*Contributed Paper*

# A genoscape-network model for conservation prioritization in a migratory bird

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**Abstract:** Migratory animals are declining worldwide and coordinated conservation efforts are needed to reverse current trends. We devised a novel genoscape-network model that combines genetic analyses with species distribution modeling and demographic data to overcome challenges with conceptualizing alternative risk factors in migratory species across their full annual cycle. We applied our method to the long distance, Neotropical migratory bird, Wilson's Warbler (*Cardellina pusilla*). Despite a lack of data from some wintering locations, we demonstrated how the results can be used to help prioritize conservation of breeding and wintering areas. For example, we showed that when genetic, demographic, and network modeling results were considered together it became clear that conservation recommendations will differ depending on whether the goal is to preserve unique genetic lineages or the largest number of birds per unit area. More specifically, if preservation of genetic lineages is the goal, then limited resources should be focused on preserving habitat in the California Sierra, Basin Rockies, or Coastal California, where the 3 most vulnerable genetic lineages breed, or in western Mexico, where 2 of the 3 most vulnerable lineages overwinter. Alternatively, if preservation of the largest number of individuals per unit area is the goal, then limited conservation dollars should be placed in the Pacific Northwest or Central America, where densities are estimated to be the highest. Overall, our results demonstrated the utility of adopting a genetically based network model for integrating multiple types of data across vast geographic scales and better inform conservation decision-making for migratory animals.

**Keywords:** birds, conservation planning, evolution, genetics, migratory

Un Modelo de Redes de Panorama Poblacional para la Priorización de la Conservación de un Ave Migratoria

**Resumen:** Los animales migratorios están pasando por una declinación mundial y se requieren esfuerzos coordinados de conservación para revertir las tendencias actuales. Diseñamos un modelo novedoso de redes de panorama poblacional que combina el análisis genético con el modelado de la distribución de especies y los datos demográficos para sobreponerse a los obstáculos con la conceptualización de los factores alternativos de riesgo en las especies migratorias durante su ciclo anual completo. Aplicamos nuestro método al chipe de corona negra (*Cardellina pusilla*), un ave migratoria neotropical que recorre largas distancias. A pesar de la falta de datos de algunas localidades de invernación, mostramos cómo pueden usarse los resultados para ayudar a priorizar la conservación de las áreas de reproducción y de invernación. Por ejemplo, mostramos que cuando se consideraron en conjunto los resultados del modelado genético, demográfico y de redes queda claro que las recomendaciones de conservación diferirán dependiendo de si el objetivo es preservar linajes genéticos únicos o el mayor número de aves por unidad de área. Más específicamente, si el objetivo es la conservación de los linajes genéticos, entonces los recursos limitados deberían enfocarse en preservar el hábitat en la Sierra de California, la Cuenca de las

Rocallosas, la costa de California (lugares en donde se reproducen los tres linajes genéticos más vulnerables) o en el oeste de México (en donde dos de los tres linajes más vulnerables pasan el invierno). Alternativamente, si el objetivo es la conservación del mayor número de individuos por unidad de área, entonces el financiamiento limitado debería aplicarse en el noroeste del Pacífico o en América Central, en donde se estima que las densidades poblacionales son las más altas. En general, nuestros resultados demostraron la utilidad de adoptar un modelo de redes basadas en la genética para la integración de datos a lo largo de escalas geográficas amplias y para informar de mejor manera la toma de decisiones de conservación para los animales migratorios.

**Palabras Clave:** aves, evolución, genética, migratorio, planeación de la conservación

**摘要:** 世界范围内迁徙动物的数量正在减少, 需要采取协调一致的保护措施来扭转目前的趋势。我们设计了一种新的遗传谱网络模型, 通过整合遗传分析与物种分布模型和种群统计数据, 来应对确定迁移物种在完整年周期中面临风险因素的挑战。我们将这一方法应用于一种长距离迁徙的新热带候鸟——黑头威森莺 (*Cardellina pusilla*)。尽管缺乏部分越冬地点数据, 我们仍展示了如何利用这些结果来确定优先保护的繁殖地和越冬地。例如, 当同时考虑遗传、种群统计和网络模型结果时, 可以明显发现, 针对不同的保护目标——保护独特的遗传谱系或确保单位面积内得到保护的鸟类数量最大化, 所得出的保护建议也不同。具体来说, 如果以保护遗传谱系为目标, 那么有限的资源应集中在保护加利福尼亚山脉、落基山盆地和加利福尼亚海岸的栖息地, 这些地区是黑头威森莺最濒危的三支遗传谱系的繁殖地, 或者集中保护墨西哥西部, 那里是三支最濒危遗传谱系中两支谱系的越冬地。然而, 如果以保护单位面积最大数量的个体为目标, 那么有限的保护资金应投向太平洋西北部或中美洲, 那里的鸟类密度估计值最高。总的来说, 我们的研究结果表明, 采用基于遗传的网络模型来整合跨越广阔地理范围的多类型数据是非常有用的, 并将更好地为迁徙动物的保护决策提供信息。【翻译: 胡怡思; 审校: 聂永刚】

**关键词:** 鸟类, 遗传学, 迁徙, 保护规划, 进化

## Introduction

Accelerating global alteration of the environment has placed new urgency on understanding and preserving biological diversity. Recent work reveals that ecologies, genomes, and habitat changes can vary greatly across the range of a species, particularly under increasing anthropogenic changes (Chen et al. 2011; Yackulic et al. 2011; Bay et al. 2018). Understanding the population dynamics and ecology of a species allows for preservation of natural biological systems (Thomassen et al. 2010; Charmantier & Gienapp 2014; Fitzpatrick & Keller 2015), thus ensuring processes that produce and maintain biodiversity can persist in a changing world (Stockwell et al. 2003; Pecl et al. 2017). Despite recent calls for improvements (Small-Lorenz et al. 2013), current tools for conservation decision-making are often limited in their ability to identify and evaluate alternative approaches.

For long-distance migratory species, ecological requirements, resource availability, and habitat suitability often have dramatic spatiotemporal variability; thus, these species face unique threats from climate and anthropogenic changes across their annual cycle (e.g., Ahola et al. 2004; Burrows et al. 2011; Rosenberg et al. 2019). Knowledge of the links between breeding and nonbreeding populations (migratory connectivity [Webster et al. 2002]) is critical for conservation of migratory species. Advancements in tracking technologies have greatly improved the ability to map population-specific movement across the annual cycle (Stutchbury et al.

2009; Bridge et al. 2013; Ruegg et al. 2014), but even when knowledge of migratory connections is extensive, integrating known patterns with demographic trends and habitat use can be difficult.

Spatial migratory networks, graph-based models composed of nodes that represent nonbreeding and breeding regions, and links that represent the degree of known migration between nodes (Taylor and Norris 2010) are particularly useful in combining disparate types of data to identify conservation priorities in migratory populations. A limitation of migratory-network analyses, however, is that breeding nodes typically are delineated based only on loosely defined environmental regions, rather than on demographically distinct subpopulations (Stanley et al. 2014; Taylor and Stutchbury 2016; Knight et al. 2018). Some methods have been developed that apply demographic attributes from long-term monitoring data to delineate natural population boundaries (Rushing et al. 2016) or use occurrence of clearly defined breeding colonies (Wiederholt et al. 2013), but these may fall short if populations that appear demographically independent are actually connected by ongoing gene flow. Thus, improved definitions of demographic units that form the basis of migratory networks would help advance the utility of such approaches for conservation of migratory animals.

Use of genetic data to define demographic units within a species is considered the benchmark for the delineation of conservation units (Moritz 1994; Palsbøll et al. 2007). Until recently, this type of designation relied on single gene approaches that might only reveal older

evolutionary splits within species. Genome-wide genetic sequencing has made it possible to also identify patterns of local and more recent adaptation (Funk et al. 2012; Smith et al. 2014), and both of these sources of genetic differentiation are important to consider in conservation planning. While using genetically defined population boundaries to delineate breeding nodes in a migratory network holds great promise, a framework for incorporating genetic data in network analysis is lacking.

We built such a framework to incorporate genetic data into a migratory network analysis of Wilson's Warbler (*Cardellina pusilla*). Although North American Breeding Bird Survey (BBS) data suggest this species' populations have declined by 61% over the past 50 years, trends vary across its range (Sauer et al. 2017), and reasons for population-specific declines remain unknown. We used Wilson's warbler for our analysis because it has a well-defined genoscape (map of genetic variation across geographic space) (Ruegg et al. 2014), known breeding and wintering ranges, and an abundance of observations across the species range. In addition, previous genome-wide genetic analyses identified 6 genetically distinct lineages with different connectivity to wintering areas, the strength of which had not been quantified (Ruegg et al. 2014). The ability to quantify migratory connections with network models may inform the designation of management units of migratory species across their full annual cycle.

To demonstrate the utility of a genoscape-network framework for managing migratory species across their full annual cycle, we combined published genetic results for Wilson's Warbler with Breeding Bird Survey (BBS) data to provide, we believe, the first migratory network model that integrates genetic information below the species level. We defined breeding nodes based on the geographic distribution of genetic lineages on the breeding grounds and wintering nodes based on information on geography and ecoregion designations. To estimate population size in species for which data may be limited, we used BBS records to derive a species distribution model and used the results to estimate habitat suitability and an index of population size within each node. We then combined genetic assignments to breeding nodes with population size estimates to estimate the strength and uncertainty of migratory connections (Procházka et al. 2017). Using these estimates, we ultimately sought to determine what conservation measures should be taken if the goal is to preserve unique genetic lineages; how would these measures differ if the goal is to preserve the largest number of birds per unit area; and the utility, potential, and possible limitations of a genoscape-network modeling approach for weighting alternative approaches for migratory species when data from different parts of the annual cycle (i.e., wintering grounds) may be limited.

## Methods

### Breeding- and Wintering-Node Definitions

We constructed a network with 2 types of nodes: breeding and wintering. "Node" refers to the geographic region and the population that inhabits the region during the relevant season. Six genetic lineages were identified using a panel of 96 single-nucleotide polymorphisms (SNPs) selected from genome-wide sequencing of ~450,000 markers with RAD sequencing methods (details in Ruegg et al. 2014). Breeding nodes were defined based on ranges of each genetically distinct lineage identified using Bayesian clustering methods (Ruegg et al. 2014) and clipped to the known geographic range of Wilson's Warbler with NatureServe range maps (Fig. 1a) (Ridgely et al. 2003). The resulting genetically distinct lineages were named as, the breeding nodes: Western Boreal, Basin Rockies, Pacific Northwest, California Sierras, California Coastal, and Eastern Boreal.

Wintering nodes were defined by dividing the known wintering range of Wilson's Warbler in Mexico and Central America into 5 regions (Fig. 1a): southern Baja, western Mexico, central Mexico, Yucatán, and Central America (Supporting Information). Little information was available for demarcation of wintering nodes for this species; thus, the 5 regions identified should be treated with discretion.

### Habitat Suitability and Relative Population Size

To develop an index of population size for breeding and wintering nodes, we constructed habitat suitability models for Wilson's Warbler with Maxent 3.4.1 (Phillips et al. 2019) (parameter settings: clamping off, all features types run except for threshold and product, regularization parameter = 1, replicates = 3, output format set to logistic, maximum 100,000 background points, 20% of data withheld for testing) (details in Supporting Information). We used presence-only records and matched the period to that of our BBS estimates (1968–2015, see below) as an exemplar of the types of data that are typically available. We suggest here, however, as others have (Elith et al. 2011; Guillera-Arroita et al. 2015; Phillips et al. 2017), that models that use only presence records carry with them inherent caveats. As such, these models should always be used with a particular purpose in mind and, when possible, compared with similar algorithms that use presence–absence data that may better model biological distributions and patterns (Brotons *et al.* 2004). Because of the general relationship between suitability and population abundance in other species (Royle et al. 2005) and the broader utility of suitability-derived estimates of population size in cases where other data may not be available, we calculated an index of relative breeding population size ($B_i$) for each breeding node ($i$) and
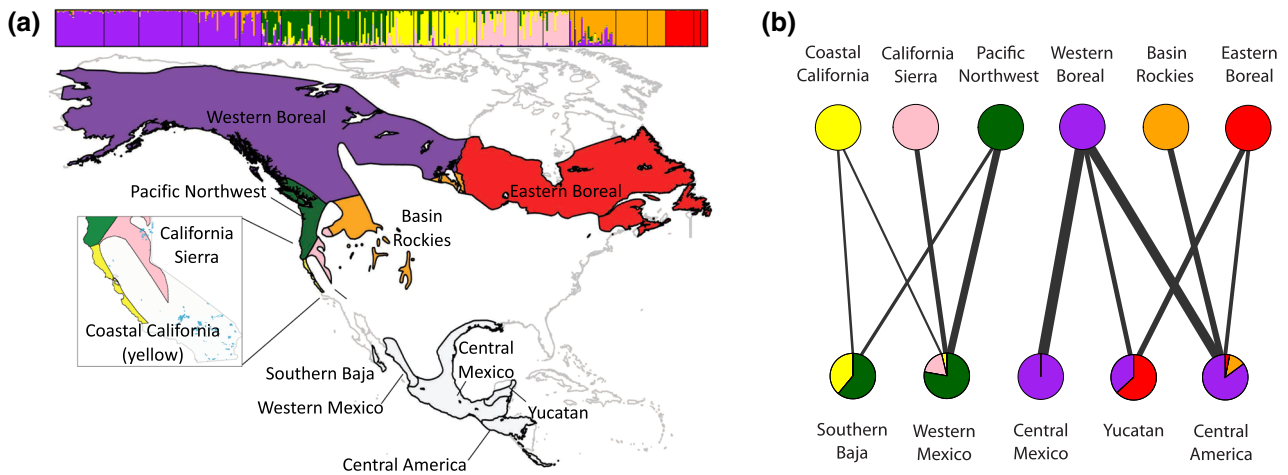
*Figure 1. (a) Genetic separation between genetic lineages of Wilson's Warbler according to the Bayesian assignment method STRUCTURE and genetic analyses detailed in Ruegg et al. (2014) and geographic location of each genetic lineage (breeding nodes in the network analysis) and (b) the warbler's migratory network (breeding nodes based on the genetic group and wintering nodes designated based on genetic groups and ecoregion; line thickness is proportional to estimated proportion of the global population using each migratory connection). Underlying estimates used to derive connectivity network are in Table 3 and Supporting Information.*

an index of relative wintering population size ($W_j$) for each winter node ($j$) by summing the suitability scores (cumulative suitability [Tables 1, 2]) across all pixels in each node. To confirm the relationship between population size estimated from cumulative suitability and population size indices derived from BBS data, we used linear regression and found a strong positive correlation ($R^2 = 0.92$ [Supporting Information]).

### Estimating Connectivity within the Network

To link the breeding nodes to the wintering nodes, we constructed a Bayesian connectivity model that calculated the proportions of the global population that comprise each link. We expressed the breeding-wintering connectivity of Wilson's Warbler as $N_B = 6 \times N_W = 5$ matrix **C**, each element of which ($c_{ij}$) represents the proportion of the global population that breeds in breeding node $i$ and spends the winter months in wintering node $j$. Connectivity can also be thought of in terms of breeding groups ($C^B$) and wintering groups ($C^W$). Each element of $C^B$ represents the proportion of breeding group $i$ that connects to wintering group $j$:

$$c_{ij}^B = \frac{c_{ij}}{\sum_{k=1}^{N_B} c_{kj}}, \quad (1)$$

whereas each element of $C^W$ represents the proportion of wintering group $j$ that connects to breeding group $i$:

$$c_{ij}^W = \frac{c_{ji}}{\sum_{k=1}^{N_W} c_{ik}}. \quad (2)$$

Three data sources were used to derive the elements of **C**: a set of individuals captured on wintering grounds that were subsequently identified as belonging to one of the six breeding genetic groups (Ruegg et al. 2014; Supporting Information), breeding population size indices ($B_i$) estimated from breeding range suitability model (Table 1), and wintering population size indices ($W_i$) estimated from winter range suitability model (Table 2).

We assumed the numbers of birds assigned to breeding nodes sampled at a given winter node (Supporting Information) followed a multinomial distribution with probabilities equal to the corresponding column of $C^W$. We also assumed the number of birds recovered at each wintering node from a given breeding node (Supporting Information) followed a multinomial distribution with probabilities equal to the corresponding rows of $C^B$ corrected (i.e., multiplied) by the sampling effort at each wintering node. Sampling effort was estimated as the proportion of the total number of samples collected at the wintering node. Finally, we assumed each population size index for a breeding and wintering node was drawn from a normal distribution with means equal to the sum of the rows and columns of $C$ multiplied by the sum of the population size indices for the season. Breeding and wintering nodes were connected if the 2.5% credible limit of the connectivity was >0.005 % of the global population. We implemented the connectivity model with JAGS 3.3.0 (Plummer 2003) and the jags function in jagsUI (Kellner 2017) in R (R Core Team 2017). We assigned vague prior distributions for all model parameters (details in Supporting Information).

**Table 1.** Demographic characteristics of breeding populations (nodes) estimated from the habitat-suitability models and Breeding Bird Survey (BBS) data for Wilson's Warbler.

| Node | Pop size index[a] (cum. suit.) | Mean suitability (SD) | Node area (km²) | No. of BBS routes | Density (mean birds/route) (CI)[b] | Pop. size index (SD)[b] | Average trend (CI)[c] | Future pop size index (SD)[d] |
|---|---|---|---|---|---|---|---|---|
| Coastal California | 25,849 | 0.81 (0.09) | 22,255 | 29 | 5.24 (3.27, 8.02) | 0.013 (0.003) | −0.93% (−1.92, to 0.05) | 0.008 (0.002) |
| California Sierra | 78,710 | 0.58 (0.21) | 89,412 | 81 | 0.78 (0.46, 1.31) | 0.008 (0.001) | −1.57%* (−3.09 to −0.06%) | 0.004 (0.001) |
| Pacific Northwest | 372,756 | 0.72 (0.18) | 318,500 | 157 | 10.01 (7.62, 13.00) | 0.370 (0.047) | −1.67%* (−2.24% to −1.06%) | 0.160 (0.026) |
| Western Boreal | 1,888,900 | 0.20 (0.17) | 4,333,000 | 301 | 7.51 (5.88, 9.59) | 4.293 (0.441) | −1.53%* (−2.16% to −0.91%) | 1.99 (0.296) |
| Basin Rockies | 342,797 | 0.49 (0.21) | 426,700 | 176 | 0.74 (0.55, 0.98) | 0.037 (0.005) | −1.31%* (−2.18% to −0.41%) | 0.019 (0.004) |
| Eastern Boreal | 911,220 | 0.20 (0.10) | 2,766,000 | 326 | 0.91 (0.65, 1.22) | 0.298 (0.034) | −0.62% (−1.64% to 0.47%) | 0.219 (0.046) |

[a]Suitability SD* number of pixels.
[b]Calculated from BBS data as the mean number of birds per route weighted by the relative area.
[c]Data from years 1968–2015. Asterisk indicates estimates whose confidence intervals do not overlap 0.
[d]Calculated using the BBS derived population size index and the long-term trend projected 50 years into the future.

## Breeding Density and Vulnerability

Because BBS data are collected in a standardized way and hierarchical models developed to account for potential biases in the data have been thoroughly vetted (Sauer & Link 2011), we used these data to separately derive an index of relative breeding population density, population size ($\hat{N}_g$ [g, genetic lineage]), and trend ($\widehat{Tr}_g$) that was independent from the suitability-derived index of population size (B). The $\hat{N}_g$ and $\widehat{Tr}_g$ were calculated using the hierarchical overdispersed Poisson model (Sauer and Link 2011) applied to BBS data; strata were defined based on breeding nodes (Supporting Information). To assess future vulnerability in the 6 breeding lineages, we estimated the future population size of each breeding node by projecting the current $\hat{N}_g$ 50 years into the future with the long-term (1968–2015) trend from BBS models: $DS_g = \exp[\log(\hat{N}_g) + 50 * \log(1 + \widehat{Tr}_g)]$. The SD in $DS_g$ was calculated from the variation in $\hat{N}_g$ and $\widehat{Tr}_g$ with the delta method. Future estimates were derived from long-term population trends (1968–2015) that may not reflect recent, dramatic changes to populations, but do represent the largest amount of continuous population data available for this species.

## Winter Density

Independent indices of Wilson's Warbler population density on wintering grounds were calculated using the same eBird records used to build the habitat suitability models. We used a kernel density estimate in ArcGIS to calculate mean and SD density for each wintering group. Kernel densities are reported as the number of individual observations per square kilometer (each unique location counted once), but point density estimates yielded comparatively similar results. Because citizen science data may be heavily biased by observation location and effort, we cross-checked all records with complete checklist records from eBird with the AWK (Strimas-Mackey et al. 2017) package in R (R Core Team 2017) and found no obvious spatial or temporal biases across wintering nodes (Supporting Information).

## Conservation Prioritization Analyses

To assign conservation priorities for Wilson's Warbler on the breeding grounds, we calculated the future population size (i.e., see above calculation of $DS_g$) for each genetic lineage. We used $DS_g$ to separate genetic lineages into high (0–0.05), moderate (0.06–0.50), and least vulnerable (0.60–2.0) categories based on their projected future population size (Table 1). To assign conservation priorities for this species on the wintering grounds, we plotted wintering population densities as estimated from eBird data (Table 2) relative to the predicted proportion of the global population in each wintering node

**Table 2.** Demographic characteristics of wintering populations (nodes) estimated from habitat suitability models and eBird data for Wilson's Warbler.

| Node | Pop size index (cum. suit.), $W_i$ | Mean suitability (SD) | Area (km²) | eBird density (mean observ/km²) (SD) |
|---|---|---|---|---|
| Southern Baja | 14,782 | 0.42 (0.10) | 28,222 | 0.0038 (0.0044) |
| Western Mexico | 98,639 | 0.56 0.12) | 147,700 | 0.0122 (0.020) |
| Central Mexico | 638,056 | 0.55 (0.10) | 950,000 | 0.0095 (+0.014) |
| Yucatan | 43,931 | 0.45 (0.07) | 83,490 | 0.0005 (0.001) |
| Central America | 133,140 | 0.53 0.12) | 248,100 | 0.0182 (0.024) |

estimated using the connectivity model (Table 3). The number of connections to each genetic lineage in each wintering node was visualized using the wintering node output from the connectivity model.

## Results

### Habitat Suitability and Relative Population Size

Our habitat-suitability-derived estimates of population size correlated significantly with estimates of population size from BBS data (Supporting Information), suggesting that cumulative suitability can be used to approximate relative abundance in cases where other sources of data are limited. Our suitability models accurately depicted the probability of occurrence of Wilson's Warbler across their breeding and wintering ranges (Supporting Information). Eastern Boreal and Western Boreal nodes had the highest population size index, whereas Coastal California had the smallest population size index. Population size indices varied between wintering nodes relative to area; the largest estimated populations were in central Mexico, followed by Central America, western Mexico, southern Baja, and the Yucatan (Table 2 & Supporting Information).

### Connectivity within the Network

The migratory network revealed variation in the use of nodes across the full annual cycle. Seventy-seven percent of the total breeding population of Wilson's Warbler was estimated to breed in the largest node (WB), whereas 23% bred in the 5 geographically smaller nodes (Table 3). The distribution of the global population among wintering grounds also showed substantial variation in distribution of birds across nodes. Central Mexico, Central America, and western Mexico had a much larger proportion of the total wintering population (93%) relative to the southern Baja and Yucatan regions (7%) (Table 3 & Fig. 1b).

Although the strength and number of connections varied across the nodes, one of the most striking patterns to emerge from the model was the prediction of a migratory divide between east and west breeding populations. Specifically, the 3 western breeding nodes (Coastal California, California Sierra, and Pacific Northwest) were connected to 2 wintering nodes (Southern Baja and Western Mexico), and the 3 eastern breeding nodes (Western Boreal, Basin Rockies, and Easten Boreal) were connected to the remaining 3 winter nodes (central Mexico, Yucatan, and Central America) (Fig. 1b). Within each network, western Mexico and Central America had significant connections (3 breeding nodes each), whereas central Mexico was connected to a single breeding node (Western Boreal). Central America had the strongest connection with Western Boreal and weaker connections to the Basin Rockies and the Eastern Boreal, whereas the Yucatan showed connections to Western Boreal and Eastern Boreal. Southern Baja showed connections to the 2 western breeding nodes: Coastal California and Pacific Northwest (Fig. 1b & Table 3).

### Breeding and Wintering Population Density and Vulnerability

The BBS data indicated the highest density of breeding birds was in Pacific Northwest, followed by the Western Boreal, Coastal California, Eastern Boreal, and California Sierra. The lowest densities were in the BR (Table 1 & Fig. 2a). Population trends showed that all genetic lineages were either significantly decreasing or showed a negative, but not significant, downward trend (Table 1). Future 50-year projections of relative population sizes of each breeding node showed California Sierra, Coastal California, and Basin Rockies breeding populations as the most vulnerable to extirpation, followed by Pacific Northwest and Eastern Boreal. The Western Boreal group was least vulnerable to extirpation (Fig. 2a & Table 1). The eBird data for each node showed warbler populations were at their highest densities in Central America, followed by western Mexico, central Mexico, southern Baja, and the Yucatan (Table 2 & Fig. 2b).

### Conservation Prioritization

Based on our conservation priority criteria, Coastal California and Basin Rockies lineages had the lowest future population sizes and were therefore categorized as highly vulnerable (Fig. 2a & Table 1). Within the 3 highly vulnerable populations, Coastal California demonstrated the highest densities of birds, whereas Basin Rockies had the lowest. Alternatively, the Pacific Northwest and Eastern Boreal lineages

**Table 3.** Estimates of mean connectivity (95% CI) of Wilson's Warbler populations across the full life cycle.[a]

| Nodes | Southern Baja n = 8 | Western Mexico n = 8 | Central Mexico n = 87 | Yucatan n = 9 | Central America n = 122 | Total in breeding nodes[b] n = 234 |
|---|---|---|---|---|---|---|
| Coastal California | 0.44 (0.27–0.62)* | 0.36 (0.20–0.54)* | 0 (0.00–0.00) | 0 (0.00–0.09) | 0 (0.00–0.00) | 0.81 (0.66–0.96)* |
| California Sierra | 0.17 (0.00–0.66) | 1.79 (0.60–3.18)* | 0.18 (0.00–0.69) | 0.11 (0.00–0.47) | 0.11 (0.00–0.47) | 2.55 (1.32–3.90)* |
| Pacific Northwest | 0.69 (0.14–1.64)* | 7.53 (4.06–10.96)* | 0.36 (0.00,1.64) | 0.21 (0.00–0.82) | 0.11 (0.00–0.46) | 8.91 (5.32–12.45)* |
| Western Boreal | 0.19 (0.00–0.78) | 1.18 (0.00–4.03) | 48.36 (43.38–53.48)* | 1.62 (0.73–2.69)* | 25.75 (22.32–29.37)* | 77.10 (72.62–81.52)* |
| Basin Rockies | 0.21 (0.00–0.82) | 1.41 (0.00–4.49) | 0.30 (0.00–1.27) | 0.22 (0.00–0.84) | 3.55 (2.09–5.39)* | 5.69 (3.06–9.29)* |
| Eastern Boreal | 0.18 (0.00–0.74)* | 0.90 (0.00–3.30) | 0.12 (0.00–0.59) | 2.77 (1.71–3.88)* | 0.95 (0.38–1.86)* | 4.94 (2.91–7.92)* |
| Total in wintering nodes[c] | 1.88 (0.85–3.11)* | 13.18 (9.74–16.62)* | 49.49 (44.55–54.46)* | 5.01 (4.35–5.68)* | 30.47 (26.61–34.42)* | |

[a]Numbers are the percentage of the global population that uses each connection. Asterisk indicates estimates whose confidence intervals do not overlap 0. Numbers under wintering node names indicate sample size of birds recovered from these nodes and assigned to breeding nodes.
[b]Sum of the rows, which is the predicted distribution of the species among breeding nodes.
[c]Sum of columns, which is the predicted distribution of the species among nonbreeding nodes.

had intermediate estimates of future population size and relatively high and low population densities respectively and were thus categorized as moderately vulnerable. The Western Boreal lineage had the second highest density and a very large relative future population size was categorized as the least vulnerable.

A visualization of wintering node conservation prioritization (Fig. 2b) showed the importance of the Western Mexico wintering node, which had the second highest density of wintering birds and was connected to three out of six genetic groups, including 2 of the 3 highly vulnerable breeding populations. The Central America node was also important; ~30% of the global population winters there, including birds from the third highly vulnerable group (Basin Rockies), and winter densities were highest there among all wintering nodes (Fig. 2b).

## Discussion

Recently developed migratory network models have made it possible to better quantify, visualize, and interpret the strength of migratory connections across the annual cycle (e.g., Wiederholt et al. 2013; Stanley et al. 2014; Knight et al. 2018), but these models are limited in their application to conservation planning by their inability to define demographically independent population boundaries. Our novel framework for combining habitat-suitability-derived estimates of population size and genetic data into a migratory network model allows identification of conservation strategies at the scale of genetic lineages within a species. We suggest our approach can be a powerful tool to help researchers and conservation scientists conceptualize trade-offs between preserving unique genetic diversity (i.e., focusing on the most vulnerable genetic lineages) and preserving the highest number of individuals per unit area.

One strategy for prioritizing conservation efforts is to focus limited resources on preserving the habitat that supports the greatest numbers of individuals per unit area (Johnson et al. 2015; Marzluff & Sallbanks 1998). Although abundance-based conservation efforts are greatly improved by estimates of relative population density across the annual cycle, such estimates are often difficult to attain in remote parts of a species range, where data are scarce (Runge et al. 2014; Johnston et al. 2015). Our results support the idea that if preservation of the largest number of individuals per unit area is the goal of conservation efforts, then limited conservation dollars should be placed in the Pacific Northwest or Central America, where densities are estimated to be the highest. Overall our results suggest that even when data are limited, multiple data sets can be combined to attain robust estimates of abundance across the full annual cycle.

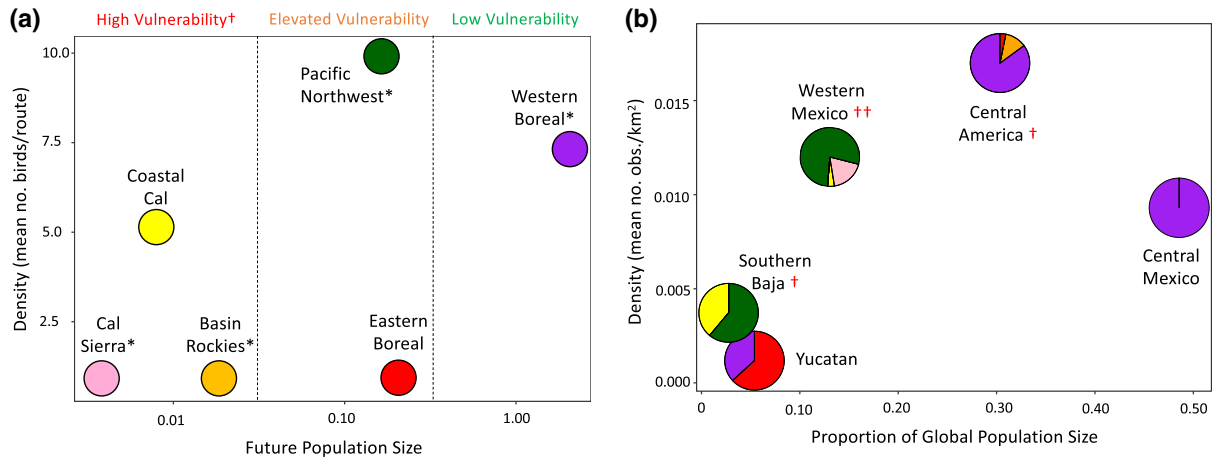Conservation prioritization is often based on threats to a species as a whole, but preserving the capacity for

*Figure 2. Estimates of Wilson Warbler (a) population size from Breeding Bird Survey (BBS) data projected 50 years into the future relative to current bird density calculated from BBS data for each genetically distinct group (∗, population trends whose confidence intervals do not cross 0 [Table 1]; high vulnerability, groups with lowest estimated future population size; moderate vulnerability, groups with relatively large future population sizes; low vulnerability, groups with largest projected future population size) and (b) density in wintering areas from eBird data relative to the proportion of the global population in each wintering node based on the connectivity model (†, number of high vulnerability breeding populations from [a] in each wintering region). Colors in [b] indicate the proportion of wintering individuals that were assigned to each breeding node depicted in [a].*

local adaptation often requires consideration of genetic uniqueness below the species level (Smith et al. 2014; Redding & Mooers 2006; Zhen et al. 2017). Our combining of genetic and demographic information in a migratory network model showed that conservation recommendations will differ depending on how much value is placed on preserving genetic lineages. In particular, our results suggest that if preservation of genetic lineages below the species level is a central goal of Wilson's Warbler conservation efforts, then limited resources should be focused on preserving habitat in the California Sierras, Basin Rockies, or Coastal California, where the 3 most vulnerable genetic lineages breed, or in western Mexico, where 2 of the 3 most vulnerable lineages overwinter. In general, our results support the idea that a combined genoscape-network modeling approach provides a robust framework for prioritizing conservation of genetic lineages below the species level across their full annual cycle.

To the best of our knowledge, our findings represent the first time that genetic data and habitat suitability modeling have been incorporated into a migratory network framework to quantify migratory connections across the full annual cycle of a migratory bird. In particular, the resulting genoscape-network model makes it possible to conceptualize how conservation actions in one breeding or wintering node may have corresponding implications for other connected nodes within the network. For example, despite limited sampling on the wintering grounds, the Wilson's Warbler genoscape-network model lends statistical support to the idea that western

and eastern genetic lineages winter in disjunct regions— a phenomenon referred to as a migratory divide (Fig. 1b). Statistical support for the existence of a migratory divide in the Wilson's Warbler suggests that western and eastern breeding birds and the distinct wintering nodes they each use are best managed separately. These findings highlight the importance of combining genetic information into migratory networks when attempting to identify unique genetic lineages for conservation and management across a species' full annual cycle.

Although our work highlights the value of a genoscape-network modeling framework for assessing conservation priorities in migratory animals, there are many ways one could incorporate additional sources of data to improve the genoscape-network approach for this and other migratory species. In particular, seasonal migrants spend only a fraction of the year in their breeding areas, but the majority of research to date has focused on the breeding grounds, leaving large data gaps across wintering areas (Faaborg et al 2010; Marra et al. 2015). The Wilson's Warbler is no exception, and, as a result of this lack of information from the wintering areas, the credible intervals surrounding some of our estimated migratory connections are large (Table 3). Such problems could be ameliorated in the future with the addition of more data from wintering grounds in the form of genetic assignments from more wintering individuals and geolocator, isotope, and banding data that span the full annual cycle (Procházka et al. 2017). Overall, the paucity of data from wintering grounds for Wilson's Warbler, and for migratory bird species in general, can serve as an impetus

for focused sampling and ecological research in these important and understudied regions (Faaborg et al 2010; Marra et al. 2015).

The network presented here also serves as an important first step in the development of more complex population models that would allow one to predict the cascading effects of threats or conservation actions in one part of the network on the species as a whole (Taylor and Norris 2010, Taylor and Stutchbury 2016). More specifically, some authors have proposed a general framework for the construction of such spatially structured population models that could be modified to specifically assess how habitat loss in one part of the range may influence population trajectories in another part of the range based on the migratory connections outlined herein (Taylor & Norris 2010; Taylor & Stutchbury 2016). Such models may also be modified to combine variables, such as land cost and anthropogenic impacts (available from public data sources such as the Global Human Influence Index [WCC 2005]), with information on genetic diversity, local adaptation, and potential climate vulnerability in each distinct lineage (measured as outputs from climate vulnerability models [Ruegg et al 2018]) to further refine weighting of the costs and benefits of different conservation options (Martin et al. 2007, Sheehy et al. 2010).

There is growing scientific consensus that preservation of biological diversity under future conditions requires incorporating information below the level of species (e.g., Purvis & Hector 2000, Garner et al. 2005, Bay et al. 2018) but such information is often challenging to attain for migratory animals whose annual cycles can span vast geographic scales and geopolitical borders (Attard et al. 2016). Recent research supports the idea that unique genetic lineages may respond differently to environmental change (Bay et al. 2018, Ruegg et al. 2018), and the ability to incorporate such information into conservation planning can help refine prioritization efforts. We harnessed recent developments in genomics and network theory to construct a framework that incorporates unique genetic lineages and current and future populations trends to inform conservation plans for migratory species. Our results make it clear that conservation recommendations will differ depending on whether the goal is to preserve genetic lineages or preserve the largest number of birds per unit area. Overall, the resulting genoscape-network framework provides a strong foundation for integrating multiple types of data across the annual cycle to better inform conservation prioritization for migratory animals in a changing world.

## Acknowledgments

## Supporting Information

Additional methods (Appendix S1), assignments of wintering individuals to breeding lineages (Appendix S2), and suitability model for Wilson's Warblers during breeding and wintering seasons, relationship between cumulative suitability and index of population size and between wintering density during the study period and full record of observations, and comparison of eBird locations on wintering grounds that had at least 1 Wilson's warbler observation with those that had no observations (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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