province-level Breeding Bird Survey population trend ($n = 81$; 2000–2015; population trend estimate ≥ 0 = stationary and/or increasing, population trend estimate < 0 = declining).

METHODS—

Geolocator data collection—

We used published geolocator data from 90 individual *Vermivora* warblers (*n* = 96 geolocator tracks; 6 individuals were tracked for 2 years) collected from 2014–2018 (Kramer et al. 2018b, Bennett 2019). Geolocators record levels of ambient light data at regular intervals (usually 2–5 minutes), which can be used to estimate geographic location based on the seasonal variation in the timing and duration of sunlight across the globe (Hill and Braun 2001, Ekstrom 2004). Most of the geolocator data (76/96 tracks; 79%; Kramer et al. 2018b) were collected from 2014–2018 from *Vermivora* warblers at 26 sites spanning the breeding distributions of both blue- and golden-winged warblers (Fig. 1; Kramer et al. 2018b). These data were previously used to identify the nonbreeding dispersion and migratory connectivity of *Vermivora* breeding populations (Kramer et al. 2017, Kramer et al. 2018a). We also used geolocator data from 20 male golden-winged warblers (20 tracks) collected by Bennett et al. (2019b) from 5 sites in Central America (Fig. 1; Bennett 2019).

In total, we analyzed 90 geolocator tracks from 85 individual *Vermivora* warblers: 25 blue-winged warblers (*n* = 26 tracks) and 60 golden-winged warblers (*n* = 64 tracks; Table S1, S2). We defined regional populations based on the Bird Conservation Region (BCR) of an individual's breeding location for figures and in analyses of overlap during migration. However, several study areas occurred in BCRs on the periphery of a species' distribution and we assigned individuals at those sites to the nearest BCR containing other study sites and a greater proportion of the species' distribution (SI Methods). Overall, we classified blue-winged warblers into three regional populations: Prairie Hardwood Transition BCR (*n* = 7 individuals, *n* = 8 tracks), Central Hardwoods BCR (*n* = 5 individuals and tracks), and the Appalachian Mountains BCR (*n* = 12 individuals, *n* = 13 tracks). We classified golden-winged warblers into two regional populations: Boreal Hardwood Transition BCR (*n* = 49 individuals, *n* = 51 tracks) and Appalachian Mountains BCR (*n* = 12 individuals, *n* = 13 tracks). For subregional analyses, we classified warblers based on the state or province where they were captured during the breeding period or based on their geolocator-inferred breeding site for individuals that were marked during the sedentary nonbreeding period.

Details on the study sites and field methods used in each study are presented in Kramer et al. (2018a) and Bennett et al. (2019b). Both studies used the same model geolocator (ML6240, 2-min light-sampling regime; Biotrak, Wareham, UK) and modified leg-loop harness design to attach geolocators to *Vermivora* warblers (Rappole and Tipton 1991, Streby et al. 2015b). Peterson et al. (2015) found no evidence for effects of geolocators on the migratory ecology or apparent survival rate of golden-winged warblers marked with geolocators using this harnessing method.

Geolocator data analysis—

We analyzed all geolocator data in R (v. 3.6.1; R Core Team 2019) using the template-fit method with 'FLightR' (v. 4.9: Rakhimberdiev et al. 2015, Rakhimberdiev and Saveliev 2019) following previously described methods (Kramer et al. 2017, 2018a; Delancey et al. 2020; see SI Methods for details). Briefly, we used the function 'find.times.distribution' in 'FLightR' to estimate commencement and termination of seasonal migrations for individuals. We summed individuals' daily probability density functions for the days spanning an individual's migration and transformed the resulting likelihood surfaces into a probability density function (cell size ~0.5°) representing space use during either autumn or spring migration with areas associated with greater probabilities representing stopover regions (i.e., areas with a higher probability of being occupied by an individual for a greater duration relative to other locations).

Delineating space use by species and populations—

To identify the general space use patterns of each species and visualize interspecific variation in space use, we created mean seasonal migration probability density functions for each species by averaging probability density functions of individuals of a given species for each season (i.e., autumn or spring). For example, we summed the autumn probability density functions of all blue-winged warblers and divided by the sum of the composite surface (i.e., the number of geolocator tracks in each sample; each individual's probability density function sums to 1) to derive the average autumn probability density function for blue-winged warblers. We used the same methods to derive mean seasonal migration probability density functions for populations of each species based on BCR.

Quantifying overlap within and among regional populations—

We identified the core areas used by each regional population during both autumn and spring migration periods (hereafter, "core-use areas") to quantify variation in space use and overlap among *Vermivora* warblers from different BCRs. Defining a threshold to delineate core-use areas can be useful to differentiate high-probability cells from low-probability cells when analyzing spatially explicit probability density functions derived from geolocators (e.g., Kramer et al. 2018a). In our analysis of population and seasonal overlap, we defined core-use areas as the top 25th percentile of each regional population's average seasonal migration probability density function. We chose the top 25th percentile as a balance between the somewhat coarse resolution of geolocator-derived location estimates (Rakhimberdiev et al. 2016) and the desire to define areas where regional, population-specific conservation efforts may be targeted (Levin 1992).

We quantified the proportion of overlap among regional populations' seasonal core-use area (i.e., different populations, same season) to identify the similarity of within-season space use patterns among populations. We calculated the total area (km^2) of overlap between two regional populations' seasonal core-use areas and divided by the total seasonal core-use area of the reference population to derive the proportion of overlap. The proportion of overlap depends on which population's core-use area is the reference (i.e., the denominator). Therefore, we used pairwise comparisons to calculate the proportion of overlap between two core-use areas (i.e., using each core-use area as the reference) and averaged estimates of proportion of overlap when comparing the relative amount of overlap observed between and among populations (SI Methods).

Selection and analysis of migration risk-factors—

To determine whether variation in space use among populations of *Vermivora* warblers was associated with variation in exposure to migration risk-factors, we identified natural ($n = 4$) and anthropogenic ($n = 4$) factors that exhibit geographic variation in occurrence and/or intensity and are known or hypothesized to be associated with increased risk of mortality or carry-over effects in migrating birds (Table 2, SI Methods). We downloaded risk-factor data from publicly available sources and standardized the extent and resolution of all rasters to match geolocator-derived probability density functions (i.e., y = 0°, 60°; x = -120°, -60°; cell size ~0.5°; Table 2). We also calculated a combined (overall) measure of the relative intensity of migration risk-factors by standardizing each migration risk-factor raster (i.e., minimum and maximum values set to 0 and 1, respectively depending on the assumed direction of the relationship between the risk factor and fitness outcomes; Table 2). We summed standardized migration risk-factor layers to create a single raster layer (assigning equal weight to individual migration risk-factors) to test whether population trends of *Vermivora* warblers were associated with this combined measure of relative exposure to migration risk-factors (Table 1). We did not differentiate between risk factors associated with direct effects (i.e., increased mortality) and those associated with indirect effects (i.e., carry-over effects) in this analysis because each factor could reasonably cause either type of effect. Consequently, we assessed potential relationships between population trends and the combined effects (i.e., both direct and indirect) of exposure to migration risk-factors. Other potential risk factors exist that we did not directly account for (e.g., exposure to disease, resource availability, predation risk). However, the risk factors chosen for this analysis are among the most frequently proposed threats to migratory birds and most can be mitigated through targeted conservation actions (Newton 2006, Loss et al. 2015).

We also extracted land-cover composition characteristics from 100-km buffers around individuals' breeding and nonbreeding sites using a subset of migration risk-factors (n = 3/period) that were also relevant to *Vermivora* warbler fitness during the breeding and sedentary nonbreeding period (Table 2; SI Methods). We chose 100-km buffers to complement the spatial resolution and accuracy of geolocator data and other data sources in our analysis.

We assumed that there was a positive association between the relative intensity of migration risk-factors within *Vermivora* warbler core use areas and the likelihood that warblers' fitness would be affected by those factors. For example, we assumed that the probability of colliding with a window, getting hit by a car, or experiencing other negative fitness consequences as a result of factors included within the variable "human footprint" would be lower for a warbler with a core-use area containing primarily forested land-cover with minimal human development compared to a warbler with a core-use area containing primarily developed land-cover. Similarly, we assumed that higher levels of variables with negative predicted relationships to fitness (e.g., "human footprint") within an individual's breeding or nonbreeding buffer area would be associated with greater risk of mortality or carry-over effects. However, we were unable to test these assumptions given the spatial resolution of geolocator data and the lack of spatially explicit data sources for singular factors that cause direct mortality in migratory birds (e.g., the surface area and orientation of glass windows across North America). Therefore, our risk-factor data (including breeding and nonbreeding factors) represent proxies for the true causes of variation in fitness of migratory birds. Technological advances allowing for the continuous, fine-scale monitoring of small migratory songbirds may provide greater insight into the rate at which individuals are exposed to factors throughout the annual cycle and the frequency and intensity of associated fitness consequences (e.g., Hewson et al. 2016).

Table 2. Natural and anthropogenic migration risk-factors known or hypothesized to affect mortality rate and/or future reproduction in migrating birds that we included in these analyses. The expected relationship between population trends of *Vermivora* warblers and potential migration risk-factors describe the expected direction (i.e., positive or negative) an effect would have if it was strong enough to lead to a measurable change in the population trends of different groups of *Vermivora* warblers. The original resolution of each data source is noted in brackets under each source and all spatially explicit data were resampled to achieve a standardized resolution equal to the resolution of the geolocator data (~0.500°).

Risk factor (expected relationship)	Explanation	Citations	Data source [resolution]
Natural			
Forest and shrub cover (positive)[1]	*Vermivora* warblers use areas with forest or shrub cover to rest and refuel during migration. We predicted that populations migrating through areas with greater amounts of forest and shrub cover would be more likely to be stationary or increasing if variation in the amount of forest and shrub cover is driving or contributing to population declines.	Rohrbaugh et al. 2016	U.S. Geological Survey (USGS) Global Land Cover Characterization (GLCC); USGS 1997 [0.008°]
Net increase in forest cover 2000-2015 (positive)[1]	If declining populations of *Vermivora* warblers are limited by the availability of forest cover along population-specific migration routes, then we expect declining populations to migrate through areas having lost relatively more forest than stationary or increasing populations.	Rohrbaugh et al. 2016	HYDE 3.1; Goldewijk et al. 2010, 2011 [0.500°]
Tornados* (negative)	Tornados and the powerful storms that produce them are known to cause mortality in migrating birds. Although tornados usually represent an acute threat to migrating individuals, these storms could contribute to population-level declines if variation in space use during migration	Weidenfeld and Weidenfeld 1995, Newton 2007, Streby et al. 2015a	National Oceanic and Atmospheric Administration (NOAA) Severe Weather Database Files; NOAA 2018 [N/A; point data]

	leads to variation in exposure to tornadic storms among populations of *Vermivora* warblers.		
Hurricanes (negative)	Hurricanes pose a risk to migratory birds, especially if encountered during overwater barrier crossing (i.e., trans-Gulf of Mexico flights). Additionally, hurricanes may destroy coastal forest cover that may be important to migrants after crossing the Gulf of Mexico.	Newton 2007, Dionne et al. 2008	Atlantic HURDAT2; Landsea and Franklin 2013 [N/A, point data]
Anthropogenic			
Agricultural cover (negative)	Landscapes dominated by agriculture are considered poor quality stopover sites for migrating, insectivorous songbirds including *Vermivora* warblers. Therefore, regions with more agricultural cover may force migrants to travel greater distances between suitable stopover sites. Additionally, rural areas with high amounts of agricultural cover may be associated with increased exposure to chemical pesticides, herbicides, and vehicle collisions.	Blake 1986, Faaborg et al. 2010, Loss et al. 2014.	USGS GLCC; USGS 1997 [0.008°]
Human footprint (negative)[1]	We used human footprint as a proxy variable to account for several correlated aspects of urbanization and human development that are known or hypothesized to increase mortality rate in migrating birds. First, urban landscapes generally contain less forest cover that many species (like *Vermivora* warblers) use during migration. Additionally, human footprint is strongly associated with increased levels of artificial light at night (ALAN), which may confuse nocturnally migrating birds and draw them into urban centers where they may be at a greater risk of colliding with buildings and windows. Human footprint is also highly correlated with population density, which	Klem 1989, Van Doren et al. 2017, Cabrera-Cruz et al. 2018, Loss et al. 2015.	Global Human Footprint Dataset; Wildlife Conservation Society 2005, National Aeronautics and Space Administration (NASA) Socioeconomic Data and Applications Center (CEDAC) [0.008°]

	may be associated with greater levels of environmental pollution, increased threats from poaching or non-native invasive predators (e.g., feral cats), and other non-fatal stressors.		
Wind energy development* (negative)	Wind energy development (i.e., wind turbines) can cause direct mortality in migrating birds.	Osborn et al. 2000, Smallwood 2007, Loss et al. 2013	United States Wind Turbine Database; Hoen et al. 2018 [N/A, point data]
Communications towers* (negative)	Communications towers (often lighted) pose a direct mortality threat to migrating birds via collisions with the tower structure or guy-wires.	Kerlinger 2000, Longcore et al. 2013, Loss et al. 2015	Federal Communications Commission (FCC) Geospatial Data; FCC 2012 [N/A, point data]

*Data for US only.

[1] Also considered as a breeding-and nonbreeding-period risk-factor.

Variation in regional populations' exposure to migration risk-factors—

We quantified *Vermivora* warblers' relative exposure to each migration risk-factor, and all risk-factors combined, by summing the values of migration risk-factor raster cells that were contained within an individual warbler's seasonal core-use area. We considered other thresholds (i.e., 10th percentile, 50th percentile) for delineating core-use areas for this portion of the analysis but present the results using 25th percentile core-use areas because the relative exposure of populations to different risk factors and the direction and strength of modeled relationships (see below) did not meaningfully differ among thresholds (Fig. S1). Completion of an annual cycle requires an individual to undergo both autumn and spring migration. Therefore, we summed the values of each migration risk-factor extracted from an individual's autumn and spring core-use areas to derive the total annual exposure for each warbler to each risk factor. We excluded individuals with geolocators that did not record both autumn and spring migration ($n = 8$).

We used one-way analysis of variance (ANOVA; differences considered significant using $\alpha = 0.05$) to assess differences in the mean exposure to individual migration risk-factors for regional populations (i.e., three populations of blue-winged warblers and two populations of golden-winged warblers; based on BCR). If we detected a difference between populations with an ANOVA, we conducted a Tukey's *post hoc* test to determine the comparison(s) that differed and the direction of the difference. Despite small sample sizes from some populations, power analyses suggested that we would be likely to detect moderate-to-large effect sizes in all our analyses (Fig. S2; Table S3, S4).

The relative importance of migration, breeding, and nonbreeding factors on subregional population trends —

We also investigated whether exposure to migration risk-factors explained variation in recent population trends (i.e., 2000–2015) of *Vermivora* warblers at the state- and province-level (i.e., subregional level). We used the 'carat' package in R (Kassambra and Mundt 2019) to perform a partial least squares (PLS) regression analysis to determine whether variation in state- and province-level population trends was more strongly associated with exposure to migration risk-factors or land-cover characteristics of breeding and nonbreeding areas. We used PLS regression analysis because it reduces the multidimensionality of large sets of explanatory variables by creating a new set of latent, orthogonal (i.e., independent) variables, thus also addressing multicollinearity (Carrascal et al. 2009). Additionally, PLS regression analysis provides similar results to those obtained through related methods (e.g., multiple regression, principal components regression) but may outperform those methods in identifying the effect size and relative importance of explanatory variables in modeling the response variable (Carrascal et al. 2009). We tested for multicollinearity among explanatory variables by calculating the variable inflation factor (VIF) of each variable using the 'mctest' package in R (Imdadullah et al. 2016, Imdadullah and Aslam 2018).

We used BBS-estimated population trends from 2000–2015 (2015 was the last year of available BBS data at the time of analysis) based on the breeding-grounds deployment site or the geolocator-estimated breeding site for individuals tracked from their nonbreeding sites as the response variable (Regional Trend Analysis Form, www.mbr-pwrc.usgs.gov/bbs/trend/tf15.html; Fig. 1, Table S1). The BBS uses a hierarchical model to estimate the annual index of abundance for a specific region (i.e., state or province) and then derives a trend from the ratio of the annual index between the first and last year in the period of interest, including an estimate of error (Link and Sauer 2002). However, we were unable to incorporate estimates of error around BBS-derived population trend estimates into our modeling approaches. Using state- and province-level estimates of population trends allowed us to assess whether finer-scale variation within broader regional populations (i.e., BCR's; Fig. 1) was more strongly associated with factors experienced during migration or during sedentary breeding and nonbreeding periods as has been observed in other systems (e.g., Hewson et al. 2016, Buchan et al. 2022).

We analyzed the relationship between the response variable (state- and province-level population trend, 2000–2015) and 14 explanatory variables associated with breeding and nonbreeding land-cover characteristics (*n* = 6; forest and shrub cover, net change in forest and shrub cover 2000–2010, and human footprint; extracted from 100-km buffers for breeding and nonbreeding points; Table 2) and risk factors experienced during migration (*n* = 8; forest and shrub cover, net change in forest and shrub cover 2000–2010, tornados, hurricanes, agricultural cover, human footprint, wind energy development, and communications towers; Table 2). We used separate PLS models to consider the effects of migration risk-factors at two spatial scales: cumulative exposure across core-use areas during autumn and spring migration, and in narrower stopover regions near the Gulf of Mexico (a major migration barrier) during autumn and spring (SI Methods, Fig. S3). Migration risk-factors experienced by individuals prior to navigating the Gulf of Mexico could have a disproportionate effect on populations if those risk-factors reduce the probability of individuals successfully navigating this barrier. We did not include the variable for overall exposure in the PLS models because our goal was to assess the importance of individual migration risk-factors relative to breeding and nonbreeding factors in models describing variation in *Vermivora* warbler population trends.

To train the PLS models and determine the number of latent variables (i.e., components) to include, we scaled and centered all explanatory variables and chose the number of latent variables that resulted in the lowest root mean squared error following 5-fold cross-validation to avoid overfitting (allowing for a maximum of 14 latent variables; Sawatsky et al. 2015). We also assessed model performance using test-set validation in which we used 80% of the dataset to train the PLS regression model and compared model predictions to observed values in the withheld portion of the dataset (Sawatsky et al. 2015). We estimated the variable importance for the projection (VIP) score and absolute value of coefficients in our PLS regression model to determine whether terms related to migration risk-factors, terms associated with land-cover characteristics within breeding and/or sedentary nonbreeding regions, or some combination of factors throughout the annual cycle were associated with variation in recent population trends. We considered variables with a VIP score > 0.8 and coefficient values > 1.0 as influential in our PLS model (Sawatsky et al. 2015). We augmented the results from PLS regression analyses using generalized linear modeling and an information-theoretic modeling approach to determine whether singular migration risk-factors exhibited biologically meaningful relationships with subregional population trends of *Vermivora* warblers in univariate models (SI Methods; Table S5, S6) and models that used proxy variables (breeding and nonbreeding site coordinates) to account for general breeding- and nonbreeding-site characteristics that are known to be associated with historical variation in population trends (i.e., nonbreeding forest cover; Kramer et al. 2018a; SI Methods; Table S7, S8).

Analysis of future threats—

We assessed whether areas used by numerically stable and increasing populations of *Vermivora* warblers were more likely to be affected by future anthropogenic land-use change compared to declining populations using a georeferenced dataset of the projected development potential (i.e., the land suitability for development of different anthropogenic land uses from 2015–2030; Development Threat Indices, v1 [2015]; Oakleaf et al. 2015, 2019). We derived the spatially explicit (cell size ~0.008°) future development potential for nine anthropogenic land uses from publicly available data and based on the amount of unexploited resources and/or past trends in land-use change to inform future development potential (see Oakleaf et al. 2015 for details). For analyses, we collapsed the nine anthropogenic land-use types into six categories: solar energy, urban expansion, agricultural expansion, wind energy, biofuel, and mining (composite of mining, coal mining, conventional oil and gas mining, and unconventional oil and gas mining; see Oakleaf et al. 2015 for details and definitions). We used identical methods as those described above to standardize raster extent and resolution. We estimated the potential future exposure of individual warblers to anthropogenic development within seasonal migration core-use areas by summing the development threat values (scaled from 0–100 for each cell) of each land-use type ($n = 6$) contained within an individual's seasonal migration core-use area (i.e., autumn or spring). We then calculated the cumulative potential annual exposure for individual warblers by summing the exposure of each future development threat in autumn and spring. We excluded individuals with geolocators that did not record both autumn and spring migrations ($n = 8$).

We classified *Vermivora* warblers into two groups based on population trend: stationary or increasing (1) vs. declining (0) based on the state- and province-level population trends from 2000–2015 (BBS Regional Trend Analysis Form). We calculated average future exposure of each development type for both groups of *Vermivora* warblers (stationary or increasing, declining) and used simple linear regression to test whether exposure differed between groups ($\alpha = 0.05$).

RESULTS

Interspecific variation in space use—

Blue-winged warblers and golden-winged warblers exhibited different patterns in space use during migration (Fig. 2). During autumn migration, both species used similar areas along the northern coast of the Gulf of Mexico: primarily eastern Louisiana, Mississippi, Alabama, and western Florida (Fig. 2). However, golden-winged warblers also used areas in Belize, Honduras, and Nicaragua in Central America (Fig. 2). During spring migration, blue-winged warblers used the Yucatán Peninsula and areas along the northern coast of the Gulf of

Mexico (i.e., eastern Louisiana, Mississippi, Alabama, and western Florida; Fig. 2) whereas golden-winged warblers used areas farther west along the northern coast of the Gulf of Mexico (i.e., eastern Texas and Louisiana) in addition to portions of the central US (i.e., Ozark Mountain region; Fig. 2).

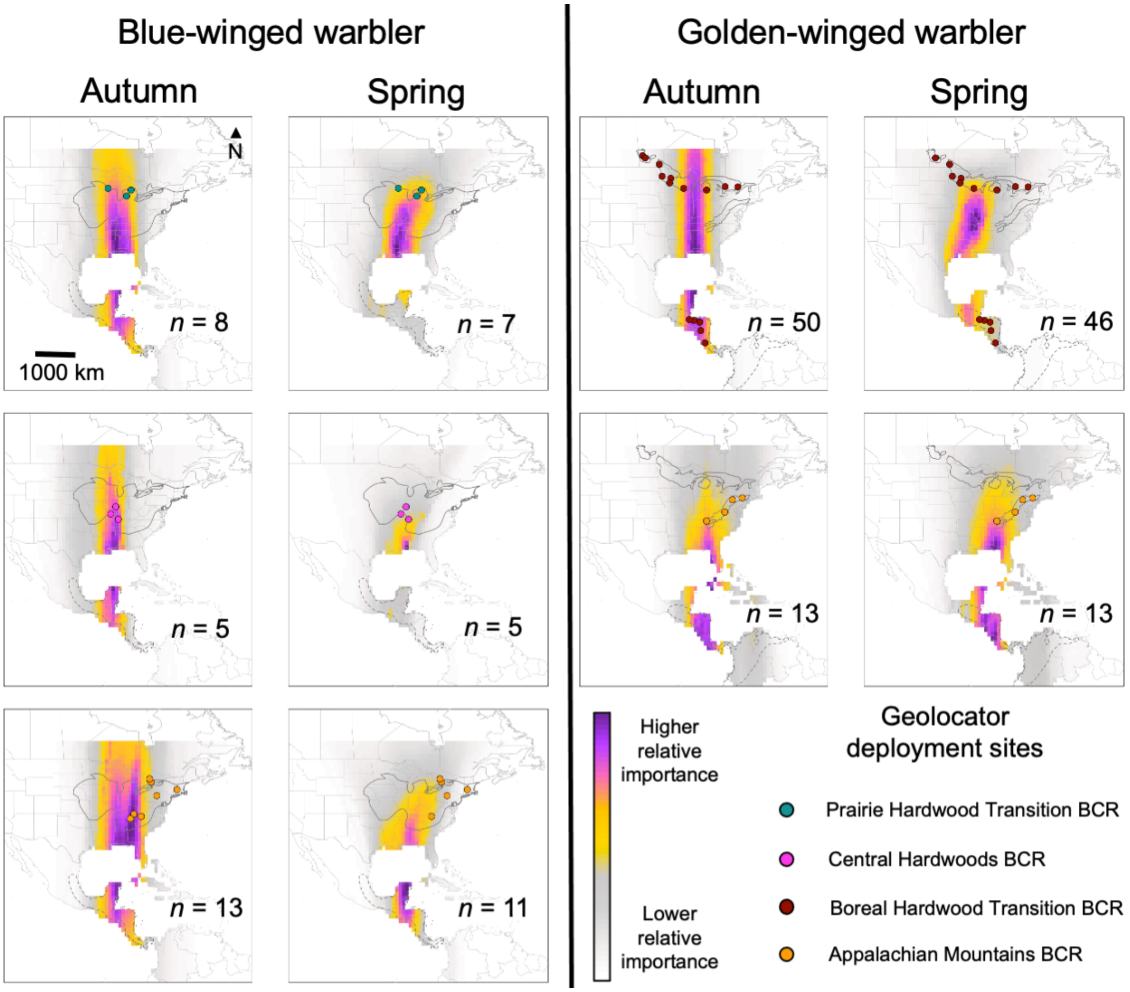

Figure 2. Average probability density functions for blue-winged warbler and golden-winged warbler populations (based on Bird Conservation Regions [BCRs]) during autumn and spring migrations. Darker purple cells represent areas of greater relative importance during migration (i.e., higher probability of use for greater durations by more individuals). We averaged the probability density functions of individual warblers derived from geolocator data spanning the duration of each warbler's seasonal migration period. Geolocator deployment sites are represented by circles and colors of circles correspond with Bird Conservation Regions (BCRs) of breeding sites. A solid gray line delineates the breeding

distribution whereas a dashed line identifies the nonbreeding distribution (including a 100-km buffer).

Intraspecific variation in space use—

Vermivora warblers exhibited intraspecific, regional variation in core-use areas during migration (Fig. 3A). During autumn migration, blue-winged warblers from the Appalachian Mountains BCR used areas farther east than western-breeding blue-winged warblers; however, there was extensive overlap in core-use areas among populations defined by BCR (mean proportion of overlap = 0.56 ± 0.13 SD, $n = 6$ pairwise comparisons; range = 0.37–0.70). During spring migration, blue-winged warblers migrating to breeding sites in the Appalachian Mountains BCR used areas in the Yucatán Peninsula and south-central US whereas the western-breeding populations primarily used areas in south-central US (Fig. 3A). Intraspecific variation in core-use areas during both autumn and spring migration was most pronounced in golden-winged warblers with individuals breeding at sites in the Appalachian Mountains BCR occurring farther east in the US and in Central America relative to individuals breeding at sites in the Boreal Hardwoods Transition BCR (Fig. 3A). The proportional overlap of core-use areas between populations of golden-winged warblers was low during autumn migration (0.28 ± 0.7 SD, $n = 2$ pairwise comparisons) and there was no overlap between core-use areas during spring migration ($n = 2$ pairwise comparisons; Fig. 3A).

The proportion of seasonal overlap (i.e., the overlap between autumn and spring core-use areas of a single population) within blue-winged warbler populations was moderate and similar (range = 0.56–0.68; Fig. 3A). Notably, the two populations of golden-winged warblers exhibited both the highest (0.78; Appalachian Mountain BCR) and lowest (0.19; Boreal

Hardwoods Transition BCR) proportion of seasonal overlap within *Vermivora* warblers (Fig. 3A).

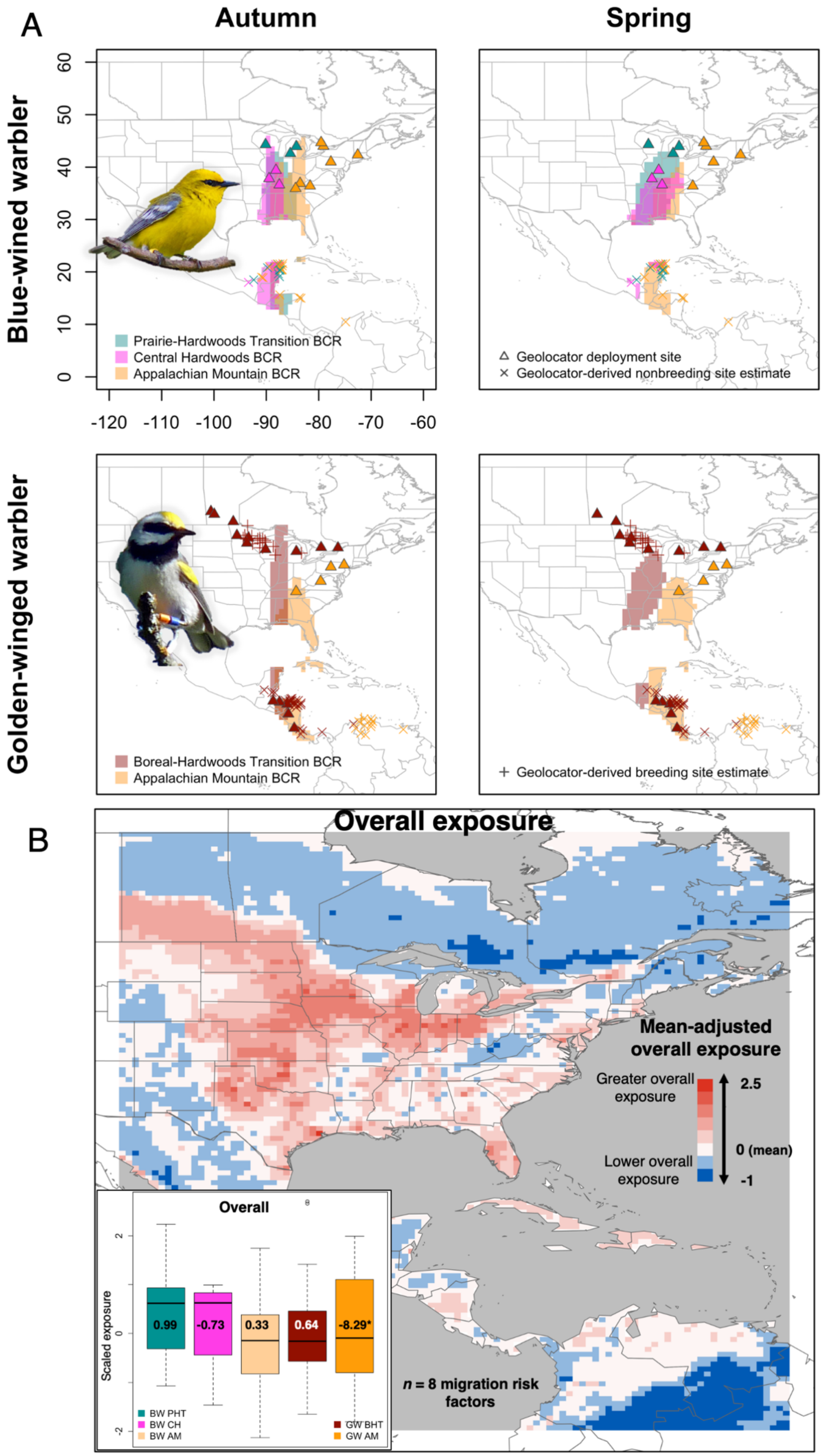
A
Autumn
Spring
Blue-wined warbler
Golden-winged warbler
60
50
40
30
20
10
0
-120
-110
-100
-90
-80
-70
-60
Prairie-Hardwoods Transition BCR
Central Hardwoods BCR
Appalachian Mountain BCR
Geolocator deployment site
Geolocator-derived nonbreeding site estimate
Boreal-Hardwoods Transition BCR
Appalachian Mountain BCR
Geolocator-derived breeding site estimate
B
Overall exposure
Mean-adjusted overall exposure
Greater overall exposure
Lower overall exposure
2.5
0 (mean)
-1
n = 8 migration risk factors
Overall
Scaled exposure
2
0
-2
0.99
-0.73
0.33
0.64
-8.29*
BW PHT
BW CH
BW AM
GW BHT
GW AM

Figure 3. (A) Regional population-specific core-use areas (25th percentile) of *Vermivora* warblers during autumn and spring migration. Blue-winged warblers and golden-winged warblers from breeding sites (triangles) associated with different Bird Conservation Regions (BCRs) are represented by different colors. Geolocator-derived nonbreeding and breeding location estimates are identified by ×'s and +'s, respectively and colored according to breeding population (i.e., BCR). (B) The spatial distribution of the mean-adjusted cumulative exposure to migration risk-factors represents the sum of standardized rasters of eight migration risk-factors considered in our analyses. Red cells indicate areas with above-average exposure to migration risk-factors whereas blue cells are associated with below-average exposure. Boxplot shows the scaled exposure of different regional populations (based on the exposure of individuals tracked within each population; colors correspond with the A) of *Vermivora* warblers to the mean-adjusted cumulative exposure to migration risk factors. Populations that experienced different levels of exposure (based on one-way ANOVA and Tukey HSD; $P < 0.05$) are denoted with letters. Values inside boxes indicate regional population trend estimates from the Breeding Bird Survey (BBS) for 2000–2015 (BBS Regional Trend Analysis Form). Asterisks specify population trends with 95% confidence intervals that do not overlap zero. Regional populations are defined by BCR and species (blue-winged warbler [BW] or golden-winged warbler [GW]) in boxplot legend: Prairie Hardwood Transition BCR (BW PHT, teal), Central Hardwoods BCR (BW CH, pink), Appalachian Mountains BCR (BW AM, light orange; GW AM, dark orange), and Boreal Hardwood Transition (GW BHT; maroon) BCR.

Variation in population-specific exposure to migration risk-factors—

We observed no evidence that regional populations of *Vermivora* warblers experienced differential exposure to the summed combination of migration risk-factors (i.e., "overall"; one-way ANOVA, $F_{4,76} = 0.53$, $P = 0.71$; Fig. 3B). However, mean exposure to 50% (4/8) of individual migration risk-factors differed among *Vermivora* warbler populations (Fig. S4). Golden-winged warblers that migrated between the Appalachian Mountains BCR and northern South America had core-use areas with greater amounts of relative forest and shrub cover (one-way ANOVA, $F_{4,76} = 3.99$, $P = 0.005$), less agricultural cover (one-way ANOVA, $F_{4,76} = 4.03$, $P = 0.005$), fewer wind turbines (one-way ANOVA, $F_{4,76} = 3.11$, $P = 0.020$), and a lower frequency of tornadic storms (one-way ANOVA, $F_{4,76} = 4.68$, $P = 0.002$) compared to ≥ 1 population of blue-winged or golden-winged warblers that migrated between the Boreal Hardwoods Transition BCR, Central Hardwood BCR, or Prairie Hardwood BCR and Central America (Fig. S4).

Linking subregional population trends with exposure to migration risk-factors

We detected moderate to high multicollinearity among explanatory variables we considered in PLS models exploring drivers of variation in subregional population trends (i.e., natural and anthropogenic migration risk-factors and breeding and nonbreeding factors associated with land-cover characteristics; variable inflation factor [VIF] range = 1.4–15.4; Table S9). The PLS regression model with the lowest root mean squared error after 5-fold cross-validation was comprised of two components that cumulatively explained 32% of the variance in the 14 explanatory variables and 40% of the variance in the response variable (subregional population trend 2000–2015) in the training dataset (test-set validation R^2 = 0.30; Fig. S5).

Among standardized, explanatory variables (n = 14) included in the PLS regression analysis, nonbreeding forest cover was the most important factor explaining variation in recent subregional population trends of *Vermivora* warblers ($|\bar{x}|$ = 1.39, variable importance on the projection [VIP] score = 0.82; Fig. 4). Additionally, breeding forest cover, net change in nonbreeding forest cover, and the relative intensity of human footprint at sedentary nonbreeding sites had relatively high regression coefficients and VIP scores (although none were > 0.80) suggesting that these variables were influential in the model (Fig. 4). None of the eight explanatory variables related to migration risk-factors had regression coefficients (absolute value) > 0.90 or VIP scores > 0.50 (Fig. 4; Fig. S1). Migration risk-factors were also not important in PLS models considering the exposure of warblers to migration risk-factors in a smaller region near the Gulf of Mexico region during both autumn and spring (Fig. S3, S6). We found no evidence of biologically meaningful relationships between migration risk-factors and subregional population trends using univariate generalized linear modeling (Table S5, S6; Fig. S7). Similarly, we found no evidence that individual migration risk-factors explained meaningful variation in subregional population trends using a hierarchical generalized linear modeling approach (Table S7, S8).

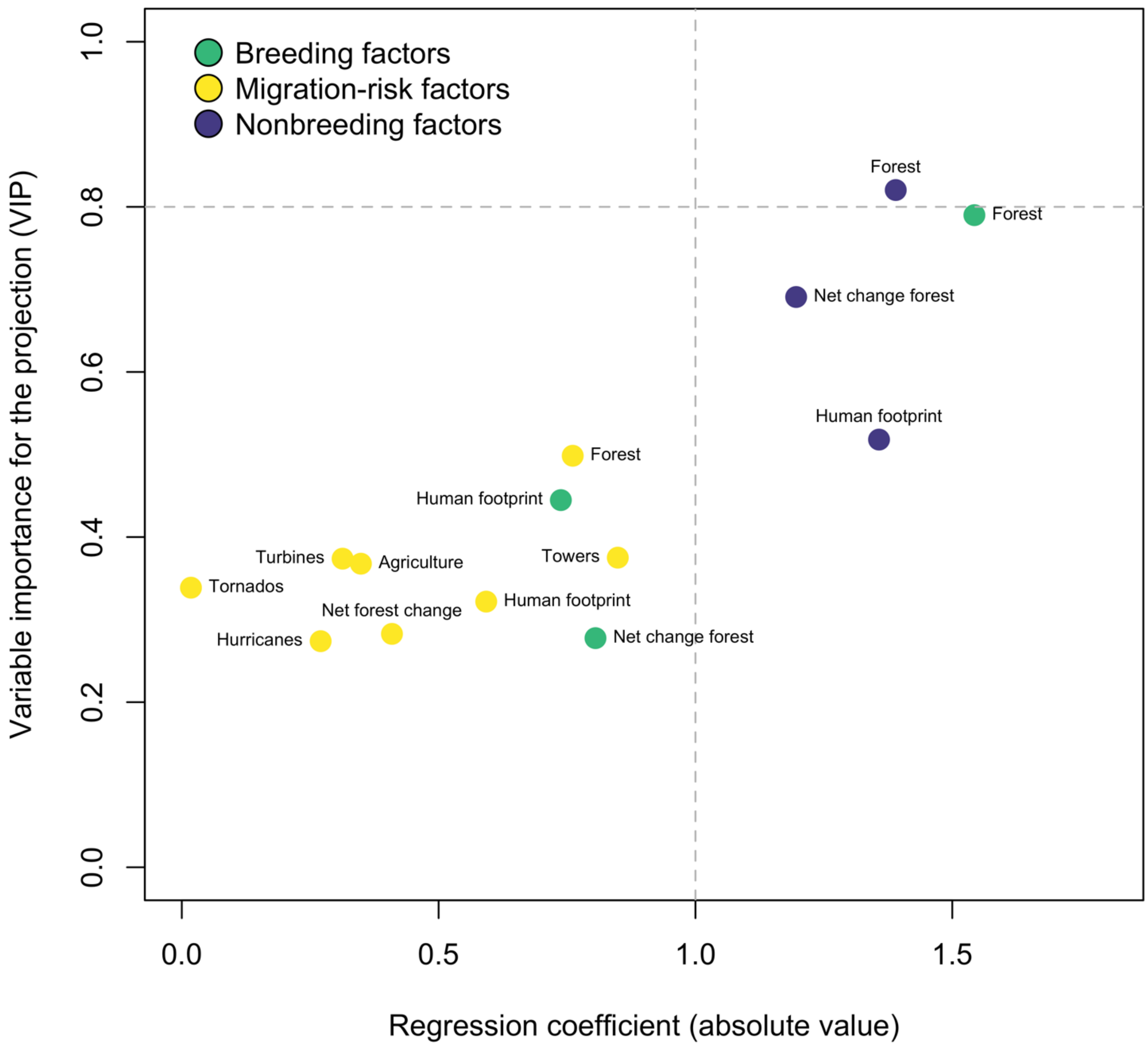

Figure 4. Comparison plot of the absolute value of regression coefficients and variable importance for the projection (VIP) of explanatory variables included in a partial least squares (PLS) regression model relating explanatory variables to variation in recent state- and province-level population trends of *Vermivora* warblers (i.e., 2000–2015). Explanatory variables comprise factors relevant to individual fitness that warblers may be exposed to in different periods of the annual cycle: migration (migration risk-factor terms; yellow circles), the breeding period (breeding factors; green circles), and the sedentary nonbreeding period (nonbreeding factors; purple circles). Gray dashed lines denote regression coefficients with absolute values > 1 and VIP > 0.8, which correspond with terms that are important in the PLS model.

Analysis of future threats—

Spatial variation in the projected threat of anthropogenic land-use change in migration core-use areas may lead to different factors affecting currently stationary and increasing, or declining populations of *Vermivora* warblers in the future (i.e., by 2030; Fig. 5).

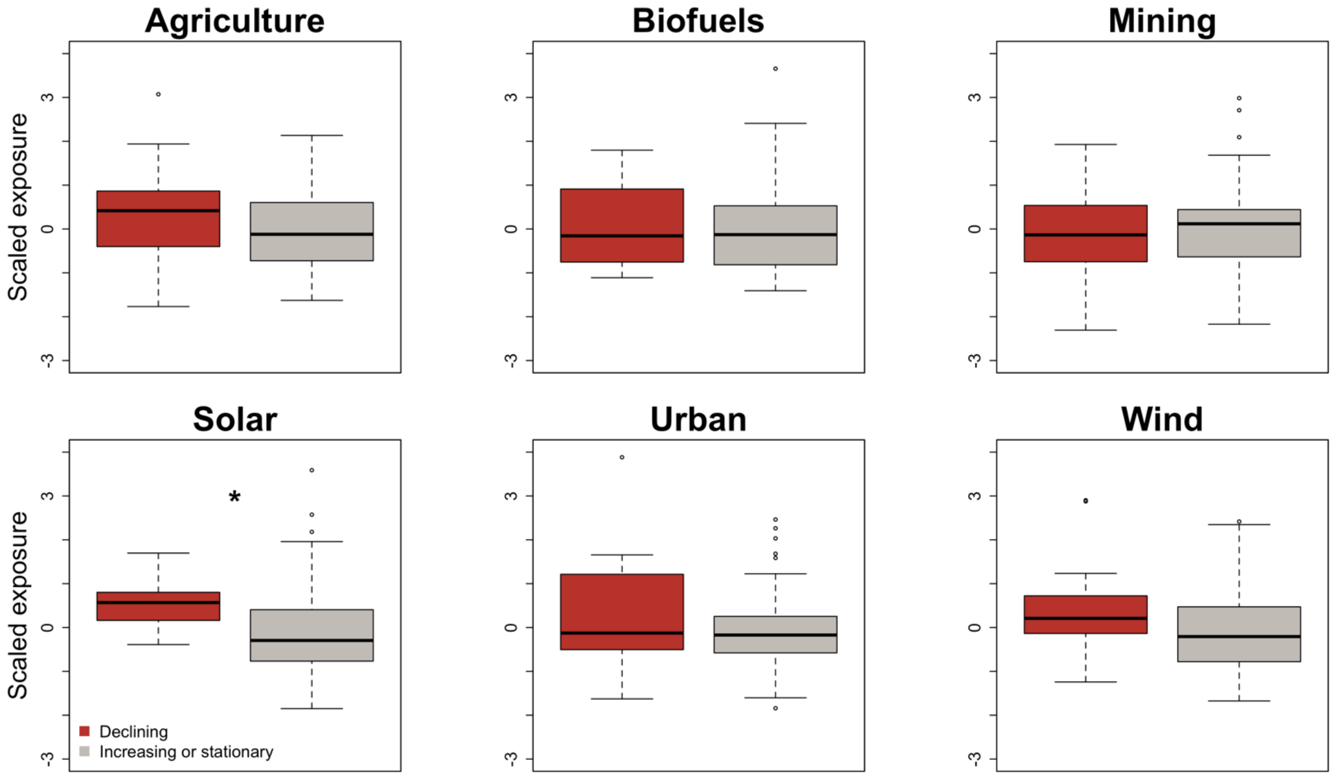

Figure 5. Boxplots displaying potential future exposure of currently stationary and increasing, or declining populations of *Vermivora* warblers to different types of anthropogenic land-use change. Asterisks indicate differences in averages that are significant at $\alpha = 0.05$. Spatially explicit data describing the suitability of land for potential future (i.e., 2030) anthropogenic development come from NASA Socioeconomic Data and Applications Center (SEDAC; Oakleaf et al. 2015, 2019).

Specifically, potential land-use change associated with solar energy development may be more likely to affect migration core-use areas of currently declining populations of *Vermivora* warblers relative to stationary or increasing populations ($|\bar{x}| = 0.67$, $t_{79} = -2.34$, $P = 0.02$). Projected land-use change associated with five additional factors is likely to occur similarly across areas used by both declining and increasing or stationary populations of *Vermivora* warblers during migration.

DISCUSSION

Regional populations of *Vermivora* warblers exhibited variation in space use during migration. Notably, the greatest observed differences in space use were between stationary (Great Lakes) and declining (Appalachian Mountains) populations of golden-winged warblers during spring migration (Fig. 3A). Generally, variation in space use did not correspond with variation in relative exposure to migration risk-factors. However, golden-winged warblers breeding in the Appalachian Mountains migrated through areas with more forest and shrub cover, less agricultural cover, and less wind energy development relative to golden-winged warblers from breeding sites in the Great Lakes region. Golden-winged warblers tend to be associated with forest and shrub cover types during migration (Rohrbaugh et al. 2016) and therefore we expected to observe a positive relationship wherein populations migrating through areas with more forest and shrub cover would be more likely to be stationary or increasing (Table 2). We observed the opposite relationship in that the population associated with the greatest amount of forest and shrub cover during migration (i.e., Appalachian Mountains golden-winged warblers) exhibited declining population trends suggesting that populations of *Vermivora* warblers are not currently limited by availability of forested stopover habitat along seasonal migration routes. However, the data used to quantify the amount of forest and shrub cover on the landscape do not account for factors such as habitat quality, pollution, or variation in predator density/richness, which may vary spatially and influence mortality rate (Gandini et al. 1994, Nicholson et al. 1997, Weber et al. 1999) or decrease future productivity (Legagneux et al. 2012).

We did not find evidence of biologically meaningful relationships between recent *Vermivora* population trends and variation in exposure to migration risk-factors across any of the scales we considered. Instead, results from multiple analyses indicated that nonbreeding factors (primarily nonbreeding forest cover) were the most important in PLS models describing variation in population trends at regional and subregional scales. Breeding forest cover was also consistently among the most important factors in our analyses suggesting that factors associated with reproduction on the breeding grounds (e.g., low fledgling survival of golden-winged warblers at some Appalachian Mountains breeding sites; Lehman 2017) may have contributed to variation in population dynamics of *Vermivora* warblers in the recent past. There is geographic variation in reproductive success of local populations of golden-winged warblers breeding within the Appalachian Mountains (Lehman 2017, McNeil 2019). At some sites, golden-winged warblers are apparently reproducing at rates that would be expected to lead to population increases (Aldinger 2018, McNeil 2019) whereas others are reproducing at lower rates that correspond with population declines (Lehman 2017). Whether ongoing population declines in the Appalachian Mountain population segment of golden-winged warblers are driven by low reproduction, habitat loss at northern South American nonbreeding sites, or some other factor or combination of factors will likely require additional study. Moreover, demographic information on golden-winged warblers in the Appalachian Mountains comes from several well-studied sites that are managed with the intention of benefitting golden-winged warblers. Therefore, it is unclear whether the trends observed at these sites are representative of the broader Appalachian Mountain population, and whether these sites are population sources or sinks (Lloyd et al. 2005, Aldinger 2018). Additional information on metapopulation dynamics among the patchily dispersed golden-winged warblers of the Appalachian Mountains may help disentangle the proximate drivers of population trends and improve the effectiveness of conservation efforts.

Golden-winged warblers have been described as super-colliders (i.e., experienced collision mortality more frequently than would be expected by chance based on population size and distribution; Arnold and Zink 2011). However, Arnold and Zink (2011) found no evidence that collision mortality experienced by golden-winged warblers and other super-collider species led to discernable changes in breeding population abundance trends. Similarly, we found limited evidence for population-level effects of a suite of natural and anthropogenic migration mortality risk-factors on the population trends of *Vermivora* warblers (including communications towers) suggesting that mortality experienced during migration may be similar among populations, the magnitude of population-level differences in mortality rate during migration is not great enough to be captured in Breeding Bird

Survey trends, or variation in population trends are associated with other factors that we were unable to consider due to data limitations.

The geolocator datasets we evaluated were comprised almost entirely of male *Vermivora* warblers because they are easier to capture and exhibit greater inter-annual site fidelity than females (Peterson et al. 2015, Kramer et al. 2018a). However, population dynamics may be more sensitive to variation in survival rate of female *Vermivora* warblers during migration if females exhibit different migratory strategies that increase their exposure to mortality risk-factors relative to males (Bennett et al. 2019a, Fischer 2020). Thus, efforts to understand the distribution, abundance, and survival of female *Vermivora* warblers throughout the annual cycle may help further refine conservation strategies (Bennett et al. 2019a, Fischer 2020). Additionally, we only recovered geolocator data from individual *Vermivora* warblers that successfully completed both autumn and spring migrations and that we detected and recaptured (see Peterson et al. [2015] and Kramer et al. [2017] for details on recovery methods). Thus, we were unable to identify when and where mortality occurred during the annual cycle for individuals that did not return to near their initial capture locations with functioning geolocators. Moreover, the relationship between putative risk factors and mortality rate in migrating *Vermivora* warblers may be acting on a finer scale than we were able to assess. Specifically, it is possible that recent variation in population trends of *Vermivora* warblers are linked to one or more of the factors considered in this analysis but that the relationship was obfuscated by noise inherent to the scale of our geolocator-based analysis. Similarly, factors affecting populations during stationary periods (i.e., breeding and nonbreeding) may be more likely to predict population trends because those location estimates are more precise than estimates of space use during migration. Technological advances leading to the availability of tracking devices that allow for delineating space use throughout the annual cycle at a finer spatial resolution may help address these questions in the future.

The spatial arrangement of migration risk-factors relative to major migration barriers (e.g., the Gulf of Mexico) may be important to consider in future efforts exploring the relationship between migration risk-factors and the population trends of migratory species. For example, the relatively high occurrence of migration risk-factors in Florida (Fig. 3B) could represent a greater risk (i.e., be more strongly associated with increased mortality rate) than other areas with similarly high occurrences of migration risk-factors but farther from the Gulf of Mexico (e.g., Iowa) if *Vermivora* warblers that stop-over in Florida prior to crossing the Gulf of Mexico are unable to sufficiently refuel and therefore initiate a trans-Gulf flight with insufficient energy reserves. However, we found no evidence of associations between variation in exposure to migration risk-factors in stopover regions near the Gulf of Mexico and *Vermivora* warbler population trends. Future efforts to quantify the relationships between migration risk-factors and survival of *Vermivora* warblers at a finer resolution (i.e., with radiotelemetry or GPS tags) may provide additional insight into the factors causing mortality during migration and patterns in their geographic arrangement that could provide opportunities for targeted conservation (Hewson et al. 2016). Despite increases in the use of tracking technology to monitor migratory species, range-wide and multi-species assessments remain uncommon (Knight et al. 2018, Kramer et al. 2018a, Hill and Renfrew 2019, Renfrew et al. 2019, Rushing et al. 2020). Our results demonstrate the potential value of tracking multiple species from many sites across their distributions to determine when during the annual cycle factors may be limiting populations.

Characterizing how populations of migratory birds are affected by factors experienced during migration is critical for informing effective conservation. For example, stopover habitat availability and the conservation of important areas used by species during migration are critical for the long-term persistence of some migratory species (Weber et al. 1999, Wilcove and Wikelski 2008). However, our results suggest populations of *Vermivora* warblers are currently not limited by the availability of appropriate stopover habitat at the landscape scale. Habitat loss at stopover sites can negatively affect populations if suitable sites are far apart and/or limited in quality or abundance (Weber et al. 1999). Species that rely on the availability of predictable resources at fewer stopover sites within an otherwise inhospitable landscape (e.g., shorebirds) may be more susceptible to habitat loss and reduced habitat quality at those stopover sites (Weber et al. 1999; Studds et al. 2017). Our findings suggest *Vermivora* warblers likely have access to sufficient forest- and shrub-dominated landscapes during migration such that targeted conservation of individual sites may not be fruitful, unless future research determines these landscapes to be of insufficient quality. Instead, using limited resources to ensure that sufficient forest and shrub cover is maintained within population-specific core-use areas may be an effective conservation strategy for *Vermivora* warblers. Ultimately, our findings join a growing body of research suggesting that successful conservation of *Vermivora* warblers may require addressing limiting factors (likely historical and ongoing habitat loss) occurring during the sedentary nonbreeding period (Kramer et al. 2018a). Lastly, migratory behavior in *Vermivora* warblers is a complex and evolving phenomenon and investigating how changes to the climate or landscape may affect future populations could be valuable for long-term conservation planning (Winger et al. 2019). Continued monitoring of *Vermivora* warbler populations may aid in identifying and mitigating the negative effects of future anthropogenic land-use change that may differentially affect populations during migration.

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Supplementary Information

Supplementary methods—

Assigning individuals to regional populations—

We defined regional populations based on the BCR of an individual's breeding location for figures and in analyses of overlap during migration. However, two of our study sites occurred near the periphery of the relevant species' distribution. Thus, we assigned blue-winged warblers breeding at two sites in southern Ontario, Canada (*n* = 2) and one site in Massachusetts, USA (*n* = 4) to the Appalachian Mountains BCR and golden-winged warblers breeding at two sites in western Manitoba, Canada (*n* = 2) to the Boreal Hardwood Transition BCR. Thus, we classified blue-winged warblers into three regional populations: Prairie Hardwood Transition BCR (*n* = 7 individuals, *n* = 8 tracks), Central Hardwoods BCR (*n* = 5 individuals and tracks), and the Appalachian Mountains BCR (*n* = 12 individuals, *n* = 13 tracks). We classified golden-winged warblers into two regional populations: Boreal Hardwood Transition BCR (*n* = 48 individuals, *n* = 51 tracks) and Appalachian Mountains BCR (*n* = 12 individuals, *n* = 13 tracks).

We also classified individuals into subregional groups based on the state or province of their breeding site (Table S1). We classified golden-winged warblers into eight subregional groups: Manitoba (*n* =4), Michigan (*n* = 2), Minnesota (*n* = 28), Ontario (*n* = 4), Pennsylvania (*n* = 3), Tennessee (*n* = 8), Virginia (*n* = 2), and Wisconsin (*n* = 14). We classified blue-winged warblers into seven subregional groups: Illinois (*n* = 4), Massachusetts (*n* = 4), Michigan (*n* = 4), Ontario (*n* = 2), Pennsylvania (*n* = 4), Tennessee (*n* = 3), and Wisconsin (*n* = 4).

Geolocator analysis—

We omitted hybrid warblers (*n* = 4 individuals, *n* = 5 geolocator tracks) and one golden-winged warbler that returned with mud caked over the geolocator's light sensor from analysis (Table S1, S2). We analyzed geolocator data using 'FLightR' (v. 4.9: Rakhimberdiev et al. 2015, Rakhimberdiev and Saveliev 2019). 'FLightR' uses the template-fit method to derive location estimates from raw light data using the timing and slope of transitions (i.e., sunrises and sunsets; Ekstrom 2004, Rakhimberdiev et al. 2015). We identified transition events with the package 'BAStag' (Wotherspoon et al. 2016) using a threshold of 1.5 (Kramer et al. 2017, 2018a). We calibrated geolocator data in 'FLightR' using the period that individuals were known (or assumed) to be resident at breeding or nonbreeding deployment sites (Kramer et al. 2018a, 2018b, Bennett et al. 2019b). We followed the workflow of Kramer et al. (2018a) to derive probability density functions using data spanning the duration of an individual's autumn and spring migrations. We analyzed data from each geolocator using the movement model in 'FLightR' (optimized with one million particles) to derive location estimates (i.e., spatially explicit likelihood surfaces) for individual transitions throughout the year with a behavioral mask that prevented stationary location estimates >25 km from land (Kramer et al. 2018a, Delancey et al. 2020).

We also constrained the maximum distance between subsequent twilights to 1,200 km, which limited the effects of erroneous location estimates, and used the automatic outlier exclusion capability in 'FLightR' to identify and eliminate extreme location estimates during the movement modeling process (Rakhimberdiev and Saveliev 2019). We used the function find.times.distribution in 'FLightR' to estimate commencement and termination of seasonal migrations (median date) from known (Kramer et al. 2018a) or estimated (Bennet et al. 2019b) breeding sites to known (Bennett et al. 2019b) or estimated (Kramer et al. 2018a) nonbreeding sites. We then created a daily likelihood surface by multiplying 'FLightR'-derived likelihood surfaces (~0.5 ° cell size) for each day within the identified migratory period for which we were able to generate a likelihood surface for both sunrise and sunset transitions (generally ~95% of days). We multiplied each day's sunrise and sunset likelihood surfaces together to create a daily likelihood surface (Kramer et al. 2017, 2018a). The likelihood surface for an individual transition is generally an arc corresponding to the geographic location of the transition between dark and light (or *vice versa*). The likelihood surfaces for sunrises and sunsets are nearly perpendicular and by multiplying the sunrise and sunset likelihood surfaces from a single day, it is possible to effectively pinpoint the estimated location of a geolocator-marked animal (Rakhimberdiev et al. 2015, Kramer et al. 2017). This process assumes that *Vermivora* warblers were stationary or moved relatively short distances (i.e., <250 km) during the day, which is a reasonable assumption as *Vermivora* warblers, like many other migratory songbirds, primarily migrate at night (Lincoln 1935). The accuracy of geolocator-derived location estimates can be reduced near the equinoxes when day length is similar across the globe (Ekstrom 2004). During these periods, estimates of longitude may still be highly accurate. However, latitudinal errors may be more prominent leading to probability density functions that indicate location estimates that are biased north (autumn) or south (spring) of breeding or nonbreeding sites although it is currently impossible to determine whether these are erroneous location estimates or true movements. After creating daily likelihood surfaces for each day that 'FLightR' estimated sunrise and sunset likelihood surfaces, we added together an individual's daily likelihood surfaces spanning each seasonal migration (i.e., all of the daily likelihood surfaces from breeding-site departure to nonbreeding-site arrival [autumn migration] or nonbreeding-site departure to breeding-site arrival [spring migration]). The resulting migration likelihood surface identified areas of relative importance during seasonal migration (i.e., stopover areas; cells with higher likelihoods were associated with a higher probability of being occupied by an individual for a greater duration relative to other locations). We then created a probability density function of each individual's seasonal migration by dividing each migration likelihood surface by its sum. For individuals with two years of tracking data, we considered each year as independent because we assumed individuals may not use the same routes and/or stopover sites during different years (or may use them for a different duration; Stanley et al. 2012). We quantified the proportion of overlap among population's seasonal core-use areas to quantify similarities in space use among populations. The proportion of overlap depends on which population's core-use area is the reference (i.e., the denominator). Thus, we used pairwise comparisons to calculate the proportion of overlap between two core-use areas (i.e., using each core-use area as the reference) and averaged estimates of proportion of overlap when comparing the relative amount of overlap observed between and among populations . For example, to estimate the percent overlap between golden-winged warblers from Appalachian Mountains BCR breeding sites and from Boreal Hardwood Transition BCR breeding sites, we calculated the total area (km^2) of overlap between two populations' seasonal core-use areas and divided by the total seasonal core-use area of the reference population to derive the proportion of overlap. We then repeated these steps using the other population as the reference and then averaged both proportions.

Selection and analysis of migration risk-factors—

We limited the number of potential migration risk-factor variables in our analysis (n = 8) to those that we predicted could affect populations' trajectories due to the combination of their geographical extent and potential for causing mortality or reducing productivity. When possible, we selected variables that aggregated correlated risk factors. Specifically, we used the variable "human footprint" (Venter et al. 2016, 2018) as a proxy for a suite of highly correlated risk factors associated with urbanization and development (i.e., population density, artificial light at night, built-up area, road density; Table 2). We downloaded migration risk-factor data as georeferenced rasters or transformed them from vectors (i.e., points) to rasters in R using the 'raster' package (Hijmans 2020; Table 2). We clipped and resampled all rasters to standardize the extent (i.e., y = 0, 60; x = -120, -60) and resolution (˜0.5° × 0.5°).) because the resolution of all migration risk-factor data was finer (i.e., more precise) than the resolution of the geolocator-derived probability density functions (˜0.5°; Table 2).

Processing hurricane and tornado data—

We downloaded datasets containing spatially explicit historical hurricane (Best Track Data HURDAT2, National Hurricane Center; https://www.nhc.noaa.gov/data/) and tornado (Storm Events Database; https://www.ncdc.noaa.gov/stormevents/) data. Historical hurricane data spanned 1851–2013 and historical tornado data spanned 1950–2019. We selected tornado and hurricane tracks that occurred during migration periods (April–May, August–November) from 2000 to the most recent year available for each dataset. We transformed track data for hurricanes and tornados into point data and rasterized each layer in R using a standardized extent (i.e., y = 0, 60; x = -120, -60) and resolution (˜0.5° × 0.5°).

Selection and processing of breeding and nonbreeding factors—

We selected three variables related to general land-cover characteristics (i.e., forest and shrub cover, and human footprint) and changes in land-cover characteristics (net change in forest and shrub cover 2000–2010) in PLS models testing the relative importance of breeding, nonbreeding, and migration risk-factors in models describing variation in subregional population trends of *Vermivora* warblers. We chose breeding and nonbreeding variables associated with land-cover characteristics because breeding and nonbreeding habitat availability may affect fitness and contribute to variation in populations dynamics of *Vermivora* warblers (Buehler et al. 2007, Kramer et al. 2018a). We extracted the amount of each cover-type from 100-km buffers around breeding and nonbreeding sites of *Vermivora* warblers. Thus, we included six parameters accounting for breeding- and nonbreeding-site land-cover characteristics in our PLS models (i.e., three breeding cover-type factors plus three nonbreeding cover-type factors).

Generalized linear modeling of migration risk-factor effects—

Historical population trends in *Vermivora* warblers are strongly associated with both breeding and nonbreeding regions (Buehler et al. 2007, Kramer et al. 2018b). Including breeding or nonbreeding factors in PLS models may obfuscate biologically meaningful associations between migration risk-factors and *Vermivora* warbler population trends. We used generalized linear modeling to determine whether individual migration risk-factors exhibited statistically and biologically meaningful relationships with recent *Vermivora* warbler population trends (subregional) without controlling for breeding and nonbreeding factors. We compared univariate models to intercept-only models and considered models to be uninformative if they were < 2 ΔAIC_c from the intercept-only model (Table S8, S9; Arnold 2010).

Hierarchical linear modeling of the relationships between risk-factors and population trends while controlling for breeding and nonbreeding factors using proxy variables—

We augmented the results from PLS regression analyses using an information-theoretic modeling approach to determine whether singular migration risk-factors explained additional variation in subregional population trends of *Vermivora* warblers while using proxy variables (breeding and nonbreeding site coordinates) to account for general breeding- and nonbreeding-site characteristics that are generally associated with variation in population trends (i.e., nonbreeding forest cover; Kramer et al. 2018a; SI Methods, Fig. S3). We constructed generalized linear models within a hierarchical modeling framework to determine whether adding singular migration risk-factor parameters, including the variable for overall exposure to migration risk-factors, to a base model consisting of breeding latitude, breeding longitude, nonbreeding latitude, and nonbreeding longitude explained additional variation in state- and province-level *Vermivora* warbler population trends. We considered migration risk-factor variables to be uninformative if the more complex model (i.e., base model plus single migration risk-factor parameter) was < 2 AIC_c from the base model (Arnold 2010). We modeled the relationships between subregional population trends of *Vermivora* warblers and individual migration risk-factors experienced at two spatial scales: cumulative annual exposure across core-use areas (autumn and spring migration combined; Table S9), and in narrower stopover regions near the Gulf of Mexico (a major migration barrier) during autumn and spring (Table S7).

To test for potential associations between population trends and the amount of migration risk-factors in population-specific areas used prior to crossing a major migration barrier (Gulf of Mexico), we summed the relative amount of each migration risk-factor within an individual's 25th percentile core-use area between latitudes corresponding with regions containing likely stopover sites where individuals rest and refuel prior to initiating trans-Gulf flights during both autumn and spring migration periods (Figure S2, Kramer et al. 2017). Specifically, we extracted migration risk-factors from 25th percentile core-use areas between 25–35° latitude during autumn migration and between 15–23.5° latitude during spring migration (Fig. S3). Risk-factors experienced by individuals prior to navigating the Gulf of Mexico during autumn or spring migration may have a disproportionate effect on populations if those risk-factors reduce the probability of individuals successfully navigating this barrier.

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Table S1. Metadata of geolocator-marked *Vermivora* warblers. Individual identification code (ID), U.S. Geological Survey band number (Band #), geolocator deployment year (Deployment year), species (Species; GW=golden-winged warbler, BW=blue-winged warbler, HY=hybrid), Bird Conservation Region (BHT=Boreal Hardwood Transition, CH=Central Hardwoods, AM=Appalachian Mountains, PHT=Prairie Hardwood Transition), Subregion (IL = Illinois, MA = Massachusetts, MB = Manitoba, MI = Michigan, MN = Minnesota, ON = Ontario, PA = Pennsylvania, TN = Tennessee, VA = Virginia, WI = Wisconsin), start and end of seasonal migrations (Autumn start, Autumn end, Spring start, Spring end), breeding and nonbreeding coordinates (Breeding latitude, Breeding longitude, Nonbreeding latitude, Nonbreeding longitude). Cells for which geolocator data were not collected, or for which data were not available are denoted by "n/a".

ID	Band #	Deployment year	Species	BCR	Subregion	Autumn start	Autumn end	Spring start	Spring end	Breeding latitude	Breeding longitude	Nonbreeding latitude	Nonbreeding longitude
DMG03	2840-78903	2015	GW	BHT	MB	9/10/15	10/25/15	n/a	n/a	51.535	-100.581	15.989	-85.386
ILB04	2750-63504	2015	BW	CH	IL	9/24/15	10/23/15	2/14/16	4/8/16	37.816	-89.463	21.497	-87.890
ILB06	2750-63506	2015	BW	CH	IL	8/1/15	9/27/15	4/20/16	5/4/16	37.816	-89.463	21.497	-87.389
ILB08	2750-63508	2015	BW	CH	IL	9/21/15	11/16/15	4/17/16	5/5/16	37.816	-89.463	17.992	-93.398
ILB18	2750-63523	2015	BW	CH	IL	9/6/15	11/9/15	4/17/16	5/16/16	39.407	-88.161	21.497	-87.890
KYB14	2690-98096	2015	BW	AM	TN	9/7/15	10/3/15	n/a	n/a	36.913	-83.562	20.997	-87.389
MAB05	2750-63237	2015	BW	AM	MA	8/23/15	10/24/15	3/29/16	5/2/16	42.343	-72.568	10.481	-74.871
MAB06	2750-63238	2015	BW	AM	MA	8/5/15	11/1/15	4/12/16	5/16/16	42.343	-72.568	14.988	-83.383
MAB09	2750-63243	2015	BW	AM	MA	10/10/15	10/23/15	4/11/16	4/27/16	42.343	-72.568	20.997	-86.888
MAB12	2770-39353	2015	BW	AM	MA	9/8/15	11/7/15	3/28/16	4/25/16	42.343	-72.568	14.988	-83.383

MIB02	2750-63335	2015	BW	PHT	MI	9/3/15	11/19/15	4/11/16	5/2/16	43.948	-84.267	20.997	-86.888
MIB05	2750-63353	2015	BW	PHT	MI	8/15/15	9/3/15	n/a	n/a	42.615	-85.410	21.124	-86.953
MIB12	2750-63360	2015	BW	PHT	MI	9/20/15	9/29/15	4/11/16	4/15/16	42.615	-85.410	21.497	-87.389
MIB14	2750-63362	2015	BW	PHT	MI	10/10/15	10/17/15	4/29/16	5/18/16	42.615	-85.410	20.997	-89.392
MIG01	2750-63331	2015	GW	BHT	MI	9/8/15	11/12/15	4/20/16	5/6/16	43.948	-84.267	14.988	-83.383
MIH02[a]	2750-63351	2015	HY	BHT	MI	9/19/15	11/25/15	4/15/16	5/4/16	43.948	-84.267	20.997	-88.390
RLG12	2690-98282	2015	GW	BHT	MN	8/29/15	10/14/15	4/29/16	5/9/16	46.533	-93.407	15.489	-84.385
RLG19	2690-98043	2015	GW	BHT	MN	9/2/15	10/12/15	n/a	n/a	46.533	-93.407	14.988	-83.383
RLG18	2690-98276	2015	GW	BHT	MN	9/9/15	11/18/15	4/19/16	5/8/16	46.533	-93.407	16.991	-88.390
NCB01	2700-29578	2015	BW	AM	NC*	9/16/15	10/10/15	4/2/16	4/19/16	36.412	-81.655	20.997	-86.888
ONB02	2740-78971	2015	BW	AM	ON	9/21/15	11/4/15	4/22/16	5/26/16	44.003	-79.123	21.497	-87.389
ONB05	2740-78972	2015	BW	AM	ON	9/7/15	10/22/15	4/3/16	5/2/16	44.700	-79.545	20.997	-86.888
ONG03	2740-78953	2015	GW	BHT	ON	9/5/15	10/14/15	4/23/16	5/10/16	44.641	-76.343	14.988	-83.383
ONG05	2740-78955	2015	GW	BHT	ON	9/1/15	10/31/15	4/24/16	5/19/16	44.641	-76.343	14.988	-83.383
ONG10	2740-78968	2015	GW	BHT	ON	9/6/15	10/29/15	4/10/16	5/11/16	44.700	-79.545	10.982	-73.369
PAB01	2750-63202	2015	BW	AM	PA	9/27/15	10/17/15	3/11/16	4/23/16	40.995	-77.701	20.997	-89.392
PAB03	2750-63206	2015	BW	AM	PA	8/26/15	11/3/15	4/18/16	4/26/16	40.995	-77.701	20.997	-86.888
PAB05	2750-63211	2015	BW	AM	PA	8/26/15	10/26/15	4/17/16	4/25/16	40.995	-77.701	21.497	-87.389
PAB07	2750-63225	2015	BW	AM	PA	9/12/15	10/19/15	4/17/16	4/25/16	40.995	-77.701	18.994	-90.894

PAG12	2750-63222	2015	GW	AM	PA	8/8/15	11/14/15	4/7/16	5/15/16	40.995	-77.701	11.984	-69.864
PAH01[a]	2750-63210	2015	HY	AM	PA	9/14/15	11/16/15	3/27/16	4/26/16	40.995	-77.701	10.982	-73.869
PAH06[a]	2750-63228	2015	HY	AM	PA	8/13/15	9/25/15	3/5/16	4/19/16	40.995	-77.701	11.984	-71.867
RLG16	2750-63373	2015	GW	BHT	MN	8/25/15	10/26/15	n/a	n/a	46.533	-93.407	15.989	-85.386
RLG23	2750-63256	2015	GW	BHT	MN	9/4/15	11/1/15	4/17/16	5/12/16	46.533	-93.407	15.989	-85.386
RLGF15	2750-63255	2015	GW	BHT	MN	9/6/15	10/19/15	4/9/16	5/8/16	46.533	-93.407	14.487	-83.884
RMG02	2840-78914	2015	GW	BHT	MB	9/7/15	11/7/15	4/15/16	5/20/16	51.024	-99.941	15.489	-84.385
SHG07	2750-63448	2015	GW	BHT	MN	8/20/15	11/21/15	3/30/16	5/15/16	45.517	-93.699	9.480	-79.377
SLG12	2740-84922	2015	GW	BHT	MB	9/4/15	10/25/15	4/22/16	5/25/16	49.624	-96.307	15.989	-85.386
SLG18	2740-84929	2015	GW	BHT	MB	9/15/15	10/25/15	4/17/16	5/23/16	49.624	-96.307	14.988	-83.884
TAG07	2750-63418	2015	GW	BHT	MN	8/24/15	10/28/15	4/17/16	5/8/16	46.987	-95.611	17.492	-90.393
TAG09	2750-63410	2015	GW	BHT	MN	9/17/15	10/24/15	4/24/16	5/15/16	46.987	-95.611	15.489	-86.388
TAG14	2750-63416	2015	GW	BHT	MN	8/12/15	10/6/15	4/9/16	5/23/16	46.987	-95.611	14.988	-83.383
TNB03	2560-53231	2015	BW	AM	TN	9/4/15	10/28/15	n/a	n/a	35.927	-84.404	18.994	-90.894
TNB09	2560-53254	2015	BW	CH	TN	9/15/15	10/11/15	4/4/16	5/2/16	36.620	-87.515	21.497	-87.890
TNG13	2560-53206	2015	GW	AM	TN	8/20/15	9/12/15	3/31/16	5/11/16	36.291	-84.302	11.984	-71.366
VAG01	2770-39700	2015	GW	AM	VA	9/16/15	10/23/15	3/25/16	4/27/16	38.260	-79.627	11.984	-71.366
VAG02	2770-39698	2015	GW	AM	VA	9/12/15	11/20/15	3/23/16	4/25/16	38.260	-79.627	11.984	-69.864
WIB05	2750-63537	2015	BW	PHT	WI	9/3/15	11/28/15	3/28/16	5/18/16	44.319	-90.131	20.997	-86.888

WIB11	2750-63550	2015	BW	PHT	WI	9/2/15	11/11/15	4/16/16	5/6/16	44.319	-90.131	20.997	-89.893
WIB11	2750-63550	2016	BW	PHT	WI	9/23/16	11/10/16	3/28/17	5/12/17	44.319	-90.131	18.493	-92.396
WIB19	2750-63464	2016	BW	PHT	WI	9/11/16	11/23/16	4/26/17	5/9/17	44.319	-90.131	21.497	-87.389
WIG01	2750-63528	2015	GW	BHT	WI	8/30/15	10/28/15	4/17/16	5/7/16	44.319	-90.131	14.988	-83.383
WIG02	2750-63529	2015	GW	BHT	WI	8/15/15	10/2/15	4/4/16	5/7/16	44.319	-90.131	14.988	-83.383
WIH03[a]	2750-63553	2015	HY	BHT	WI	8/20/15	11/15/15	4/23/16	5/5/16	44.319	-90.131	18.994	-90.894
WIH03[a]	2750-63553	2016	HY	BHT	WI	9/20/16	10/27/16	4/22/17	5/7/17	44.319	-90.131	15.989	-85.386
MN03[a]	2660-29638	2013	GW	BHT	MN	n/a	n/a	n/a	n/a	46.533	-93.407	14.487	-85.386
MN05	2660-29468	2013	GW	BHT	MN	9/9/13	11/5/13	4/8/14	5/17/14	46.533	-93.407	15.489	-84.385
MN06	2690-98281	2013	GW	BHT	MN	9/10/13	11/25/13	4/16/14	5/15/14	46.533	-93.407	15.489	-84.385
MN11	2660-29675	2013	GW	BHT	MN	9/12/13	11/1/13	4/12/14	5/21/14	46.533	-93.407	15.989	-85.386
MN12	2690-98293	2013	GW	BHT	MN	9/10/13	11/11/13	4/25/14	5/28/14	46.533	-93.407	16.991	-88.891
MN14	2660-29420	2013	GW	BHT	MN	9/18/13	10/26/13	n/a	n/a	46.533	-93.407	14.988	-83.383
MN15	2660-29451	2013	GW	BHT	MN	8/29/13	11/24/13	n/a	n/a	46.533	-93.407	15.989	-85.386
MN16	2690-98294	2013	GW	BHT	MN	9/22/13	10/13/13	4/25/14	5/17/14	46.533	-93.407	14.988	-83.884
MN20	2690-98300	2013	GW	BHT	MN	9/15/13	10/19/13	3/31/14	5/19/14	46.533	-93.407	15.989	-85.386
MN25	2690-98039	2014	GW	BHT	MN	8/24/14	11/5/14	4/8/15	5/7/15	46.533	-93.407	15.489	-84.385
MN29	2690-98043	2014	GW	BHT	MN	8/24/14	11/28/14	4/23/15	5/16/15	46.533	-93.407	14.988	-83.383
MN36	2690-98276	2014	GW	BHT	MN	9/1/14	10/28/14	4/22/15	5/6/15	46.533	-93.407	17.492	-90.393

PA05	2520-97749	2014	GW	AM	PA	9/3/14	10/25/14	3/18/15	5/10/15	41.380	-75.180	11.984	-69.864
PA11	2670-48410	2014	GW	AM	PA	9/14/14	10/26/14	3/25/15	5/8/15	41.380	-75.180	9.981	-63.855
TN05	2550-08479	2013	GW	AM	TN	8/14/13	9/10/13	3/21/14	4/11/14	36.291	-84.302	11.483	-72.367
TN06	2470-16207	2013	GW	AM	TN	9/13/13	11/8/13	3/18/14	4/29/14	36.291	-84.302	10.042	-70.539
TN09	2560-53002	2013	GW	AM	TN	8/30/13	9/27/13	3/24/14	4/27/14	36.291	-84.302	11.984	-69.864
TN10	2470-16213	2013	GW	AM	TN	9/8/13	10/10/13	3/19/14	4/19/14	36.291	-84.302	11.984	-71.366
TN13	2560-53004	2013	GW	AM	TN	8/17/13	9/13/13	3/27/14	4/30/14	36.291	-84.302	11.984	-71.366
TN13	2560-53004	2014	GW	AM	TN	8/14/14	9/11/14	3/19/15	4/16/15	36.291	-84.302	11.984	-71.366
TN16	2560-53009	2013	GW	AM	TN	9/10/13	10/3/13	3/8/14	4/17/14	36.291	-84.302	11.984	-71.867
B1	n/a	2016	GW	BHT	WI	9/11/16	10/24/16	4/15/16	5/15/16	44.650	-91.260	14.786	-86.029
B2	n/a	2016	GW	BHT	MN	9/3/16	10/20/16	4/27/16	5/20/16	46.920	-92.760	14.784	-86.032
B3	n/a	2016	GW	BHT	WI	9/17/16	10/26/16	5/1/16	5/22/16	46.340	-91.630	14.786	-86.033
B4	n/a	2016	GW	BHT	WI	8/27/16	11/21/16	4/14/16	5/10/16	46.500	-91.260	14.787	-86.025
B5	n/a	2016	GW	BHT	MI	9/5/16	10/13/16	4/17/16	5/27/16	43.640	-83.290	10.215	-84.659
B6	n/a	2016	GW	BHT	WI	9/15/16	11/8/16	4/29/16	5/16/16	45.690	-90.070	12.945	-85.778
B7	n/a	2016	GW	BHT	WI	9/5/16	11/12/16	4/28/16	5/25/16	46.050	-91.170	12.937	-85.782
B8	n/a	2016	GW	BHT	MN	9/2/16	10/28/16	4/16/16	5/12/16	47.570	-92.510	12.928	-85.780
B9	n/a	2016	GW	BHT	WI	9/17/16	10/24/16	4/20/16	5/18/16	45.570	-91.200	13.234	-86.050
B10	n/a	2016	GW	BHT	MN	9/5/16	10/17/16	4/29/16	5/9/16	46.460	-93.280	13.236	-86.054
B11	n/a	2016	GW	BHT	WI	9/17/16	10/19/16	4/18/16	5/10/16	44.890	-88.670	13.242	-86.055
B12	n/a	2016	GW	BHT	WI	8/29/16	10/26/16	3/25/16	5/16/16	44.620	-90.700	13.240	-86.052
B13	n/a	2016	GW	BHT	WI	8/30/16	11/10/16	4/23/16	5/29/16	45.400	-92.600	15.178	-87.480
B14	n/a	2016	GW	BHT	WI	9/11/16	10/9/16	4/20/16	5/11/16	46.020	-90.260	15.364	-88.690
B15	n/a	2016	GW	BHT	MN	8/29/16	10/26/16	4/6/16	5/9/16	46.520	-94.420	15.377	-88.702

B16	n/a	2016	GW	BHT	MN	8/24/16	11/9/16	4/28/16	5/17/16	46.310	-93.870	15.671	-88.684
B17	n/a	2016	GW	BHT	ON	8/28/16	10/23/16	4/30/16	5/17/16	48.860	-93.570	15.364	-88.677
B18	n/a	2016	GW	BHT	WI	9/10/16	10/11/16	4/11/16	5/3/16	43.250	-88.280	14.787	-86.025
B19	n/a	2016	GW	BHT	WI	n/a	n/a	4/22/16	5/11/16	46.320	-90.690	12.941	-85.780
B20	n/a	2016	GW	BHT	MN	8/27/16	10/31/16	4/15/16	5/16/16	47.040	-94.110	15.208	-87.505

[a] Individual omitted from analysis.

*Population trends could not be estimated for blue-winged warblers in North Carolina. We combined blue-winged warblers tracked from breeding sites in North Carolina (*n* = 1) with blue-winged warblers tracked from nearby sites in Tennessee.

Table S2. Summary table of the geolocators used in this analysis and collected from *Vermivora* warblers at 26 sites across the North American breeding distribution and five sites within the Central America nonbreeding distribution. Breeding sites are stratified by Bird Conservation Region (BCR).

	Autumn migration					Spring migration				
Breeding Bird Conservation Region	2013	2014	2015	2016	**Total**	2014	2015	2016	2017	**Total**
Golden-winged warblers										
Boreal Hardwood Transition	8	3	20[a]	19	**50**	6	3	37[a]	0	**46**
Appalachian Mountains	6	3[b]	4	0	**13**	6	3[b]	4	0	**13**
Blue-winged warblers										
Appalachian Mountains	0	0	13	0	**13**	0	0	11	0	**11**
Prairie Hardwood Transition	0	0	6	2[c]	**8**	0	0	5	2[c]	**7**
Central Hardwoods	0	0	5	0	**5**	0	0	5	0	**5**
Total	14	6	48	21	**89**	12	6	62	2	**82**

[a] Includes one female golden-winged warbler and two male golden-winged warblers that were also tracked in autumn 2014 and spring 2015.

[b] Includes one male golden-winged warbler also tracked in autumn 2013 and spring 2014.

[c] Includes one male blue-winged warbler also tracked in autumn 2015 and spring 2016.

Table S3. Summary of a power analysis of multiple linear regression models with five parameters (not including the intercept) corresponding with multiple linear regression models with proxy terms for breeding and nonbreeding factors (Breeding latitude, Breeding longitude, Nonbreeding latitude, Nonbreeding longitude and an additional migration risk-factor term. Small, medium, and large effect sizes are generally considered to correspond with f^2-values of 0.02, 0.15, and 0.35, respectively.

Number of coefficients (u)[a]	Number of observations (v)[b]	Model R^2	Effect size (f^2)[c]	Significance level	Power
5	9	0.05	0.05	0.05	0.10
5	9	0.20	0.25	0.05	0.32
5	9	0.40	0.67	0.05	0.67
5	9	0.60	1.50	0.05	0.95
5	9	0.63*	1.68	0.05	0.97

[a] Number of coefficients that are being estimated in the model (not including intercept)

[b] Number of observations (unique subregional breeding population trend) minus the number of coefficients minus one: effectively the degrees of freedom

[c] Effect size is calculated as $R^2/(1- R^2)$

* Actual R^2 of multiple linear regression model including migratory connectivity terms (Br Lat, Br Lon, NB Lat, NB Lon, and Forest and Shrub Cover.

Table S4. Summary of a power analysis of simple linear regression models of the relationship between individual migration risk-factors and subregional (state- and province-level) population trend from 2000–2015. Small, medium, and large effect sizes are generally considered to correspond with f^2-values of 0.02, 0.15, and 0.35, respectively.

Number of coefficients (u)[a]	Number of observations (v)[b]	Model R^2	Effect size (f^2)[c]	Significance level	Power
1	13	0.01	0.01	0.05	0.07
1	13	0.03	0.03	0.05	0.10
1	13	0.07	0.08	0.05	0.17
1	13	0.13	0.15	0.05	0.28
1	13	0.26	0.35	0.05	0.57
1	13	0.52	1.08	0.05	0.96

[a] Number of coefficients that are being estimated in the model (not including intercept)

[b] Number of observations (unique subregional breeding population trend) minus the number of coefficients minus one: effectively the degrees of freedom

[c] Effect size is calculated as $R^2/(1- R^2)$

Table S5. Performance of linear regression models assessing the relationship between annual exposure to individual migration risk-factor variables and subregional *Vermivora* warbler population trends (i.e., state- and province-level). We used migration risk-factor data extracted from 10%, 25%, and 50% core-use areas. Model name (Model), the number of variables in each model (k), difference between Akaike's Information Criterion adjusted for sample size of top-performing model (ΔAIC_c), and model deviance (-2*log-likelihood) are provided. Models in bold are >2 AIC_c from the intercept-only model.

Model	*k*	ΔAIC_c	-2*log-likelihood
10% core-use area			
Agriculture	3	0.0	502.3
Wind energy	3	0.8	503.1
Null (intercept-only)	2	1.7	506.1
Tornados	3	3.0	505.3
Forest and shrub cover	3	3.5	505.7
Communications towers	3	3.5	505.8
Human footprint	3	3.6	505.8
Net change in forest cover 2000–2010	3	3.6	505.9
Hurricanes	3	3.8	506.1
25% core-use area			
Agriculture	**3**	**0.0**	**501.6**
Tornados	3	1.5	503.1
Forest and shrub cover	3	1.7	503.3
Net change in forest cover 2000–2010	3	2.1	503.7
Wind energy	3	2.2	503.7
Null (intercept-only)	2	2.4	506.1
Communications towers	3	3.6	505.2
Human footprint	3	4.0	505.6
Hurricanes	3	4.1	505.7
50% core-use area			
Wind energy	**3**	**0.0**	**498.1**
Tornados	**3**	**0.6**	**498.7**
Forest and shrub cover	**3**	**0.8**	**498.9**
Agriculture	**3**	**2.8**	**500.9**
Human footprint	3	5.1	503.2
Net change in forest cover 2000–2010	3	5.4	503.5
Null (intercept-only)	2	5.9	506.1

Hurricanes	3	5.9	504.0
Communications towers	3	7.9	505.9

Table S6. Coefficient estimates of linear regression models assessing the relationship between individual migration risk-factor variables (sum of autumn and spring migration periods) and subregional (state- and population-level) *Vermivora* warbler population trends. We used migration risk-factor data extracted from 10%, 25%, and 50% core-use areas. Shown are models from Table S8 that were >2 AIC$_c$ from the intercept-only model. Coefficient being estimated (Parameter), the standard error of the coefficient estimate (Std. Error), *P*-value, and whether the direction of the relationship was congruent with expectations are provided.

Parameter*	Estimate	Std. Error	*P*-value	Direction of effect congruent with expectations?
10% core-use area				
N/A				
25% core-use area				
Agriculture	1.29	0.61	0.04	No, expected negative relationship
50% core-use area				
Wind energy	1.70	0.59	0.005	No, expected negative relationship
Tornados	1.64	0.60	0.007	No, expected negative relationship
Forest and shrub cover	-1.38	0.60	0.02	No, expected positive relationship
Agriculture	1.62	0.60	0.008	No, expected negative relationship

*All parameters are scaled (mean-centered)

Table S7. Performance of generalized linear models considered in an information-theoretic, hierarchical regression analysis exploring whether the addition of individual migration risk-factor variables (sum of autumn and spring migration periods) explains additional variation relative to a base model of migratory connectivity terms (breeding location, nonbreeding location) with previously described associations with *Vermivora* warbler population trends. Model name (Model), the number of variables in each model (k), difference between Akaike's Information Criterion adjusted for sample size of top-performing model (ΔAIC_c), and model deviance (-2*log-likelihood) are provided. Base model (Base) included five estimated parameters: intercept, breeding latitude, breeding longitude, nonbreeding latitude, nonbreeding longitude.

Model	*k*	ΔAIC_c	-2*log-likelihood
10% core-use area			
Base + Forest and shrub cover	7	0.0	424.5
Base	6	0.3	427.2
Base + Tornados	7	0.3	424.8
Base + Agriculture	7	0.6	425.0
Base + Net change in forest cover 2000-2010	7	1.0	425.5
Base + Hurricanes	7	1.7	426.2
Base + Communications towers	7	2.2	426.7
Base + Wind energy	7	2.3	426.8
Base + Human footprint	7	2.3	426.8
Full model	14	10.7	416.4
25% core-use area			
Base + Communications towers	7	0.0	424.3
Base	6	0.4	427.2
Base + Wind energy	7	1.8	426.1
Base + Agriculture	7	1.8	426.1
Base + Tornados	7	2.1	426.4
Base + Hurricanes	7	2.1	426.5
Base + Forest and shrub cover	7	2.2	426.6
Base + Net change in forest cover 2000-2010	7	2.8	427.1
Base + Human footprint	7	2.8	427.2
Full model	14	9.9	415.4
50% core-use area			

Base	6	0.0	427.2
Base + Communications towers	7	1.8	426.5
Base + Hurricanes	7	2.1	426.9
Base + Agriculture	7	2.3	427.1
Base + Forest and shrub cover	7	2.4	427.2
Base + Tornados	7	2.4	427.2
Base + Wind energy	7	2.4	427.2
Base + Net change in forest cover 2000-2010	7	2.4	427.2
Base + Human footprint	7	2.4	427.2
Full model	14	18.4	424.4

Table S8. Model performance of factors considered in an information-theoretic, hierarchical regression analysis exploring whether the addition of individual migration risk-factor variables experienced before crossing the Gulf of Mexico (25th percentile core-use area) in both autumn and spring (Fig. S3) explains additional variation relative to a base model including proxy terms (breeding location, nonbreeding location) intended to account for previously described associations between *Vermivora* warbler population trends and factors occurring within breeding and nonbreeding periods. Model name (Model), the number of variables in each model (*k*), difference between Akaike's Information Criterion adjusted for sample size of top-performing model (ΔAIC_c), and model deviance (-2*log-likelihood) are provided. Base model (Base) included five estimated parameters: intercept, breeding latitude, breeding longitude, nonbreeding latitude, nonbreeding longitude. The variable "Overall" was calculated by summing standardizing individual migration risk-factor rasters ($n = 8$; assigning equal weight to all risk factors).

Autumn	*k*	ΔAIC_c	-2*log-likelihood
Base[a]	6	0.0	466.8
Base + Wind energy	7	0.3	464.7
Base + Net change in forest cover 2000–2010	7	0.7	465.1
Base + Communications towers	7	1.4	465.8
Base + Hurricanes	7	1.9	466.3
Base + Forest and shrub cover	7	2.1	466.6
Base + Agricultural cover	7	2.3	466.7
Base + Human footprint	7	2.3	466.7
Base + Overall	7	2.3	466.7
Base + Tornados	7	2.3	466.8
Spring*	***k***	ΔAIC_c	**-2*log-likelihood**
Base[b]	6	0.0	349.6
Base + Forest and shrub cover	7	0.9	348.0
Base + Overall	7	1.8	348.9
Base + Human footprint	7	2.0	349.2
Base + Net change in forest cover 2000–2010	7	2.3	349.4
Base + Agricultural cover	7	2.4	349.5

[a] AIC_c of top model = 493.7

[b] AIC_c of top model = 363.1

*Data for wind energy, communications towers, hurricanes, and tornados not available for area considered during spring migration (i.e., only available for United States).

Table S9. Variable inflation factors (VIF) used to assess the multicollinearity of terms used in the partial least squares (PLS) regression analysis. The PLS analysis modeled the relative importance of migration risk-factors (experienced during migration; 25th percentile core-use area) and breeding and nonbreeding factors (land-cover characteristics at breeding and nonbreeding sites) in explaining recent population trends in *Vermivora* warblers. VIF scores > 5 denote moderate to strong multicollinearity and are bold.

Variable category	Variable name	Variable inflation factor (VIF)
Migration risk-factor	Wind turbines	**5.7**
Migration risk-factor	Communications towers	2.7
Migration risk-factor	Hurricanes	3.3
Migration risk-factor	Tornados	**5.7**
Migration risk-factor	Agriculture	**9.3**
Migration risk-factor	Forest and shrub cover	**9.4**
Migration risk-factor	Human footprint	**15.2**
Migration risk-factor	Net change forest cover 2000-2010	2.3
Breeding factor	Forest and shrub cover	1.5
Breeding factor	Human footprint	2.1
Breeding factor	Net change forest cover 2000-2010	1.8
Nonbreeding factor	Forest and shrub cover	1.9
Nonbreeding factor	Human footprint	1.3
Nonbreeding factor	Net change forest cover 2000-2010	1.40

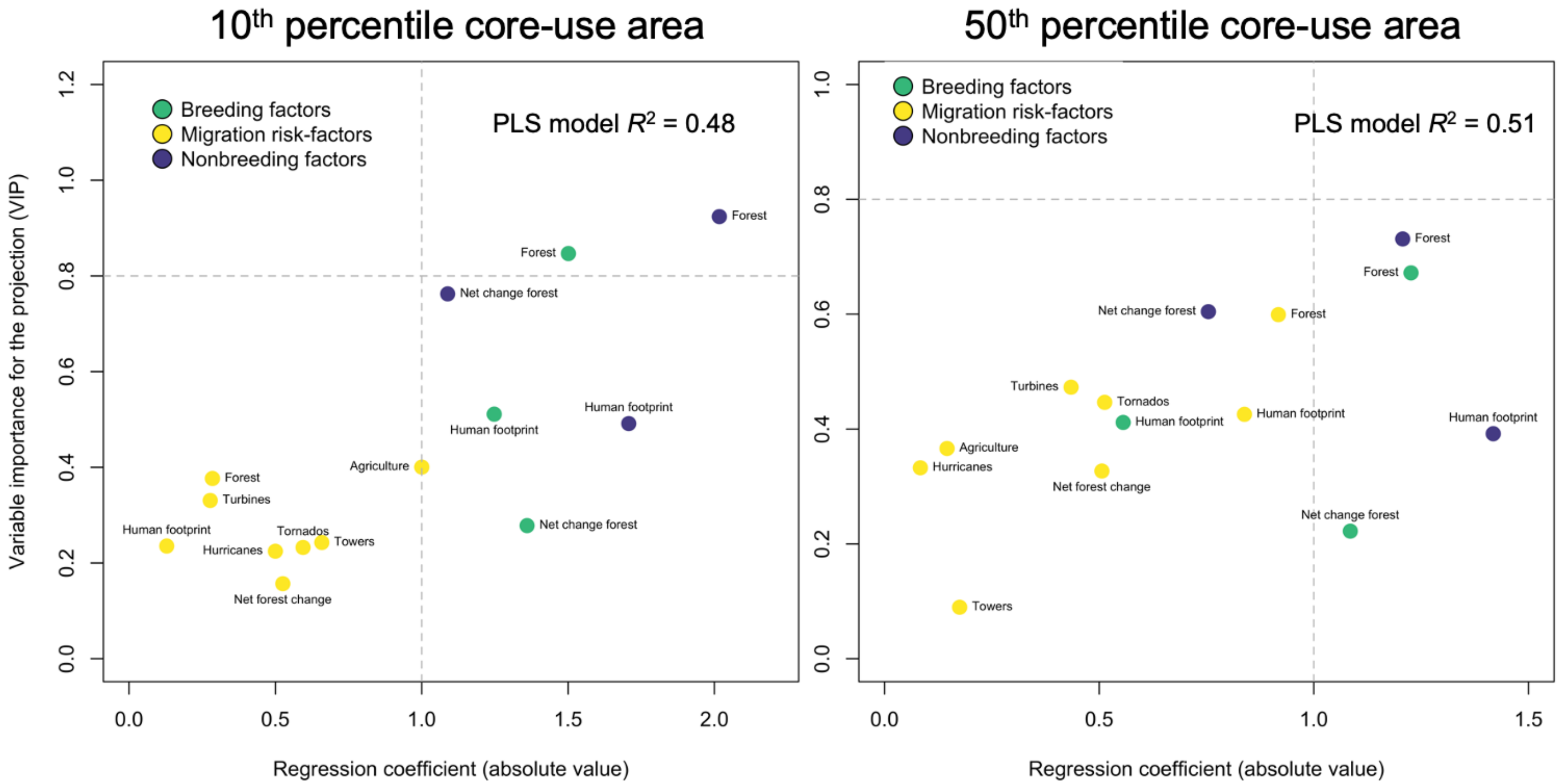
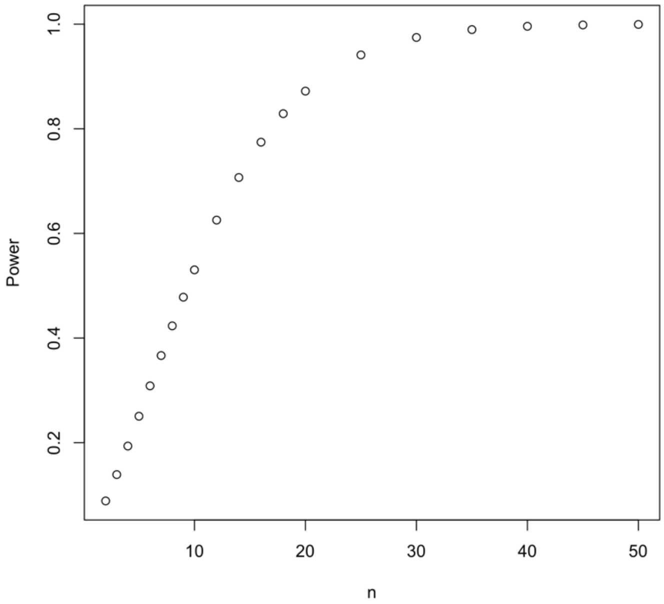


Figure S1. Comparison plots of the absolute value of regression coefficients and variable importance for the projection (VIP) of explanatory variables included in partial least squares (PLS) regression models relating explanatory variables to variation in recent population trends of *Vermivora* warblers (i.e., 2000–2010) at two different core-use area scales (10th percentile, 50th percentile). Explanatory variables fall into three categories: those associated with migration risk-factors (migration risk-factors terms; yellow circles), factors associated with the breeding period, and factors associated with the sedentary nonbreeding period. Gray dashed lines denote regression coefficients with absolute values > 1 and VIP > 0.8, which correspond with terms that are important in the PLS model. Test set validation of PLS model performance is presented (R^2).

Figure S2. Predicted power versus sample size of one-way analysis of variance (ANOVA) given the scaled mean, within-group, and among-group variances of the “Hurricane” migration risk-factor variable calculated for 81 *Vermivora* warblers. Warblers were classified into five groups based on Bird Conservation Region (BCR) and species. Sample size increments in the plot below are not constant: 2–10, by 1; 12–20, by 2; 22–50, by 5. We estimated the among-group variance without blue-winged warblers from breeding populations in the Central Harwood Bird Conservation Region (i.e., *n* = 4 groups) because the rate of within-group variance was an order of magnitude greater than any of the other groups.



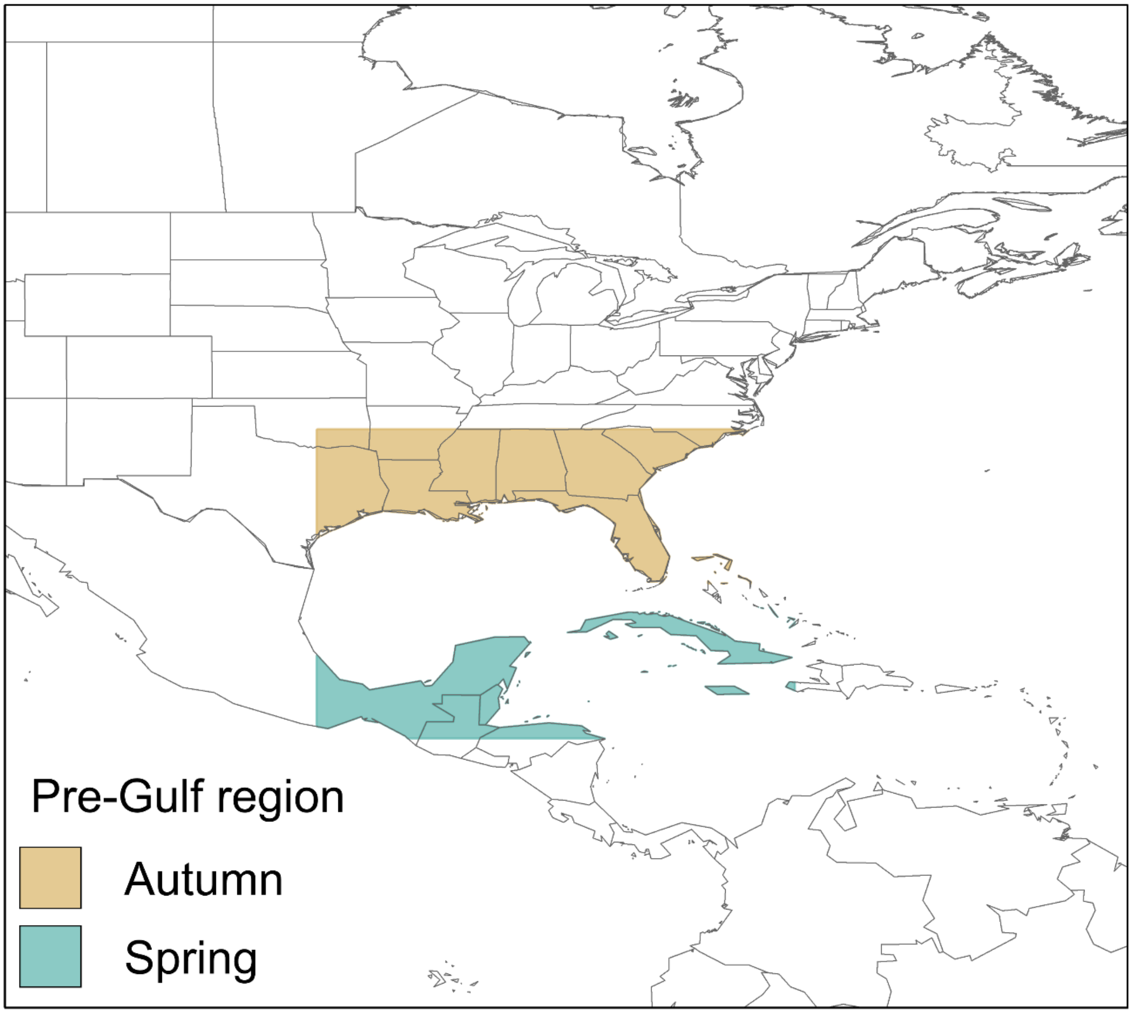


Figure S3. Map of region used to test for associations between *Vermivora* warbler population trends and migration risk-factors experienced in stopover regions before crossing the Gulf of Mexico during autumn (25–35°; tan) and spring (15–23.5°; blue) migration periods.

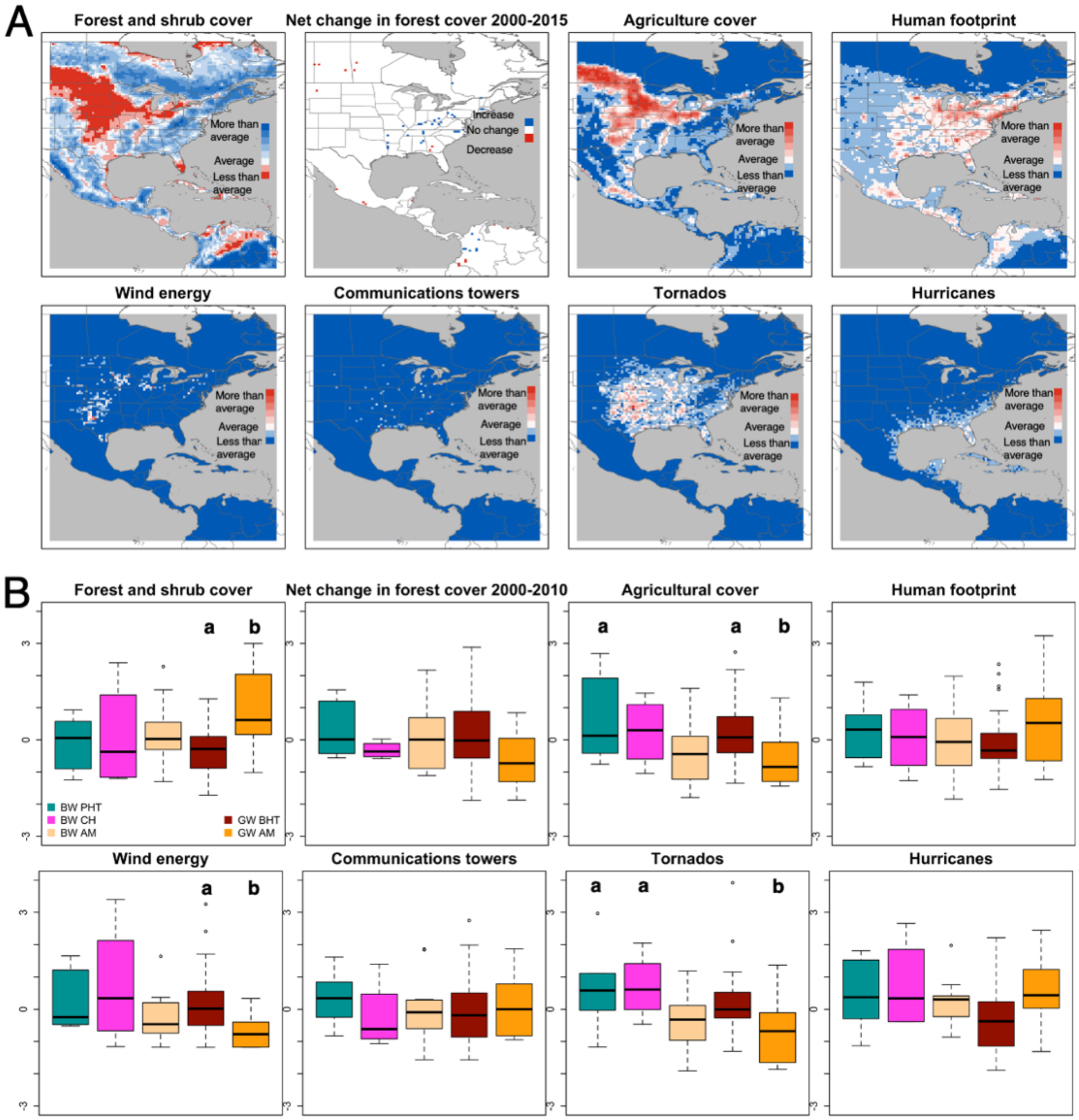


Figure S4. The spatial distribution of mean-adjusted individual migration risk-factors we considered ($n = 8$; A) are displayed using color schemes corresponding with their expected association with population-trends (i.e., positive association = blue for higher-than-average values, negative association = red for higher-than-average values; see Table 1). Boxplots (B) show the scaled exposure of different populations (based on the exposure of individuals tracked within each population; colors correspond with the center panel) of *Vermivora* warblers to each migration risk-factor. Populations that experienced different levels of exposure (based on one-way ANOVA and Tukey HSD; $P < 0.05$) are denoted with letters. Populations are defined based on BCR and species (blue-winged warbler [BW] or golden-winged warbler [GW]) in boxplots: Prairie Hardwood Transition BCR (BW PHT, teal), Central Hardwoods BCR (BW CH, pink), Appalachian Mountains BCR (BW AM, light orange; GW AM, dark orange), and Boreal Hardwood Transition (GW BHT; maroon) BCR.

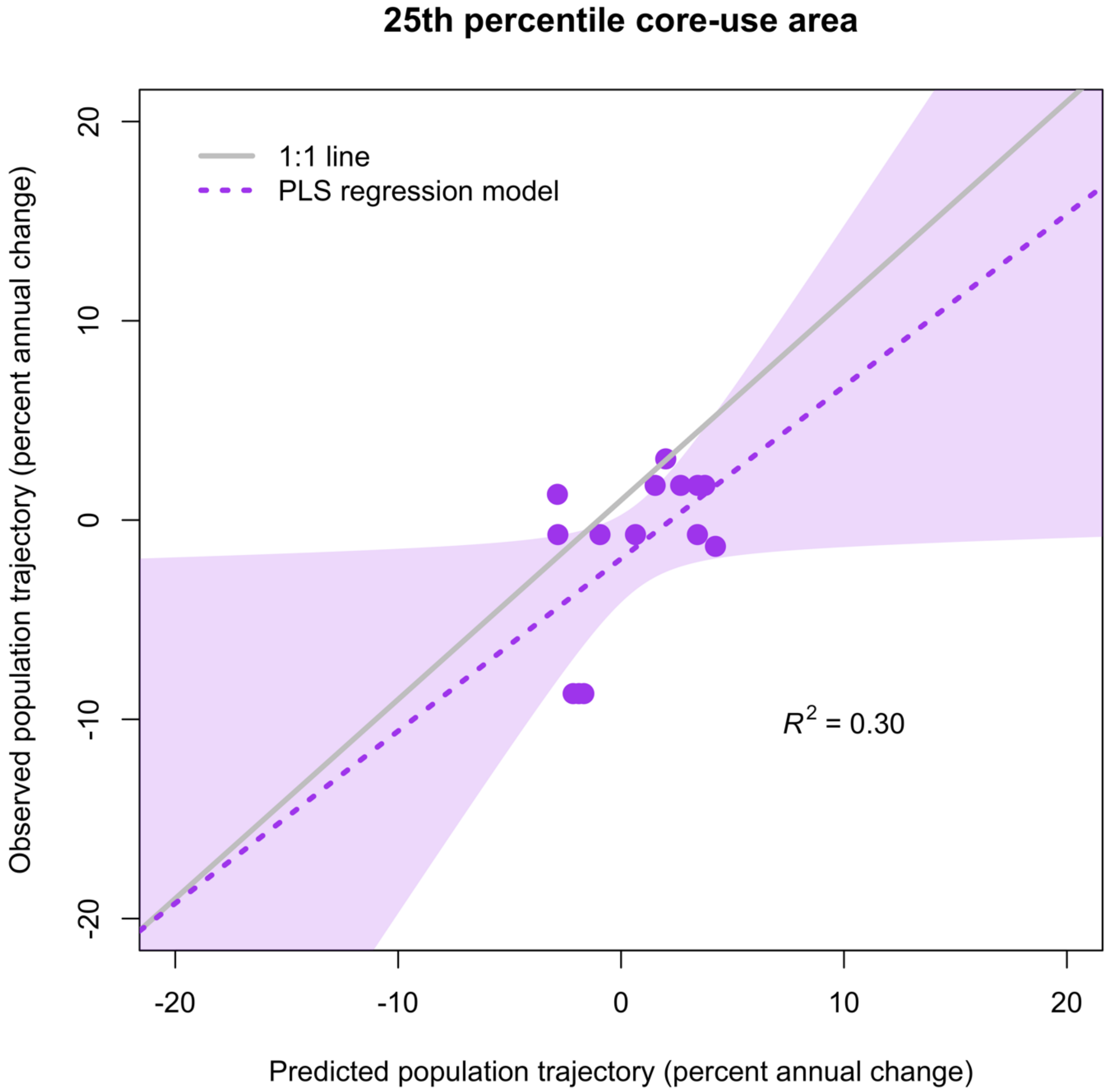


Figure S5. Test set validation of partial least squares (PLS) regression model (predicted vs. observed population trends). We trained a PLS regression model using 80% of the data and predicted the withheld (test) data to assess model accuracy. Predicted points are shown in purple and the fitted model is represented by a dashed purple line (shaded area = 95% CI).

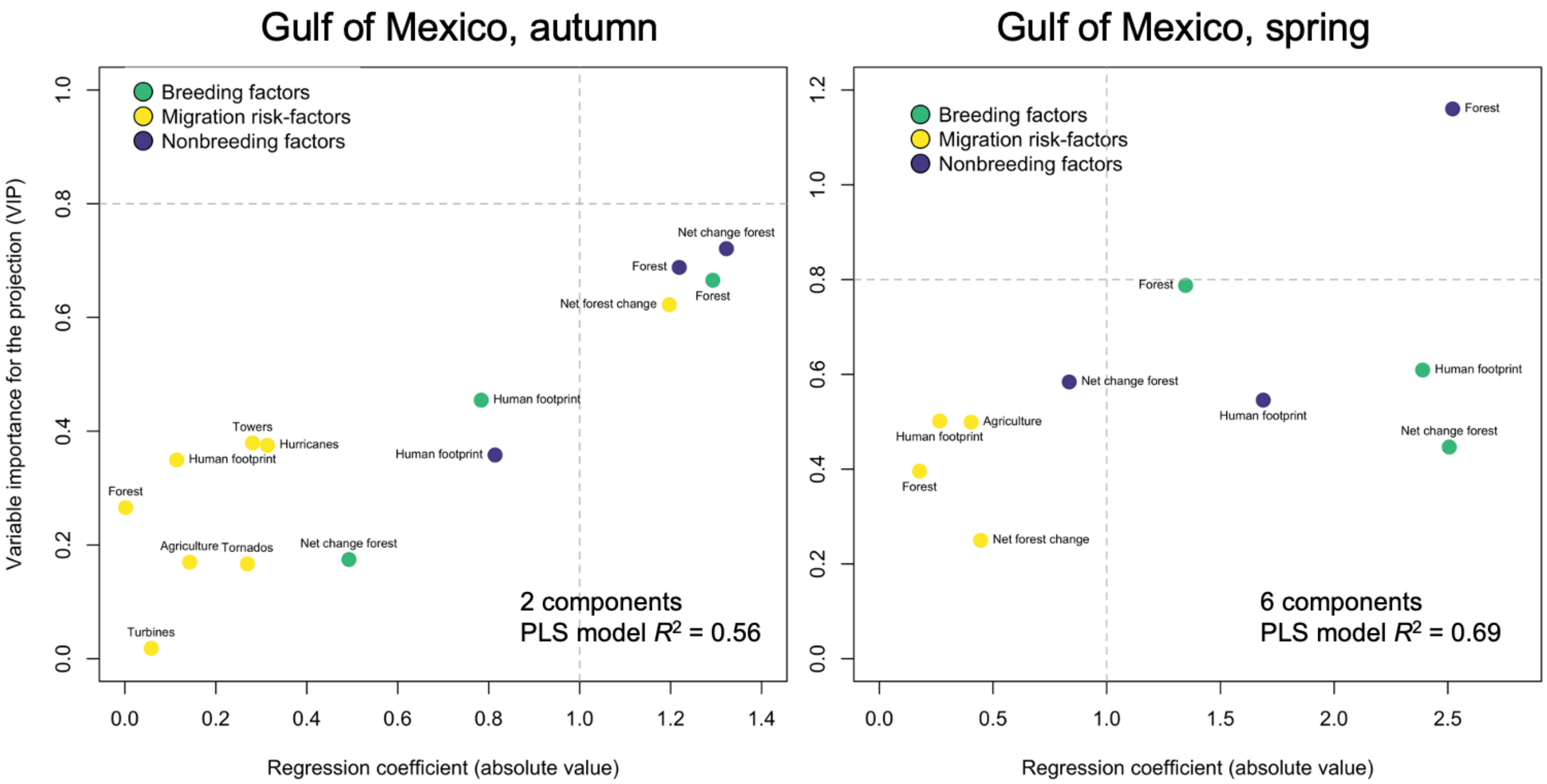


Figure S6. Comparison plots of the absolute value of regression coefficients and variable importance for the projection (VIP) of explanatory variables included in partial least squares (PLS) regression models relating explanatory variables to variation in recent population trends of *Vermivora* warblers (i.e., 2000–2010) in areas near the Gulf of Mexico during autumn and spring migrations. Explanatory variables fall into three categories: those associated with migration risk-factors (migration risk-factors terms; yellow circles), factors associated with the breeding period (breeding factors; green circles), and factors associated with the sedentary nonbreeding period (nonbreeding factors; purple circles). Gray dashed lines denote regression coefficients with absolute values > 1 and VIP > 0.8, which correspond with terms that are important in the PLS model. Test set validation of PLS model performance is presented (R^2).

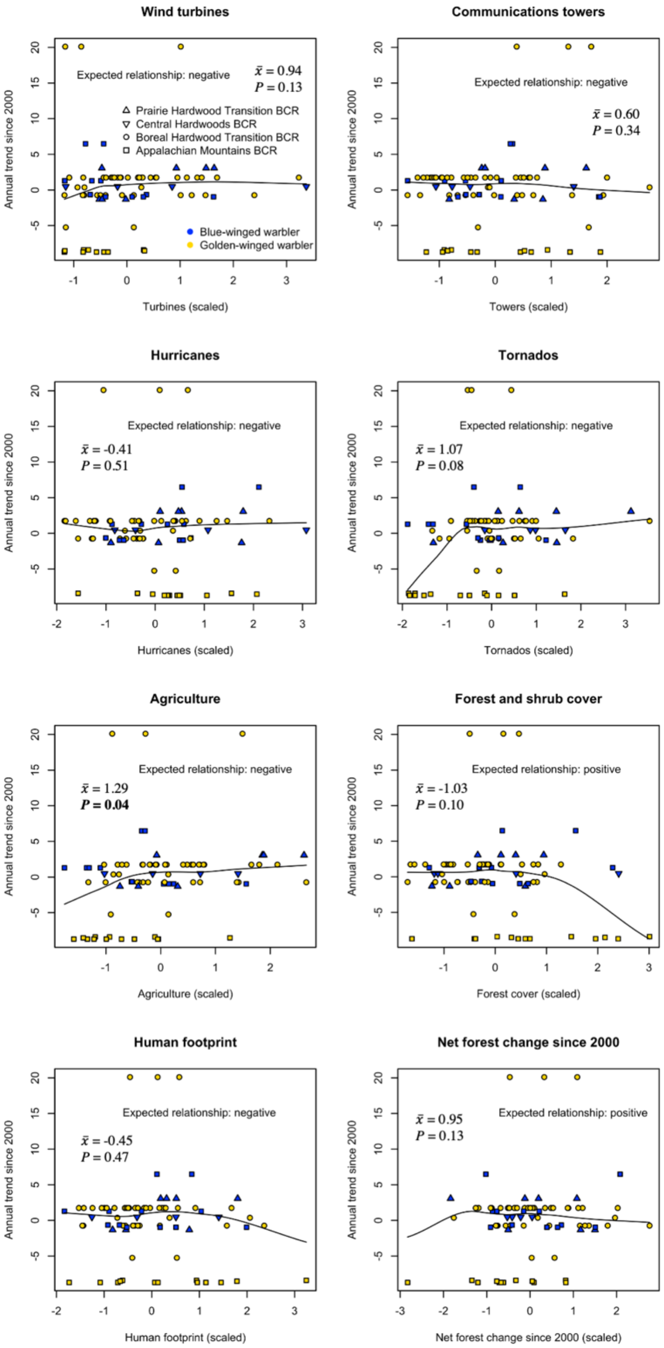


Figure S7. Scatterplots of the association (loess curve; black line) between recent annual population trend (since 2000) and exposure of individual *Vermivora* warblers to migration risk-factors. Blue-winged warblers (blue) and golden-winged warblers (gold) from different Bird Conservation Regions are presented with different shapes. Statistical relationships (slope and *P*-value) between individual risk factors and subregional (state- and province-level) population trends assessed with simple linear regression also are presented with statistically significant relationships appearing in bold.